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# Plant Water Balance

*In diverse habitats, where water often is scarce, plants display a variety of mechanisms for managing this essential resource*

E.-D. Schulze, R. H. Robichaux, J. Grace, P. W. Rundel, and J. R. Ehleringer

**A**lthough water is the earth's most abundant compound, lack of water is the major factor limiting terrestrial plant productivity on a global scale (Turner and Kramer 1980). Worldwide losses in crop yields from water deficits probably exceed the losses from all other causes combined (Kramer 1980). In natural plant communities, water deficits influence the distribution and abundance of many species. About half the earth's terrestrial communities, including dry tropical woodlands, savannahs, and grasslands, mediterranean woodlands and scrub, and temperate steppes, semideserts, and deserts, regularly experience extended periods of limited rainfall. Even very wet communities, such as lowland tropical rainforests, may experience moderate water deficits on a regular diurnal basis, with severe water deficits occurring every few

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## Water deficits influence the distribution and abundance of many plant species

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years (Robichaux et al. 1984).

On a local scale, competition for water among neighboring plants in a population can be very intense (Ehleringer 1984). Figure 1 illustrates just how pronounced this competition can be in a desert community where vegetation occupies less than 20% of the land surface. Following the removal of neighboring individuals, biomass of the remaining *Encelia farinosa* shrubs increased 80% over 18 months. Biomass of the control shrubs, in contrast, increased only six percent. Leaf water potential, canopy leaf area, and reproduction also improved significantly when there were no neighboring plants to compete for water.

The limitation imposed by atmospheric CO<sub>2</sub> abundance also makes water use an important issue in plant life (Cowan 1977). Both CO<sub>2</sub> and water vapor enter and exit the leaf by diffusion. The relative magnitudes of the diffusional gradients inevitably result in a proportionally greater water loss than CO<sub>2</sub> uptake. The CO<sub>2</sub> concentration in the atmosphere is only 0.35 mbar/bar, and the diffusional gradient that plants can develop is typically only about half this value. The difference in water vapor concen-

tration between the hydrated leaf tissue and the atmosphere, in contrast, is usually greater than 10 mbar/bar, and may exceed 80 mbar/bar in deserts. The ratio of transpiration to photosynthesis (expressed as the gradient in water vapor concentration over the gradient in CO<sub>2</sub> concentration) is usually greater than 50, and may be greater than 100. Thus, for terrestrial plants, there is a tradeoff between opening the stomata to increase photosynthesis and closing the stomata to prevent desiccation. The corresponding situation for animals is quite different because the oxygen concentration in the atmosphere is 210 mbar/bar, almost a thousandfold higher than the CO<sub>2</sub> concentration. In addition, breathing maximizes the oxygen diffusional gradient, so that the gradient in water vapor concentration over the gradient in oxygen concentration is always less than one.

The influence of water availability on plant performance in natural and managed ecosystems has been the subject of a large body of research in plant physiological ecology and related disciplines. A topic of major concern has been the control of water movement along the pathway leading from the soil through the plant to the atmosphere. A related topic, the interaction of water vapor and heat transport between plants and the atmosphere, has received considerable attention, particularly with regard to developing accurate leaf energy balance equations. Mechanisms of adaptation to drought, ranging from decreases in canopy leaf area to increases in turgor maintenance ca-

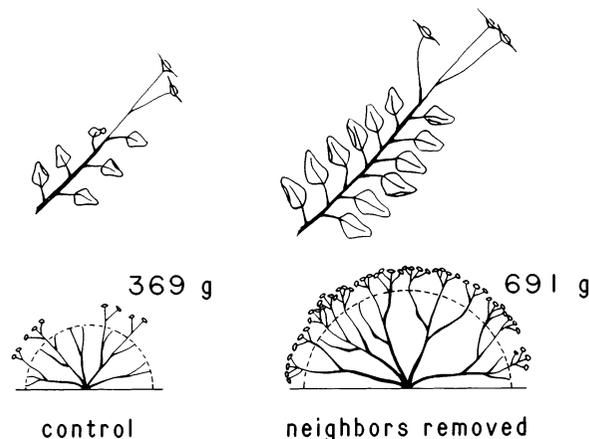
capacity, have also been studied intensively. A fourth topic of major interest has been the relationship between water balance, growth, and carbon partitioning, with recent advances having been made at both the cellular and whole-plant levels. In the following sections, we highlight some of the classical and recent advances on these topics and point to research areas that show promise of providing important insights in the near future.

## The soil-plant-atmosphere continuum

Since the cohesion theory for the ascent of sap was proposed at the end of the last century, advances in our understanding of water movement in the soil-plant-atmosphere continuum have been stimulated by two major developments. First, van den Honert (1948) and Cowan (1965), among others, developed mathematical models describing water flow along thermodynamic gradients in water potential. Second, new instruments enabled rapid and reliable measurements of water potential and water flow on plants growing in the field. These include the pressure chamber for measuring water potential, the porometer for measuring transpiration, and the controlled-environment cuvette for simultaneously measuring transpiration and photosynthesis. Following these developments, studies on species from a wide variety of communities elucidated factors influencing water uptake by roots, water flow and storage in stems, and water loss by leaves.

**Water uptake by roots.** To maintain access to water, plants extend new roots into previously unexplored soil and continually re-explore the same soil with the established root system (Caldwell 1976). Hence, root biomass and productivity are often quite high. In shortgrass prairie, cold desert, and arctic tundra, for example, root biomass accounts for 60–80% of total plant biomass (Caldwell and Richards 1986). Even in forested ecosystems, where root-to-shoot biomass ratios are smaller, annual root productivity can account for a large fraction of total plant productivity (Caldwell and Richards 1986). Thus, a substantial fraction of the net carbon

midday $\psi_{\text{leaf}}$	-33 bars	-26 bars
leaf area per twig	13.0 cm <sup>2</sup>	44.8 cm <sup>2</sup>
achenes per twig	98	329
shrub LAI	1.13	3.31



**Figure 1.** Leaf water potential ( $\psi_{\text{leaf}}$ ), canopy leaf area, reproduction, and biomass in the Sonoran Desert shrub, *Encelia farinosa*, under natural conditions in the spring and under similar conditions when competing neighbors have been removed. In this species, twigs switch from vegetative to reproductive growth in the late spring only if they have acquired the necessary minimal resources. LAI, the leaf area index, equals the ratio of leaf area to ground area. Adapted from Ehleringer (1984).

assimilated by plants may go toward maintaining root systems.

Mathematical models describing water uptake by roots have provided significant insight into its sensitivity to various soil and root parameters (Tinker 1976). However, these models have typically included a set of simplifying assumptions, such as that water flows radially through the soil to the root, that the uptake of water per unit length of active root is uniform, and that each root has sole access to water within a hollow cylinder of soil, the dimensions of which are some function of the root length per unit volume of soil and the root radius (Passioura 1981). These assumptions are unlikely to be met for many plants growing under natural conditions in the field. Hence, more complex models are required to account for such phenomena as the intricate three-dimensional distribution of competing roots in the soil, the dynamic aspects of root growth and senescence, the nonuniform uptake of water per unit length of active root, and the shifting nature of soil water resources resulting from new wetting fronts within the soil profile (Caldwell and Richards 1986). An addi-

tional complexity arises when roots promote the development of soil aggregates, thus altering soil hydraulic properties (Gunzermann 1986).

One parameter that may have a significant influence on water uptake is rooting density, or the root length per unit volume of soil (Passioura 1982). Despite the potential importance of this parameter, data on rooting densities for nonagricultural species are very limited, particularly for species growing under competitive conditions in the field. Caldwell and Richards (1986) have recently shown that rooting density may play a significant role in determining the outcome of competitive interactions between perennial grasses and shrubs in the cold deserts of the Great Basin. Grasses with a greater rooting density deplete soil water resources more rapidly, especially at greater depths in the soil profile, and thus occupy below-ground space more effectively in competition with neighboring shrubs.

In addition to rooting density, root system architecture may influence the pattern and extent of water uptake from the soil. The application of morphometric analyses to complex root systems is beginning to provide in-

sight into the relationship between root branching patterns and optimal exploration of belowground space (Caldwell and Richards 1986).

Water loss by leaves may be closely coupled with water uptake by roots (Mansfield and Davies 1985). A decrease in soil water availability below a critical level may result in a decrease in root cytokinin production and its transport to leaves (Davies et al. 1986). Decreased leaf cytokinin levels may lead, in turn, to partial closure of stomata (Blackman and Davies 1985). Such regulatory coupling between roots and leaves may permit plants to achieve the most efficient long-term use of soil water supplies.

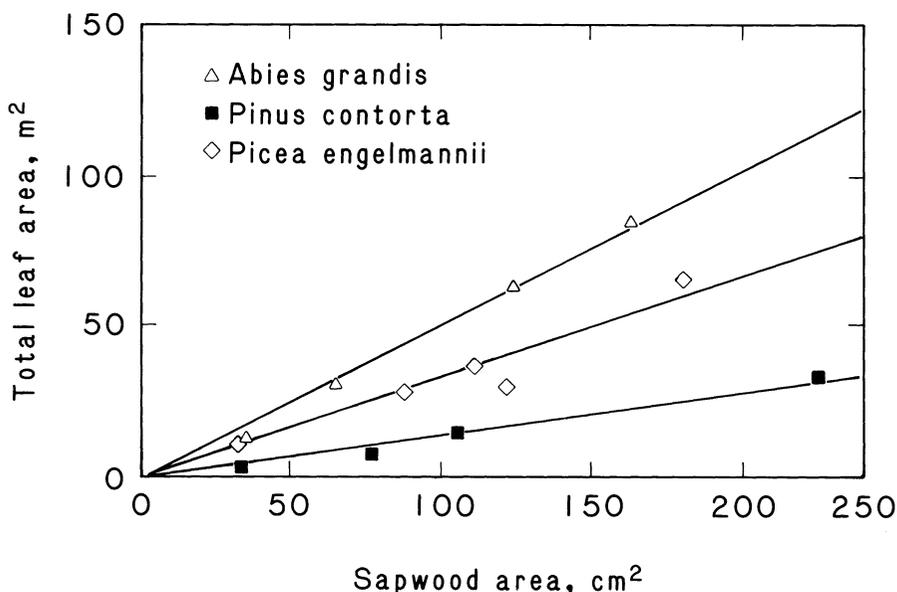
**Water flow and storage in stems.** Water flow within the stems of vascular plants occurs through a pathway of specialized cells consisting mainly of tracheids in gymnosperms and vessel elements in angiosperms. Together with parenchyma cells and fibers, these specialized cells form the xylem or wood. According to the Hagen-Poiseuille law, the water flow rate in the xylem is a function of the magnitude of the hydrostatic pressure gradient, the radius of the xylem elements (taken to the fourth power), and the viscosity of the xylem solution (Nobel 1983). For a given hydrostatic pressure gradient, water flow in vessel elements is typically much greater

than in tracheids, since vessel elements have much greater radii. In addition, the pits in the connecting walls of the tracheids impose a substantial resistance to water flow (Nobel 1983).

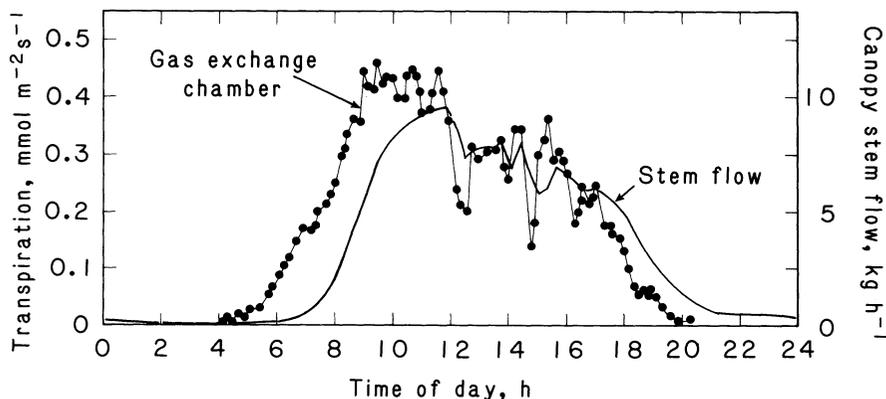
The size of the canopy available for transpiration may be closely coupled with the amount of stem tissue available for water flow. In many tree species, for example, the relationship between leaf area and sapwood area appears to be linear, though the slope of this relationship may differ between species (Figure 2) (Waring et al. 1982). This linear relationship appears to hold even when the transpiring leaves belong to a species different from the one supplying the water. In host-parasite systems involving mistletoe, for example, the leaf area of the mistletoe is proportional to the sapwood area of the host branch, even when there is no host foliage on the branch (Schulze and Ehleringer 1984).

Stems and other organs often shrink during transpiration. Most stem shrinkage occurs in living tissues external to the xylem, where the cells have elastic walls that contract when water is withdrawn (Kozłowski 1972). This type of water storage is particularly important in herbaceous plants and succulents. By contrast, the elastic modulus of cell walls in the sapwood of trees is much higher, so that shrinkage is negligible. The sapwood of trees may still serve as an important source of water, however, for meeting daily transpirational demands. Schulze et al. (1985) reported that water flow in the stem of a *Larix* tree lags behind canopy transpiration by about two hours (Figure 3), suggesting that the morning water supply for transpiration comes from the sapwood of branches and twigs rather than from the soil. Recharging of water in the sapwood occurs after transpiration has declined in the late afternoon and evening. Such water storage may allow stomata to remain open during stress periods, such as when soils are cold and the rate of water uptake by roots is reduced.

**Water loss by leaves.** Most of the water taken up by roots is lost through transpiration; with very little of it being used directly for plant growth. Stomatal control of transpi-



**Figure 2.** Relationships between the total leaf area supported by a tree and the sapwood area available for water conduction in three common conifers of the Pacific Northwest. Adapted from Waring et al. (1982).



**Figure 3.** Daily courses of transpiration (as measured in a gas exchange chamber) and water flow in the stem of a *Larix* tree. Adapted from Schulze et al. (1985).

ration, particularly in relation to photosynthesis, greatly influences plant performance in many terrestrial communities. Though stomata respond to a variety of environmental factors, their responses to atmospheric humidity and to leaf and soil water status are linked most directly to plant water balance (Schulze 1986).

The discovery by Lange et al. (1971) that stomata respond directly to atmospheric humidity was a major advance in plant physiological ecology. This humidity response, which is readily reversible, enables stomata to close when the leaf-to-air vapor pressure gradient increases. Even in epidermal sections isolated from the mesophyll, individual stomata can be shown to respond independently to local humidity conditions (Figure 4). Although the humidity response of stomata has been demonstrated for plants native to a wide variety of habitats (Figure 5), the events within the leaf that lead to the response have not yet been identified. However, the application of new instruments, such as miniaturized pressure probes that measure turgor pressure, hydraulic conductivity, and wall elasticity in individual cells, promises to yield new insight into the dynamics of this response (Shackel and Brinckmann 1985).

The direct response of stomata to humidity is an example of a feedforward response (Cowan 1977, Farquhar 1978). A feedforward response occurs when an environmental perturbation causes a change in the controller (e.g., the stomata) that is independent of any change in the flux being controlled (Farquhar 1978, Mansfield and Davies 1985). This feedforward response, which enables plants to restrict excessive water loss before they develop severe water deficits, may significantly enhance the ability of plants to use soil water supplies efficiently (Cowan 1986) and thus may be particularly important for species growing in semi arid and arid habitats.

The response of stomata to leaf water status has long been considered to be a classical feedback response (Raschke 1975). When the leaf water potential declines below a critical level, stomata begin to close, thereby reducing water loss and allowing the leaf water potential to recover (Lud-

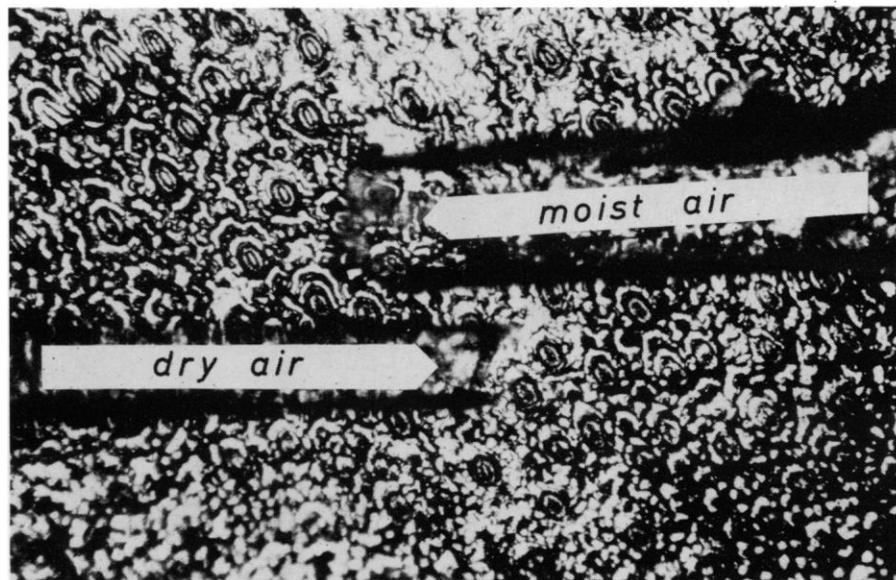


Figure 4. Treatment of an epidermis of *Polypodium* with dry and moist air through two faintly visible capillaries (arrows). Stomata close on exposure to dry air and open on exposure to moist air. The response is reversible. Adapted from Lange et al. (1971).

low 1980). As the leaf water potential increases, stomata may then begin to reopen.

Recent work suggests, however, that some aspect of root or soil water status may be more important than leaf water status in terms of influencing the degree of stomatal opening. For example, Gollan et al. (1985) manipulated leaf water potential by controlling transpiration from a single leaf and from the entire canopy. They observed that soil water content, rather than leaf water potential or turgor pressure, was the primary factor influencing stomatal conductance (Figure 6). Thus, the rate of water loss by the canopy may be closely coupled with the moisture environment of the roots. Such regulatory coupling between roots and leaves may have major implications for plant performance under water-limited conditions in the field.

Stomata control not only the amount of water lost by leaves but also the amount of carbon gained. Thus, stomatal function often represents a compromise between two conflicting demands. In a major step toward understanding stomatal function in relation to leaf metabolism and environment, Cowan and Farquhar (1977) developed a model for predicting how stomatal conductance should vary during the day in order to maximize carbon gain for a

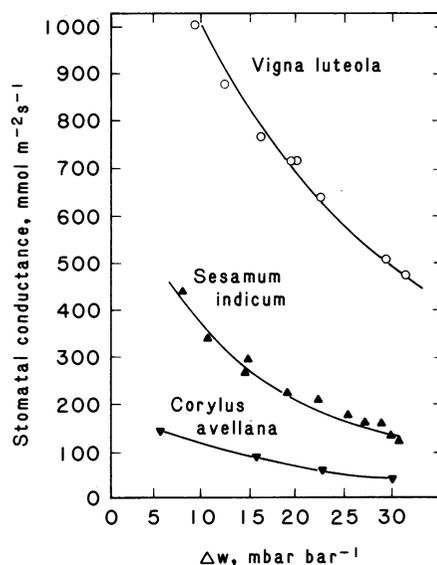
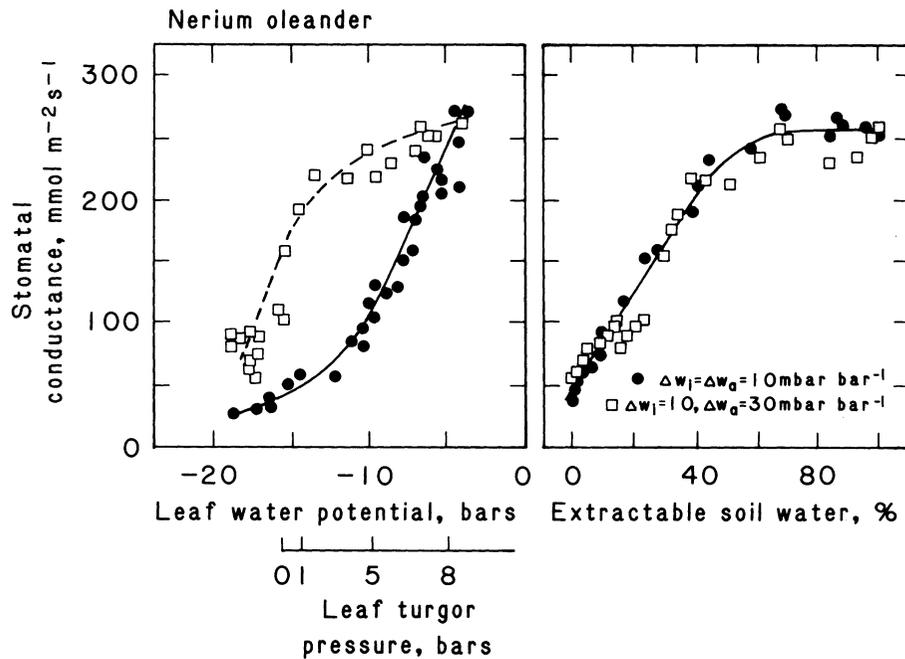


Figure 5. Stomatal conductance to water vapor as a function of the leaf-to-air vapor pressure gradient ( $\Delta w$ ) in *Vigna luteola*, *Sesamun indicum*, and *Corylus avellana* (from Schulze and Hall 1982).

given amount of water loss. The model predicts that the ratio of the partial derivatives of carbon assimilation and transpiration with respect to stomatal conductance, the gain ratio, should remain constant during the day. Subsequent tests suggest that the gain ratio remains constant under some conditions (e.g., Farquhar et al. 1980) but not others. For example, carbon



**Figure 6.** Stomatal conductance to water vapor as a function of leaf water potential and turgor pressure (left) and extractable soil water (right) in *Nerium oleander*. In the two experiments, the test leaf was maintained under a constant leaf-to-air vapor pressure gradient ( $\Delta w_l$ ) of 10 mbar/bar, while the remainder of the plant was exposed to a  $\Delta w$  of either 10 mbar/bar (closed symbols) or 30 mbar/bar (open symbols). Adapted from Gollan et al. (1985).

assimilation and transpiration are sometimes so constrained by the microenvironment that stomatal conductance has almost no effect on them (Williams 1983). Although the model will undoubtedly be modified as new data become available, it serves an extremely valuable role in integrating information on the metabolic and environmental responses of stomata.

### Leaf energy balance

Water vapor and heat transport between plants and the atmosphere are intimately related (Grace 1983). Although water vapor loss is controlled primarily by stomata, both water vapor and heat transport are influenced by the aerodynamic properties of leaves, as both involve laminar and eddy-assisted diffusion from the leaf surface. In addition, the driving force for water vapor loss depends on the vapor pressure of the saturated air in the substomatal cavity, which is a function of leaf temperature. Hence, any change in heat transport affecting leaf temperature will also affect water vapor transport.

Our understanding of the complex interactions between water vapor and

heat transport has been enhanced by the use of leaf energy-balance equations (Grace 1983). Though numerous methods have been developed for solving leaf energy-balance equations, the important parameters for describing the flux processes in all cases are the aerodynamic and stomatal conductances. Aerodynamic conductances for individual leaves, analyzed using standard relationships developed for laminar boundary layers (Monteith 1973), are typically expressed as a function of windspeed and leaf dimension. However, leaf roughness and uneven topography make boundary layers partly turbulent, thus promoting water vapor and heat transport in the air layers near the leaf. As a result, the relationship between water vapor or heat loss and windspeed is often steeper than would be expected on the basis of established relationships for laminar boundary layers. Moreover, the patterns of water vapor and heat transport vary over the surface of a leaf in a manner that depends on leaf shape (Grace 1983).

When there is no wind, air movement around a leaf is small and depends on the vertical currents set up

by the warming and cooling of air in contact with the leaf surfaces. There have been few determinations of aerodynamic conductances in this natural convection mode, which has usually been neglected in calculations of water vapor and heat transport. The few published studies indicate higher rates of transport under natural convection than expected (Dixon and Grace 1983).

Despite these limitations, leaf energy-balance equations have provided valuable insight into relationships between transpiration, leaf temperature, and metabolism. As a result, we now have a much better understanding of the ecological significance of leaf size and shape (Smith 1978), spectral characteristics (Ehleringer and Mooney 1978), and orientation (Ehleringer and Werk 1986).

### Adaptation to drought

Drought periods of varying duration occur during the growing season in many terrestrial communities. Whereas some species experience significant drought-induced mortality, others are adapted to survive and grow during these periods. Mechanisms of adaptation to drought vary, and include traits promoting the maintenance of high tissue water contents, as well as those promoting tolerance to low tissue water contents (Jones et al. 1981).

Perhaps the most obvious mechanism of drought adaptation is a decrease in canopy leaf area. Along many moisture gradients in nature, the fraction of vegetation exhibiting drought-deciduous leaves increases as precipitation decreases. A decrease in canopy leaf area enables drought-deciduous species to avoid severe tissue water deficits. Whereas this may represent an advantage relative to evergreen species, drought-deciduous species experience a time lag between the onset of rain and full canopy development (Mooney and Dunn 1970). According to Comstock and Ehleringer (1986), this time lag can last several weeks in a common Sonoran Desert shrub, leading to a significant decline in potential productivity.

Stomatal closure is another mechanism for maintaining high tissue water contents during drought periods, though it is not without costs. Stomatal closure under high irradiance may

lead to photoinhibition (Powles 1984) or high leaf temperatures (Gates 1980), which may cause significant metabolic damage (Berry and Björkman 1980).

Various mechanisms, particularly increases in leaf angle, can reduce the solar irradiance absorbed by leaves, so that stomatal closure does not result in metabolic damage (Ehleringer and Werk 1986). Within individual plants, leaves potentially exposed to the greatest water deficits often are vertically inclined, whereas those in more protected portions of the canopy are horizontally inclined. In some evergreen species from the California chaparral, seasonal changes in leaf angle reduce incident irradiances during the drought period (Comstock and Mahall 1985). In other species, adjustments in leaf angle occur rapidly, thus providing a mechanism for responding quickly to stress conditions. Several herbaceous species from semiarid and arid habitats have leaves that move diurnally, thus maintaining leaf surfaces perpendicular to the sun's rays (Ehleringer and Forseth 1980). With adequate soil water, this may allow the leaves to operate at high photosynthetic rates. When water is limited, however, the leaves reorient, such that their surfaces are always parallel to the sun's rays (Figure 7). This reorientation not only substantially reduces leaf temperatures and transpiration rates (Forseth and Ehleringer 1983), but also minimizes the likelihood of photoinhibitory damage to the leaves (Ludlow and Björkman 1984).

A second mechanism reducing the solar irradiance absorbed by leaves is a decrease in leaf absorptivity. Leaf hairs (Ehleringer and Mooney 1978), salt glands (Mooney et al. 1977), and waxes (Mulroy 1979) represent different anatomical means for reducing leaf absorptivity. Such traits can result in substantially lower leaf temperatures and transpiration rates.

Other mechanisms of drought adaptation include traits promoting the maintenance of high turgor pressures as tissue water contents decline (Jones et al. 1981). In higher plants, an increased turgor maintenance capacity is accomplished either by a decrease in the tissue osmotic potential at full hydration or by an increase in tissue elasticity (Tyree and Jarvis

1982). Changes in both osmotic and elastic properties appear to enable certain species to occupy dry habitats (Robichaux et al. 1986).

### Water balance, growth, and carbon partitioning

Expansive growth can be viewed as an integrator of the metabolic and environmental events that influence overall plant productivity (Bradford and Hsiao 1982). Cell expansion, for example, is closely coupled through various feedback channels to virtually all aspects of metabolism. At the whole-plant level, the rate of leaf expansion determines the rate at which new photosynthetic surface area is produced. This sets limits, in turn, on the future growth potential of the plant (Bradford and Hsiao 1982).

In its simplest formulation, cell expansion consists of two separable processes: plastic deformation of the

cell wall to encompass a larger cell volume and permeation of water across the cell membrane (Tyree and Jarvis 1982). The first process depends on the extensibility of the cell wall, the turgor pressure of the cell, and the yield threshold for cell wall extension. The second process depends on the hydraulic conductance of the cell membrane and the water potential gradient between the internal and external regions of the cell. Using a new guillotine thermocouple psychrometer for measuring all of these parameters in a single tissue, Boyer et al. (1985) demonstrated that cell expansion in soybean seedlings is simultaneously limited by wall extensibility and hydraulic conductance. These results, which imply that seedling growth will be affected not only by changes in turgor pressure but also by changes in water potential gradients, have significant implications in terms of understanding seedling es-



Figure 7. Changes in leaf orientation in response to decreased soil water availability in the annual *Kallstroemia grandiflora* (upper plates) and the prostrate perennial *Macroptilium atropurpureum* (lower plates) from the Sonoran Desert. In both species, leaves diurnally orient perpendicular to the sun's direct rays under well-watered conditions (left) and parallel to the sun's direct rays under water-stressed conditions (right).

establishment under conditions of low water availability.

For plants growing in the field, one of the first responses to reduced water availability is a decrease in the rate of canopy production (Bradford and Hsiao 1982). This results from the marked sensitivity of leaf expansive growth to water deficits. If canopy development is reduced early in the life cycle of the plant, when growth is normally exponential, the effects on adult plant size may be very pronounced, particularly under competitive conditions.

This decrease in the rate of canopy production often is accompanied by an increase in the root-to-shoot biomass ratio (Bradford and Hsiao 1982). Water deficits that are not too severe may reduce the rate of leaf expansion more than the rate of photosynthetic carbon assimilation, such that more assimilates become available for root growth. An increase in the root-to-shoot biomass ratio may enable the plant to match its water supply more closely to the evaporative demand of its leaves. However, the attendant respiratory costs of such an increase may significantly reduce the efficiency of water use (Pasioura 1981).

Schulze et al. (1983) used a simulation model to examine the relationship between optimal carbon partitioning and water use in annual plants. Carbon partitioning was considered optimal whenever total plant biomass reached a maximum without adversely affecting plant water status, defined as the difference between water uptake and water loss. The calculated values compared favorably with the actual carbon partitioning patterns of an annual *Vigna* species grown under several different moisture regimes.

## Future prospects

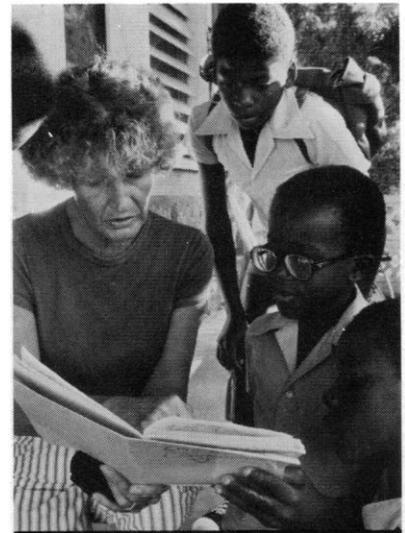
Although significant progress has been made toward understanding the influence of water availability on plant performance in natural and managed ecosystems, much remains to be learned. Several research areas, in particular, are likely to yield significant insights in the near future. First, new techniques are being developed for measuring water potential, turgor pressure, and water content simulta-

neously as leaf water deficits develop (e.g., Shackel and Brinckmann 1985). As a result, new opportunities exist for analyzing the mechanisms by which leaves transduce changes in water status into changes in metabolism. Second, carbon isotope ratios have recently been used to estimate integrated, long-term photosynthetic water-use efficiencies (Farquhar and Richards 1984). Thus, a powerful approach is now available for examining the ecological significance of water-use efficiency under different competitive regimes. Third, plant growth substances or other signals may serve as important means for integrating root water uptake with leaf water loss (Davies et al. 1986). The importance of such higher levels of integration for plant water use in different environments is virtually unexplored.

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