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Constraints by Water Stress on Plant Growth

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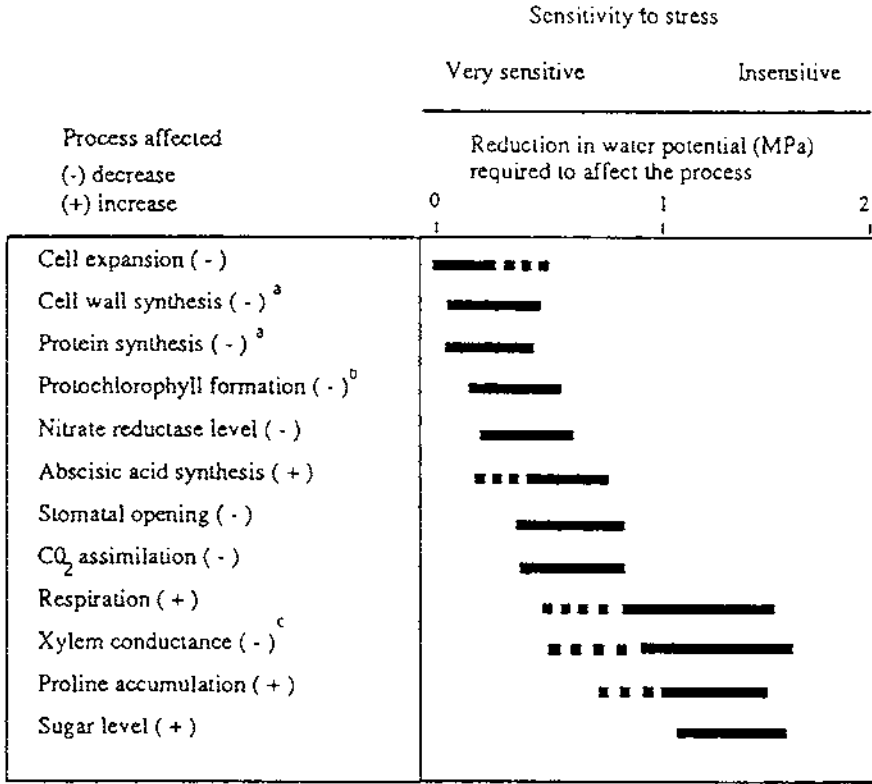
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INTRODUCTION

In regions where temperature allows plant growth, water is among the most limiting factors for plant productivity and growth rates are proportional to water availability. Because of its essential role in plant metabolism, at both the cellular and whole-plant levels, any decrease in water availability has an immediate effect on plant growth, and processes ranging from photosynthesis to solute transport and accumulation are seriously affected (Fig. 1) [1]. Plants are generally subjected to shortages in water availability varying in length from hours to days. Water lost by transpiration causes transient water deficits even in plants growing in wet places, so that most plants suffer at least regular and daily water shortages [2]. When drying soil causes water absorption to lag behind loss by transpiration, permanent water deficits develop that may result in permanent wilting and death by dehydration. Therefore, most plants must deal with some water stress. Plants have evolved physiological responses as well as ecological strategies to cope with water shortages by either stress avoidance or stress tolerance. These responses allow them to survive and even to maintain some growth under very harsh circumstances [3].

Water stress has been defined as the induction of turgor pressure below the maximal potential pressure [4,5]. The magnitude of such stress is determined by the extent and duration of the deprivation. Therefore, plant responses depend on the nature of the water shortage and may be classified as (a) physiological responses to short-term changes, (b) acclimation to a certain level of water availability, and (c) adaptations to drought. Short-term responses to water stress, acting within seconds after the onset of stress, are primarily linked to stomatal regulation, thereby reducing water loss by transpiration and maximizing CO₂ intake. An optimum efficiency in this process would lead



^a Rapidly-growing tissue ^b etiolated leaves ^c should depend on xylem dimensions

FIGURE 1 Relative sensitivity to water stress of various plant processes. The solid horizontal bars indicate the range of stress levels within which a process is first affected; the broken bars refer to the portion of the water potential range in which the response is not well established. (From Ref. 1.)

to a constant ratio of transpiration to photosynthesis [6]. Midterm responses (acclimation) include the adjustment of the osmotic potential by solute accumulation, changes in cell wall elasticity, and morphological changes. Long-term adaptation to drought includes genetically fixed patterns of biomass allocation, specific anatomical modifications, and sophisticated physiological mechanisms, with an overall growth reduction to balance resource acquisition [7,8].

EFFECT OF WATER STRESS ON NUTRIENT UPTAKE

Nutrients are less mobile in a drying soil, because the pores between soil particles are replaced by air and the pathway from the soil to the root surface is less direct [9]. Since the rate of ion diffusion to the root is very often the step limiting nutrient uptake, a decrease in soil water availability can affect plant growth. Whenever water stress limits growth more strongly than it limits nutrient uptake, tissue nutrient concentrations are higher than if water stress limits nutrient uptake more than growth [10]. Normally, the concentrations of growth-limiting nutrients decline during water stress, showing

that the indirect effects of soil water content on nutrient uptake may be as important as the direct effects of water stress on plant growth [8].

CONTROL OF STOMATAL CLOSURE

Gas-Exchange Dynamics

A certain degree of water stress is generally experienced by plants irrespective of life cycle and habitat [2]. Particularly in trees, the decrease in water potential may be greater, since hydraulic resistance increases through embolism in the xylem. The plant water content recovers at night, equalizing the soil water potential and allowing the plant to reach its highest water potential just before dawn.

In light, stomata open and begin to lose water; the leaf reaches its lowest water content when transpiration is maximum near midday. Stomata have a high capacity of response to changes in the plant water status, and they close as the leaf water potential decreases. They are even more sensitive to changes in atmospheric humidity [11,12], however, and they close as the vapor pressure deficit between the leaf and the air increases (Fig. 2). Stomatal response to ambient humidity is a species-specific trait of the guard cells [4]. Since stomata are the way by which CO_2 enters the leaf, the changes that water stress induces on stomatal apertures affect CO_2 intake and assimilation and therefore plant growth. Apparently the evolution of leaf structures favorable for high rates of photosynthesis had more survival value than that of structures favorable to low rates of transpiration except in

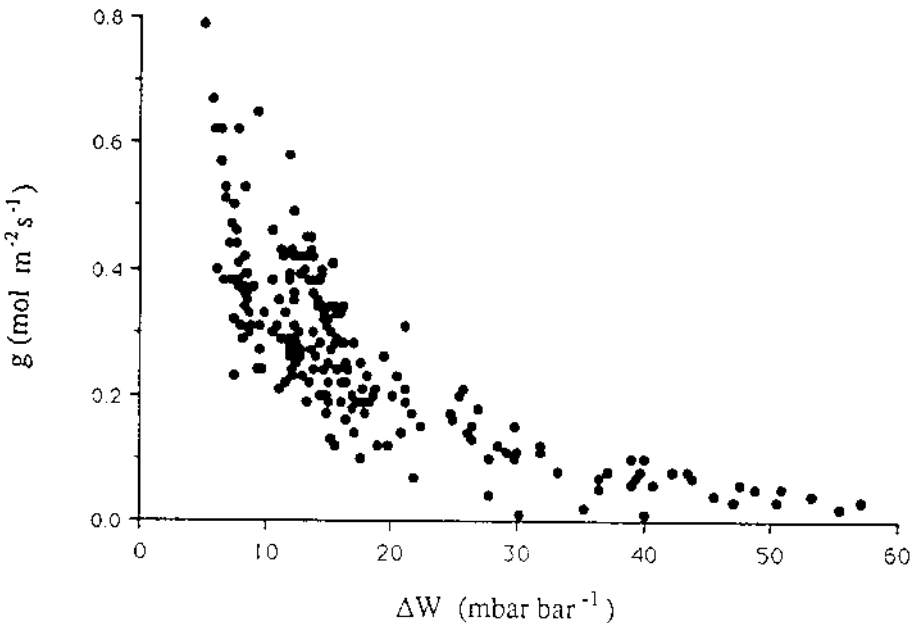


FIGURE 2 Decrease in stomatal conductance (g) as leaf-to-air water vapor mole fraction difference (ΔW) increased in field-grown *Eucalyptus globulus* trees. Conductance and ΔW were measured at midday between February and December 1991. Temperature ranged from 21 to 40°C and dawn water potential from -0.21 to -2.6 MPa during this period. (From L. Serrano and J. Pardos, unpublished observations.)

very dry habitats [13]. Stomatal opening is affected by the CO₂ concentration, and responses of isolated pairs of guard cells suggest a sensing mechanism that responds to low levels of internal CO₂ [14]. Under water stress, internal CO₂ drops in the stomatic chamber, thereby decreasing CO₂ assimilation. Since water stress directly affects photosynthetic capacity at the chloroplast level, the stomatal limitation to growth is presumed to be modest [15]. However, the stomatal or nonstomatal inhibition of photosynthesis is still a controversial topic [6].

Many trees often reach xylem pressures close to that provoking cavitation [16]. This small safety margin between minimum pressures experienced by trees and that at which cavitation is initiated induces a reduction in the transpiration rate and consequently in the stomatal conductance [17].

The process of cavitation involves a restriction on xylem pressure and a decrease on hydraulic conductance that affects the stomatal response to water stress in order to regulate leaf water potential [18]. Changes in stomatal conductance related to cavitation tend to match the progressive reduction in leaf-specific hydraulic conductance. Under these conditions, plants avoid an uncontrolled reduction in leaf water potential that otherwise would cause cavitation to continue until all xylem is embolized [18,19].

When water content in the soil diminishes, cavitation could be interpreted to be an adaptive mechanism having important implications in the control of water use [18].

Role of Growth Regulators

There is substantial evidence for the physiological role played by abscisic acid (ABA) in the regulation of the stomatal aperture [20]. Endogenous ABA increases after a period of wilting, and when applied to plants, ABA strongly inhibits transpiration. It has been hypothesized that ABAs accumulation in leaves during water stress is responsible for stomatal closure, but its overall role at the whole-plant level is still not clear. Some aspects concerning the form (free or conjugated) and location of ABA within the mesophyll cells (mainly determined by pH) must be taken into consideration.

The stomatal aperture is regulated by ABA, which is synthesized in the cytosol and accumulates in chloroplasts of the mesophyll cells [21]. Water stress results in the release of the accumulated ABA to the apoplast, from which it is carried by the transpiration stream through the leaf to the guard cells [15]. Epidermal water relations have been suggested [22] as modulators of the responses of stomata to ABA. Environmental factors and plant development also influence the process, so N-deficient media increase the release of ABA, with older leaves being more responsive than younger ones [23]. Plants with dried root systems may exhibit increased stomatal resistance despite unchanged leaf water potential, indicating that this reaction is the result of a hormonal sign sent by the roots to the shoots [24–27].

Other growth regulators influence stomatal opening. Cytokinins open stomata, but usually in environmentally stressed plants (e.g., with some nutrient deficiency) [28], and both cytokinins and auxin antagonize the action of ABA [27].

Overall, water stress triggers a change in hormonal balance, including an increase in leaf ABA and/or a decline in cytokinins. The increase in leaf ABA reduces cell wall extensibility and therefore causes a decline in leaf elongation. In other plants, the altered hormonal balance reduces root hydraulic conductance and tissue turgor, thereby reducing leaf growth. Regardless of the mechanism by which it is achieved, the decline in growth reduces the plant demand for carbon, so carbohydrates accumulate and photosynthesis declines to match the reduced requirement for carbohydrates. These rapid changes in response to environmental stress serve as an early warning system that reduces plant growth and alters allocation before there is a severe imbalance in C- and N-containing metabolites [8,29].

TURGOR AND GROWTH

Because plant growth is the result of cell division and enlargement, water stress directly reduces growth by decreasing CO₂ assimilation and reducing cell division and elongation. The effect of

water stress is more evident on cell wall expansion [13], because cell enlargement involves the extensibility of the cell wall under turgor pressure. Therefore, any loss in turgor pressure as a consequence of the imbalance in the plant water content could result in reduced growth and even in the total absence of growth under dry environmental conditions. Nevertheless, the relationship between turgor loss and cell enlargement is unclear [30].

Cell growth rate, Gr , can be expressed as a function of turgor pressure, P , and the extensibility coefficient, Φ , by the equation

$$Gr = \Phi (P - Y)$$

where Y is the yield threshold pressure [31]. The equation shows that growth rate decreases as P decreases, but it could also be maintained if either Φ increases or Y decreases. Therefore, reduced growth rate may not rely only on reduced turgor caused by desiccation [32]. There is some evidence of reduced growth without loss of turgor in plants subjected to desiccation stress [33], but this reduction may be part of the osmotic adjustment process [34]. Some mechanism may control cell wall extensibility through the perception of soil dryness [32], giving rise to smaller plants and, hence, lower water requirements and higher survival.

RESPONSES TO DROUGHT STRESS

Conversion of light energy into carbon-based energy implies loss of water. Indeed, water loss is considerably greater than C gain on a molar basis, because the diffusion gradient from water vapor in the leaf to the atmosphere is steeper than the gradient in CO_2 from the atmosphere to the leaf. Therefore, plant adaptations dealing with water conservation have a special meaning in dry environments when water stress is either permanent or temporary and severely limits plant growth. Since a large proportion of the Earth's surface is arid or semiarid, and since even in temperate regions, those environments with a Mediterranean-type climate suffer seasonal water stress, the distribution of natural vegetation and yield of cultivated plants are largely restricted by water availability. Plants living in such environments have adapted by increased drought tolerance and water use efficiency.

There are a number of modifications in plant structures and processes as a consequence of drought stress. These include sensitivity of stomatal response, osmotic adjustment, smaller cell volume, reduced leaf area, increased leaf thickness, hairy leaves, and increased root-shoot ratio, as well as several changes in enzyme and hormone production and activity.

Depending on their response to drought, plants may be classified as drought avoiders or drought tolerators [3,13,35]. Drought-avoidance strategies include short seasonal cycles, as in desert annuals, or earlier maturity, as in C_3 grasses in Mediterranean climates [36]. The drought-tolerance strategy includes either dehydration postponement or dehydration tolerance.

Drought Avoidance

Plants avoiding drought show adaptations leading to the acquisition of the maximum amount of available water or restrict their activities to the periods of water availability. A greater allocation to roots is a main feature of drought-avoidance plants in dry environments where roots consist of 60–90% of plant biomass. In contrast, in coniferous forests, the root biomass is 21–25%, and this figure reaches 30–40% in drier, tropical savanna woodlands [4]. With decreasing water availability, root growth is enhanced at the cost of aboveground biomass production [7,37].

Under well-watered conditions, plants extract water very intensively from the upper soil layers; deep rooting and subsoil water extraction become increasingly important under limited water supply. Perennial shrubs in dry habitats usually have unbranched root systems tapping water to 30 m below the surface [38,39]. In tropical savanna grasslands and North American prairies, the pattern of rooting is a profuse branching in the top layer of soil and deep roots, so that water and nutrients are efficiently absorbed from the top soil layers during wet periods and deep stored moisture is

tapped during the dry season [4]. Root growth and distribution follow the water reserves of the soil, but severe drought may promote initiation and elongation of lateral roots [40]. As a consequence of greater root allocation, aboveground biomass is smaller and the growth rate is decreased to reduce overall resource requirements [8,41]. Most plants adapted to dry environments also have mycorrhizal symbiosis, which improves water and nutrient supply but is also a sink for carbohydrates and may consume 5–10% of total photosynthate [42,43].

Among the plant adaptations to water stress, leaf modifications are especially important [44]. Since the diffusive resistance offered by a leaf to CO_2 uptake is greater than that offered to water loss, any change in the resistance of the common part of the pathway has a greater influence on the transpirational loss of water than on CO_2 intake. Therefore, many species have features that favor photosynthesis over transpiration by increasing the diffusive resistance of stomata using depressions in the epidermis, pores, or cutin or waxes. [4]. By reducing their evaporative surface, plants may reduce water loss, and for this reason, leaves tend to be smaller (Fig. 3) and thicker in dry habitats [45] but maintain a high photosynthetic rate [46]. Also, by reducing leaf size, the convective heat flux to the atmosphere is increased, and by adjustment of leaf angle, the interception of solar radiation can be reduced [47]. Leaf pubescence is a feature of dry habitats that increases light reflectance, decreases leaf temperature, and allows the leaf to gain a higher rate of carbon under arid conditions than the leaf could acquire without hairs. Pubescence also allows the plant to avoid potentially lethal high leaf temperatures and to lower daily water loss, allowing the plant to extend its growth for a longer period into the drought [48]. All these mechanisms help to maintain the leaf energy balance and tend to optimize plant growth and functioning.

High water use efficiency (expressed as a ratio between A and E) could be considered as an adaptive feature of plants submitted to extended periods of drought or growing under competition [49]. Variations observed in A and E after environmental changes occurring as a consequence of stomatal regulation can be optimized when a constant ratio is maintained through time [50]. This optimal stomatal behavior might be seen as one of many possible functional adaptations against drought [17]. However, this only has been confirmed in some species [12,51].

Sclerophylly is regarded as being a typical feature of Mediterranean-type plants and is interpreted as an adaptation to drought [52,53]. However, similar sclerophyllous plants differ broadly

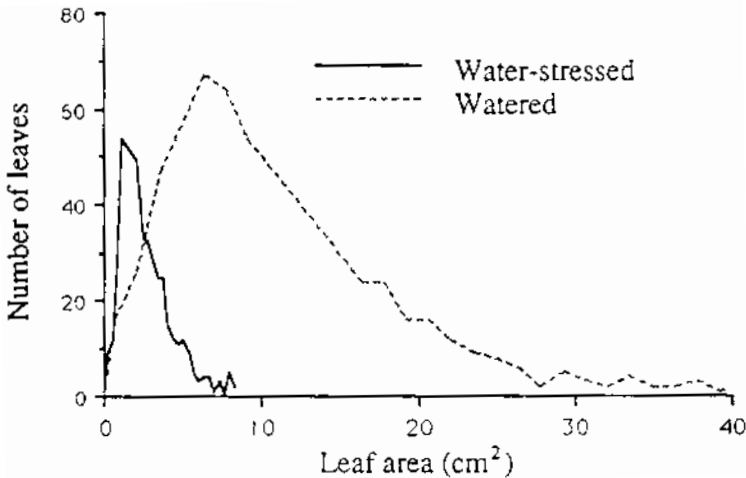


FIGURE 3 Frequency of leaves by size in clonal plants of *Eucalyptus globulus* after being watered and after several cycles of drought reaching the wilting point. (From L. Serrano and J. Pardos, unpublished observations.)

in water relations [54], leading to the hypothesis [55] that sclerophylly cannot be considered significantly related to a drought-avoiding strategy but rather to nutrient limitation [56]. Wax of sclerophyllous leaves keeps cuticular transpiration at a minimum once stomatal transpiration and CO₂ exchange have ceased, thereby conserving water. Since the production and maintenance costs of sclerophyllous leaves are higher than the costs of more mesic leaves [57], the slow growth of Mediterranean evergreen shrubs may be partially due to a greater investment in leaves along with resource limitation.

Drought deciduous shrubs (the most characteristic desert group) rely on morphological changes in the quality and the quantity of their foliar biomass to remain metabolically active through most of the year. Typically, these species develop a relatively large canopy of mesomorphic leaves when water is available and therefore maintain a relatively high rate of productivity. These leaves are replaced by smaller and more xeromorphic summer leaves as seasonal water stress increases [58]. These changes in total canopy leaf area reduce sharply the productivity of xeromorphic plants. However, the increase in water use efficiency (WUE), combined with adaptations in tissue water relations, allows photosynthetic activity through all but the most extreme water stress. Early shedding of leaves during drought often prevents death by desiccation in tropical and temperate zone woody plants [6]. A gradual leaf fall seems to be an adaptation in water stress-prone environments to maximize photosynthetic gain and nutrient cycling [59]. The capacity for leaf shedding during drought varies appreciably among species, but because water deficits frequently limit the growth and survival of trees, selective pressure for adaptation to drought is often high [6]. Because nutrient cycling and nutrient use efficiency are related to leaf fall [60,61], water stress at the time of leaf shedding may severely affect the plant's nutrient budget by decreasing nutrient resorption from leaves [62]. Leaflessness is another feature of dry habitats that allows for a reduced water loss, relying on photosynthetic stem tissues. Cortical stem tissue is structurally very similar to leaf tissue but maintains a net positive rate of photosynthesis even in drought-stressed shrubs and allows a quick recovery from herbivory [63].

Dehydration Postponement

Increased stomatal sensitivity is a functional mechanism that allows plants to maintain high water status during drought periods. This response occurs as a consequence of various events: soil water depletion, increase in the vapor pressure deficit (VPD) in the atmosphere, or both together [17].

The effect of water stress acclimation has been shown in different species to be a further reduction in stomatal conductance [64]. Other species exhibit a variation in stomatal conductance concomitant with changes in VPD and no great variations in leaf water potential [12].

Stomatal closure, although an effective means of postponing dehydration, can reduce photosynthesis to below the compensation point and, especially in dry environments, may cause heat imbalance because of the reduced transpiration rate and photoinhibition [65,66]. Furthermore, no general statement can be made concerning the adaptive value of sensitivity of guard cells to ambient humidity [67], since the response to humidity in a large number of species surveyed was not related to their natural habitat [68]. Thus, changes in the stomatal sensitivity are quite variable; nevertheless, they can be considered as an adaptive response to drought which is species-specific [4].

Metabolic adaptations to water stress cause plants with different photosynthetic pathways to differ in their sensitivity to atmospheric humidity and the resultant gradient in water vapor pressure from leaf to air. Clearly associated with dehydration postponement are CAM and C₄ photosynthetic pathways.

In CAM plants, the daytime closure of stomata combined with dark fixation of CO₂ reduces water loss without limiting photosynthesis. CAM plants, mostly desert succulents, show the highest water use efficiency but the lowest growth rate. Nevertheless, the productivity of some CAM plants may be high, for example, *Opuntia ficusindica* in Mexico and Chile (47 ton ha⁻¹ year⁻¹) or some *Agave* species (38–42 ton ha⁻¹ year⁻¹), which surpass the average 30–40 ton ha⁻¹ year⁻¹ of such crops as wheat, sugar beet, and alfalfa or many tree species over a range of productive soils [69].

The C₄ species evolved as a response to a reduction in atmospheric CO₂ levels that began during the Cretaceous era and continued until the Miocene [70]. Stomata of C₄ species are less sensitive to a desiccating atmosphere than those of C₃ plants, which would provide a greater C gain in low-humidity atmospheres [71]. The ecological advantage of a C₄ photosynthetic pathway is still unclear even though it allows a greater WUE than in the C₃ species [72]. Plant traits other than those related to the photosynthetic pathway should be responsible for the adaptation of some C₄ species to dry habitats [67,73]. When water and N are available, C₄ plants show a high growth rate, and photosynthetic N use efficiency is highest [46]. When limited in either of them, however, C₄ productivity is lower than in ecologically similar C₃ species [72].

Water storage is generally of little importance in drought avoidance because of the high leaf water turnover. Only in a few plants, such as baobab (*Adansonia digitata* L.) and saguaro (*Carnegiea gigantea* L.), is water stored in a significant amount [13]. In general, the cost of water storage is high, and most plants have little or nothing in terms of water-storing structures [74].

Dehydration Tolerance

During dry periods, plants may delay dehydration, but as drought continues, dehydration may become severe, causing injury and death. Dehydration tolerance is a species-specific trait, ranging from -1.2 MPa in aquatic plants to -10 MPa or higher in some xerophytes, but differences in species tolerance are not well understood [13]. Many species of algae, lichens, and mosses, as well as some 70 higher plant species, can be air dried and later recover [75].

Dehydration usually causes severe damage and disorganization of membranes and organelles, mechanical rupture of protoplasm, degradation of cell membranes, protein denaturation, and gene mutations. Chlorophyll content remains relatively unaffected by water stress, but the content of proteins, glycolipids, and phospholipids in chloroplasts generally decreases [76]. Damage caused by desiccation particularly affects photosystem II [77]. Reduction in C assimilation by water stress is also caused by the decreased activity of many enzymes of the Calvin cycle. This effect is completely reversible as long as the water stress is not too severe [78]. The activity of nitrate reductase is also depressed [79] and dark respiration enzymes are enhanced, so that dissimilation processes are more than doubled.

Different experiments have indicated that desiccation tolerance involves changes in the viscosity of the cytoplasm during drought hardening, the protection of membrane properties by the release of organic solutes, and a reduction in the number and reactivity of thiol groups carried by macromolecules [4].

A means of increasing drought tolerance is by decreasing osmotic potential by accumulation of solutes, so that turgor and turgor-dependent processes may be maintained at a significantly lower water availability. This osmotic adjustment allows cell enlargement and plant growth at high water stress and keeps open stomata and CO₂ assimilation at otherwise inhibitory levels [13]. However, evidence indicates that osmotic adjustment may maintain growth only for short periods of time and may not contribute greatly to continued leaf growth in water-stressed plants [80] or play a major role in the distribution of the species [81]. Nevertheless, osmotic adjustment can accomplish two functions: (a) extend the lifetime of active tissues between ephemeral showers and (b) extend the period of tissue preparation for drought (drought hardening) [71]. Furthermore, although stomatal control or reduction in leaf area gives an almost certain reduction in productivity, osmotic adjustment provides the potential for maintaining photosynthesis and growth of at least some parts of the plant as the water deficit increases. Thus, in terms of growth, the cost of osmotic adjustment must be lower even though the solute accumulated cannot be used elsewhere [35]. Osmotic adjustment is reversed when water stress is removed and may reach up to -0.7 MPa in daily changes, although values of -0.1 MPa are more usual [35,80]. It seems that there is a metabolic ceiling for each species [80].

Many solutes may be used in osmotic adjustment. Inorganic ions, such as Na⁺, K⁺, and Cl⁻, accounted for most of the osmotic potential in several species [82,83], but sugars and amino acids,

especially proline [84,85], are major osmoregulators in vascular plants [86]. The reason is probably the convenience of osmolyte storage in large, osmotically inactive molecules, such as starch or protein, which may serve several functions and from which they can be retrieved under conditions of stress. It appears that neither the synthesis of new compounds nor biochemical pathways are involved during osmotic adjustment [35]. Rather, it appears that the disturbance of normal metabolic pathways by water stress is responsible for producing the solutes involved in osmotic adjustment.

Some studies have indicated that the degree of drought tolerance is associated with the ability to undergo changes in the cell elastic properties. A drought-induced increase in the bulk modulus of elasticity, ϵ , would permit the maintenance of a large water potential gradient through the soil-plant-atmosphere continuum, with little change in the relative water content [87], therefore increasing the ability to extract soil moisture from progressively drier soil. Although increases in ϵ have been observed in response to drought stress [88], seasonal patterns differed among wild plants under the same environmental stress [54] and were inconclusive in cultivated plants [81].

CONCLUSIONS

Generally, the daily or seasonal water stress to which a plant is subjected induces a range of plant responses that depends on the extent of the water shortage. Water stress causes primarily stomatal closure, decreasing assimilation and therefore growth. Water stress also reduces plant growth by reducing cell division and enlargement and causes a decline in ion transport to the root surface, which leads to a further decrease in plant growth.

Multiple responses allow the plant to tolerate water stress. These range from stomatal sensibility to soil and atmosphere dehydration to changes in cell wall elasticity and osmotic adjustment. In plants adapted to dry environments, anatomical and morphological changes at the leaf and whole-plant levels (such as reduced leaf size, hairy leaves, sclerophyll, or higher allocation to roots) prevent metabolic imbalance and help to improve water relations. These adaptations impose a cost on plant growth, with the overall effect of reducing growth to match all levels of resource acquisition. The C_4 photosynthetic pathway may have some remarkable advantages in water-limited environments, but CAM plants represent a higher degree of plant adaptation to dry environments.

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