

Chapter 6

Water Use Strategies of Plants Under Drought Conditions

Eunice L. V. A. Bacelar, José M. Moutinho-Pereira,
Berta M. C. Gonçalves, Cátia V. Q. Brito, José Gomes-Laranjo,
Helena M. F. Ferreira and Carlos M. Correia

Abstract The growing concerns about water scarcity have focused more attention on water management in agriculture and promotion of water conservation through improved water use efficiency (WUE). Depending on the main purpose of the study, WUE can be estimated at multiple scales, from leaf to whole plant, crop, yield, and ecosystem levels. Drought resistance and WUE are not synonymous and their association is often misunderstood. Effectively, two water use strategies may be employed by woody plants under drought conditions. The prodigal water use behavior is beneficial in conditions where water supply is interrupted for short periods only. The conservative water use is favorable in conditions where a long dry period prevails and is associated with high capacity for drought resistance and slow growth rates. In this chapter, we also examine how human manipulation such as breeding and agricultural management techniques will offer new opportunities to improve plant water use under drought conditions.

6.1 Introduction

Climate change has emerged in recent years as one of the most critical phenomena affecting our planet. The latest scientific findings reported by the Intergovernmental Panel on Climate Change (IPCC), show changes in some extreme events, particularly daily temperature extremes and heat waves. Precipitation has

E. L. V. A. Bacelar (✉) · J. M. Moutinho-Pereira · B. M. C. Gonçalves · C. V. Q. Brito · J. Gomes-Laranjo · H. M. F. Ferreira · C. M. Correia
Centre for the Research and Technology of Agro-Environmental and Biological Sciences (CITAB)/Department of Biology and Environment, Universidade de Trás-os-Montes e Alto Douro (UTAD), Apartado 1013, 5001-801 Vila Real, Portugal
e-mail: areale@utad.pt

generally increased over land north of 30°N from 1900 to 2005, but there is evidence that droughts will intensify over the coming century in southern Europe and the Mediterranean region, central Europe, central North America, Central America and Mexico, northeast Brazil, and southern Africa (IPCC 2011). Given these facts, the question is which are and will be their impacts on plants, animals, and ecosystems.

Climate change can have both beneficial and detrimental impacts on plants. Researchers believe that climate change will increase productivity in certain crops and regions, and reduce productivity in others (Karl et al. 2009). Many species show positive responses to elevated carbon dioxide and low levels of warming, but higher levels of warming often negatively affect growth and yields. Nevertheless, it is expected that heat, drought, climate-associated pests and diseases, flooding, and extreme weather events will all contribute to a decline in plant productivity.

As a result of increasing populations and unsustainable practices in water usage, severe strains on freshwater resources are being felt around the world, especially in the rapidly developing countries. Water is an important component of the metabolism of all living organisms, facilitating many vital biological reactions by being a solvent, a transport medium, and an evaporative coolant (Bohnert et al. 1995). In plants and other photoautotrophs, water plays the additional role of providing the energy necessary to drive photosynthesis. Thus, any limitation in the availability of water has a great influence on plant life. The growing concerns about water scarcity have focused more attention on water management in agriculture and promotion of water conservation through improved water use efficiency (WUE). The way to increase WUE in plants is through human manipulation such as breeding or crop management techniques. Manipulating plant drought resistance mechanisms will offer new opportunities to improve WUE in water-scarce environments.

6.2 Water Use Strategies and Drought Resistance Mechanisms

Many environmental conditions can lead to water deficit in plants. Periods of little or no rainfall can lead to drought episodes. The period of time without rainfall actually needed to produce a drought episode depends mainly on the water holding capacity of the soil and the rate of evapotranspiration (ET) (Jones 1992; Larcher 1995; Kozłowski and Pallardy 1997). Water deficit in plants can also occur in environments in which water is not limiting (Bray et al. 2000). In saline habitats, the presence of high salt concentrations makes it more difficult for plant roots to extract water from the environment. Soil temperatures between 0 and 15 °C reduce soil and plant hydraulic conductance and eventually water uptake through an increase in the viscosity of water. However, the decrease in water viscosity cannot

fully explain the decrease in the root water uptake rate (Bloom et al. 2004) and the reduction of root hydraulic conductivity has also biological–metabolic causes (Aroca et al. 2012). It has been suggested that the decrease in root hydraulic conductivity upon exposure to low temperatures could be caused by an inhibition of aquaporin activity (Wan et al. 2001; Murai-Hatano et al. 2008; Ionenko et al. 2010; Aroca et al. 2012). Exposure to temperatures below 0 °C, known as freezing temperatures, can lead to cellular dehydration as water leaves the cells and forms ice crystals in the intercellular spaces. Occasionally, well-watered plants will show periodic signs of water stress such as transient loss of turgor during some periods of the day. In this case, wilting indicates that the transpirational water loss has exceeded the rate of water absorption.

The ability of plants to survive the consequences of drought is termed drought resistance. It is important not to confound the significance of drought resistance and WUE. In fact, these terms are not synonymous, although this is often the case in the literature (Blum 2005; Morison et al. 2008). Both features are often conferred by plant traits that are mutually exclusive (Blum 2005). In some situations, higher drought resistance is linked to identical (Nelson et al. 2007) or even lower (Moutinho-Pereira et al. 2007; Bacelar et al. 2009) WUE, whereas in others enhanced WUE does not necessarily mean an improved drought resistance (Masle et al. 2005). In other cases, however, increased drought resistance can be associated with higher WUE (Bacelar et al. 2007a; Moutinho-Pereira et al. 2007; Rivero et al. 2007). Differences in the time of the day and season when they are determined and on the genotypes, plant age, and the experimental environmental conditions may explain these discrepancies.

Drought adaptation depends on the severity of water deficit and two different water use strategies may be employed by woody plants (Passioura 1982). The prodigal water use behavior is beneficial in conditions where water supply is interrupted for short periods only. In this situation there is little danger of serious desiccation despite rapid water use, and it enables a plant to grow quickly. In this strategy, plants present high stomatal conductance, high C_i/C_a ratio, and low WUE_{leaf} that are positively correlated with high photosynthetic rate (Bacelar et al. 2009). The conservative water use behavior is beneficial in conditions where a long dry period prevails, enabling the plant to use the available water efficiently. Conservative water use strategies are associated with high WUE_{leaf} , high capacity for drought resistance, and slow growth rates.

There is no universal way by which drought resistance can be achieved and in consequence the different components of such capacity have been classified in different ways by different authors. Classically, plant resistance to drought has been divided into escape, avoidance, and tolerance strategies (Levitt 1972; Turner 1986). Nevertheless, these strategies are not mutually exclusive and, in practice, plants may combine a range of response types (Ludlow 1989).

6.2.1 Drought Escape

Plants that escape drought, like desert ephemerals and annual crop and pasture plants, exhibit a high degree of developmental plasticity, being able to complete their life cycle before water deficit occurs. Escape strategies rely on successful reproduction before the onset of severe stress. Improved reproductive success also includes better partitioning of assimilates to developing fruits and seeds. This is associated with the plant's ability to store reserves in some organs (stems and roots) and to mobilize them for fruit production, a response well documented in crop plants, such as cereals (Bruce et al. 2002) and some legumes (Chaves et al. 2002).

6.2.2 Drought Avoidance

Plants that tend to avoid drought generally have tissues that are very sensitive to dehydration, and thus they have to avoid water deficits whenever water shortage occurs (Ludlow 1989). Dehydration avoidance is common to both annuals and perennials and is associated with a variety of adaptive traits. The most effective protection against drought is a deep, extensively branched root system that can absorb water from a large volume of soil (Arndt 2000). Moreover, roots with low hydraulic conductance or few but long roots can permit a slow but sustainable supply of water to the plant (Passioura 1983).

Water movement from the roots to the atmosphere is controlled by the conductance of the components of the water pathway (Lovisolo and Schubert 1998). Traditionally, stomatal conductance and root conductivity have been considered the main controlling factors of water flow in the plant (Jones 1992). However, the efficiency of water transport depends on constraints to water movement that affect hydraulic conductivity (Tyree and Ewers 1991). It has been reported that water stress affects shoot conductivity by inducing embolism in xylem vessels (Schultz and Matthews 1988; Tyree and Sperry 1989; Tognetti et al. 1996) or by a reduction in the vessel diameter (Lovisolo and Schubert 1998). Adaptation requires a fine balance because features that reduce vulnerability to cavitation, narrow conduits, and many inter-conduit connections, also reduce hydraulic conductivity that generates the high xylem tensions that trigger embolism (Sperry 2003). In general, vessels with narrow diameters are less susceptible to embolism (Lovisolo and Schubert 1998). However, variations in xylem conduit diameter can radically affect the function of the conducting system because of the fourth-power relationship between radius and flow through a capillary tube, as described by the Hagen-Poiseuille law (Fahn et al. 1986). Under water stress conditions, some plants are able to increase or maintain the level of protection against cavitation and turn more efficient the water transport through the xylem, revealing a trade-off between safety (low vulnerability to cavitation) and efficiency (large hydraulic conductivity) (Bacelar et al. 2007a).

Leaves growing under water stress usually develop smaller but more densely distributed stomata. This modification makes a leaf able to reduce transpiration by a quicker onset of stomatal regulation (Larcher 1995). Stomata are mainly confined to the abaxial surface and are often hidden beneath dense hairs (peltate scales or trichomes) or in depressions (grooves or crypts). In this way the boundary layer resistance is increased and the air outside the stomata becomes moister (Larcher 1995). Other morpho-anatomical traits that help to minimize water loss during drought include leaf rolling (Schwabe and Lionakis 1996), dense leaf pubescence (Karabourniotis and Bornman 1999; Liakoura et al. 1999; Bacelar et al. 2004), a thick cuticle and epicuticular wax layer (Leon and Bukovac 1978; Liakoura et al. 1999; Richardson and Berlyn 2002; Bacelar et al. 2004), heavily lignified tissue (Richardson and Berlyn 2002), smaller mesophyll cells and less intercellular spaces (Bongi et al. 1987; Mediavilla et al. 2001). Moreover, leaf movements, such as paraheliotropism, can also prevent damage by high temperatures, dehydration, and photoinhibition (Ludlow 1989). Another common feature in water stressed plants is the reduction of the canopy leaf area through reduced growth and shedding of older leaves (Bacelar et al. 2007a). This usually begins with the oldest leaves and progresses toward stem tips. Although the loss of leaves results also in a reduction of the photosynthetic surface it consequently reduces water loss and prolongs survival (Kozłowski et al. 1991).

Because of their ability to postpone or avoid tissue water deficits, plants that avoid drought could be said to have good short-term survival. However, they have poor long-term survival, because the avoidance mechanisms eventually fail to prevent dehydration of tissues that are relatively sensitive to desiccation (Ludlow 1980).

6.2.3 Drought Tolerance

Drought tolerance is the ultimate drought strategy (Connor 2005) and it refers to adaptations that allow the plant to withstand the stress, with or without a reduction in performance.

Osmotic adjustment is generally regarded as an important drought tolerance mechanism. Most of the adjustment can usually be accounted for by increases in concentration of a variety of common solutes including sugars, organic acids, and ions, especially K^+ (Taiz and Zieger 1998). Enzymes extracted from the cytosol of plant cells have been shown to be severely inhibited by high concentrations of ions. These accumulations during osmotic adjustment appears to occur mainly in the vacuoles, that are kept out of contact with enzymes in the cytosol or subcellular organelles (Taiz and Zieger 1998). Because of this compartmentation of ions, other solutes must accumulate in the cytosol to maintain water potential equilibrium within the cell. These other solutes, called compatible solutes or compatible osmolytes, are organic compounds that do not interfere with enzyme functions. These compatible solutes may protect the cell membrane and the metabolic machinery under dehydration (Chaves et al. 2003).

The osmotic compounds synthesized in response to water stress include amino acids like proline, aspartic acid, and glutamic acid (Samuel et al. 2000; Hamilton and Heckathorn 2001; Bacelar et al. 2009), methylated quaternary ammonium compounds (Rathinasabapathi et al. 2001), carbohydrates (Vijn and Smeekens 1999), polyols (Smirnov 1998) and low-molecular-weight proteins (Ingram and Bartels 1996).

One of the most studied compatible solutes is the amino acid proline. Accumulation of high proline content in cells has also been associated with prevention of protein denaturation, preservation of enzyme structure and activity (Rajendrakumar et al. 1994; Samuel et al. 2000), and protection of membranes from damage by reactive oxygen species (ROS) produced under drought and high light conditions (Hamilton and Heckathorn 2001).

Betaines are quaternary ammonium compounds in which the nitrogen atom is fully methylated (Chen and Murata 2002). The most common betaines in plants include glycine betaine (GB, the most widely studied betaine), as well as proline betaine, β -alanine betaine, choline-O-sulfate, and 3-dimethylsulfoniopropionate (Rhodes and Hanson 1993; McNeil et al. 1999). GB is widely distributed in higher plants and is synthesized in many species at elevated rates in response to environmental stresses, appearing to be a critical determinant of stress tolerance (Rhodes and Hanson 1993). In addition, studies *in vitro* have shown that GB is effective as a compatible solute in stabilizing the quaternary structures of enzymes and complex proteins, as well as in maintaining the highly ordered state of membranes (Papageorgiou and Murata 1995).

In several species, polyols accumulate in leaves in response to water stress (Noiraud et al. 2000). The most common polyols in plants include acyclic forms, mannitol, glycerol, sorbitol, and cyclic forms (cyclitols), ononitol, and pinitol (Ashraf and Harris 2004). In addition to their role in osmoregulation, polyols also function as oxygen radical scavengers. For example, mannitol was found *in vitro* to act as a scavenger of hydroxyl radical (Halliwell and Gutteridge 1999), thereby protecting the proteins from oxidative damage in drought stressed plants (Moran et al. 1994). Recent studies support that species like olive tree cope with drought and salinity by coordinating mannitol transport with intracellular metabolism (Conde et al. 2011).

In general, soluble sugar content tends to be maintained in the leaves of droughted plants, in spite of lower rates of carbon assimilation (Chaves et al. 2003). This is achieved at the expenses of starch, which drastically declines (Chaves 1991). This response favors osmoregulation, enhances desiccation tolerance and allows metabolic activity to be regained more quickly in young leaves (Chaves et al. 2003).

During drought periods, plants undergo many physiological changes and induce a large number of genes for adaptation (Ingram and Bartels 1996). A typical change in gene expression is the induction of genes involved in the synthesis of low-molecular-weight proteins, e.g., dehydrins and late embryogenesis abundant (LEA) proteins (Ingram and Bartels 1996). The functions of LEA proteins are multiple as they are involved not only in seed maturation and desiccation but also in vegetative organs, where they can stabilize enzyme complexes and membrane structures and promote

ion sequestration (Close 1996; Garay-Arroyo et al. 2000). Dehydrins are involved in a range of responses to abiotic stress that share a dehydration component. However, the mechanisms by which dehydrin synthesis is enhanced and functions in vivo remain poorly understood (Cellier et al. 2000). There is increasing evidence that another class of proteins, the small heat-shock proteins (sHsps), may play a role in cellular protection during dehydration (Alamillo et al. 1995; Alpert and Oliver 2002). Strong evidence supports that sHsps function as molecular chaperones (Hendrick and Hartl 1995; Hong and Vierling 2000) that bind to partially folded or denatured substrate proteins and thereby prevent irreversible aggregation or promote correct substrate folding (Sun et al. 2002). They are also described as being developmentally regulated, being abundant in dry mature seeds, and disappearing during germination (Wehmeyer et al. 1996).

Membrane-associated carriers or transporters are probably involved in differentially distributing osmolytes within the cell and may also participate in regulating the transport and distribution of these solutes throughout the plant (Bray et al. 2000). Aquaporins have been implicated as the major facilitators for the movement of water across membranes (Chrispeels and Agre 1994; Bray et al. 2000). In addition, the capacity of aquaporins to transport small neutral solutes and/or gases has raised the intriguing possibility that aquaporins may work as membrane channels with multiple functions (Tyerman et al. 2002). Aquaporins may facilitate water movement in drought stressed tissues and promote the rapid recovery of turgor on watering (Bray et al. 2000).

Changes in the elastic properties of plant cell walls can also contribute to turgor maintenance under drought (Patakas and Noitsakis 1999). An inelastic cell wall should act to increase the uptake of water from drying soil because more negative water potentials would result from a relatively small decrease in water content (Schulte 1993). On the other hand, a more flexible cell should allow shrinkage during water loss, thus maintaining high turgor for a given change in water content (Patakas and Noitsakis 1999). In a study with olive tree (Bacelar et al. 2009) it was observed that cultivars that employ a prodigal water use strategy revealed high tissue elasticity, whereas conservative water use cultivars revealed high tissue rigidity.

An extreme desiccation tolerance is found in the resurrection plants as well as in some ferns, non-vascular plants, algae, and lichens (Chaves et al. 2003). The leaves of resurrection plants, like *Craterostigma plantagineum*, can equilibrate with air close to 0–2 % (v/v) relative humidity and are still able to fully recover their physiological activity upon rehydration (Bartels et al. 1990). When water is withheld from mature individuals of *C. plantagineum*, changes rapidly occur at the messenger RNA and protein levels, eventually leading to the tolerant state (Ingram and Bartels 1996).

The disadvantage of tolerance of water deficits is that the continued carbon fixation is inevitably accompanied by water loss. Thus, plant water status must ultimately fall, what can result in some cases in death (Arndt 2000).

When the use of absorbed light in either photosynthesis or photorespiration and the thermal dissipation are not enough to cope with excess energy, the production of highly reactive molecules is exacerbated (Chaves et al. 2003). The excess of

reducing power determines a redirection of photon energy into processes that favor the production of ROS, mainly in the photosynthetic (Asada 1999) and mitochondrial electron transport chains (Møller 2001). To mitigate the oxidative damage initiated by ROS, plants have developed a complex antioxidative defence system that includes enzymatic and non-enzymatic antioxidants. These compounds and enzymes are not distributed uniformly, so defence systems vary among specific subcellular compartments. The degree to which the activities of antioxidant enzymes and the amount of antioxidants increase under drought stress are extremely variable among several plant species and even between cultivars of the same species (Bacelar et al. 2006; Bacelar et al. 2007b).

6.3 Estimation of WUE at Multiple Scales

WUE could be defined in many ways, depending on the scale of measurement and the main purpose of the studies. For plant physiologists, the basic unit of production could be moles of carbon gained in photosynthesis (A) in relation to water used in transpiration (E) or to stomatal conductance (g_s), which permits the calculation of instantaneous WUE_{leaf} (A/E) or intrinsic WUE_{leaf} (A/g_s), also found as WUE_i in the literature. For farmers and agronomists, the unit of production is much more likely to be the accumulated plant biomass or the yield of harvested product achieved from the water made available to the plants through precipitation or irrigation. With this in mind, in this chapter we present the concepts of whole plant WUE (WUE_{WP}), crop WUE (WUE_C), and yield WUE (WUE_Y). Finally, mainly for forestry and environmental issues the concept of ecosystem WUE (WUE_E) is important, defined as the net carbon uptake per amount of water lost from the ecosystem.

Intrinsic WUE_{leaf} presents substantial intra and interspecific variation and is also dependent on environmental conditions, mainly drought and co-occurring stresses such as elevated temperature, high vapor pressure deficit, and elevated photosynthetic photon flux density. For instance, A/g_s was shown to range between around 20 and 80 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ during a typical summer day, with low values generally in the afternoon, when comparing three Portuguese grapevine cultivars (Moutinho-Pereira et al. 2007). On the other hand, in Touriga Nacional grapevine cultivar WUE_{leaf} decreased during the day in the more stressful conditions of Port wine country, while it increased more than 100 % in other sites of the Douro Valley, to values higher than 100 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ (Moutinho-Pereira et al. 2004). Meanwhile, Bacelar et al. (2007a) found in olive tree intrinsic WUE_{leaf} values in the range of 80–130 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$, being the higher values under regulated deficit irrigation (RDI), at midday and during the afternoon, whereas in droughted trees it decreased from 110 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ in the morning to 80 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ at midday. Meanwhile, in full irrigated trees, WUE_{leaf} increased from 80 to 90 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ between these periods. Thus, although A/g_s typically increases under water stress conditions (Bota et al. 2001;

Flexas et al. 2002), under some environmental conditions this may not occur, such as in some regions of the inland Iberian Peninsula or other regions with Mediterranean weather conditions. Thus, these results support the possibility of improving WUE_{leaf} by genetic engineering. WUE_{leaf} could be ameliorated by the increment of net carbon assimilation at leaf level (i.e., the difference between carbon gain in photosynthesis and carbon loss in respiration), or by the reduction in stomatal conductance or transpiration rate.

The carbon isotope discrimination ($\Delta^{13}\text{C}$), a measure of the $^{13}\text{C}/^{12}\text{C}$ ratio in plant material relative to the value of the same ratio in the air on which plants feed, can be used as a long-term indicator of WUE_{leaf} . Negative correlations between $\Delta^{13}\text{C}$ and water use efficiency have been demonstrated in many species, as predicted by theory (reviewed in Farquhar et al. 1989). These observations point to $\Delta^{13}\text{C}$ as a potential candidate for use in breeding for greater agronomic water use efficiency (Condon et al. 2004). In addition, the measurements of the O isotope enrichment of plant organic material ($\Delta^{18}\text{O}$) can provide complementary information to that inferred from $\Delta^{13}\text{C}$ in analyses of plant water use efficiency. Specifically, $\Delta^{18}\text{O}$ could provide information about the ratio of ambient to intercellular vapour pressures, and thus about the leaf to air vapor pressure difference, during photosynthesis (Cernusak et al. 2008).

Whole plant WUE represents the whole plant carbon and biomass acquisition per amount of transpired water. Thus, higher WUE_{WP} could be obtained by the drop of plant water losses, the decrease of growth respiration and, mainly, the decrease of maintenance respiration, that uses a substantial proportion of the total carbon assimilated (Amthor 2000), or the increase of photosynthesis by either increasing total leaf surface or increasing leaf photosynthetic capacity. Water losses depend on leaf transpiration rate, which is a function of leaf conductance (including cuticular and especially stomatal conductances) to water vapor, and on dimension and structure of canopy, such as leaf area index and leaf orientation. Leaf conductance depends on well-identified morpho-anatomical and physiological traits that may be targeted for genetic manipulation. Meanwhile, the dimension and structure of the canopy could be regulated by agronomic management techniques.

Closely related with WUE_{WP} is WUE_{C} , although in this case the water consumed by the crop includes the transpired water plus the water lost by physical processes, such as soil evaporation and runoff. Thus, in addition to the aspects reported before to WUE_{WP} , higher WUE_{C} could be achieved by the implementation of agronomic practices that reduce the amount of water lost without being used by the plants.

WUE_{Y} is a variant of WUE_{WP} that represents the carbon and biomass allocated to yield components (mainly fruits and seeds, but also to other plant organs, depending on plant species and the aim of the production). Therefore, higher partitioning to yield organs could increase WUE_{Y} .

It is important to emphasize that improving WUE_{leaf} may not necessarily result in improving WUE_{WP} , WUE_{C} , and WUE_{Y} , because of the interference of canopy and ambient processes (Flexas et al. 2010). The absence of a significant association between A/g_s and WUE_{WP} was found by our group in olive tree (Bacelar et al.

2007a) reflecting the difference in timescale of both processes (from seconds to months) and non-accounted energy expenses in growth and maintenance in the long-term water use (Maroco et al. 2000). The study of Bacelar et al. (2007a) also shows that WUE_{WP} was enhanced by 64 % in Cobrançosa cultivar under drought conditions, while in the rest of the genotypes it was either unaffected ('Verdeal Transmontana') or considerably decreased ('Madural'). Thus, for production on relatively dry sites, cultivars that are characterized by high values of WUE_{WP} , such as 'Cobrançosa', appear to be the most promising.

For the determination of WUE_E , two different methods based on Bowen ratio and eddy covariance systems could be used to evaluate the H_2O and CO_2 fluxes (Emmerich 2007). One method uses the ratio of net ecosystem exchange (NEE) of carbon dioxide to ET by the ecosystem for the growing season or some other time period (Tubiello et al. 1990). A more instantaneous evaluation method of WUE_E is the regression of daily daytime NEE versus ET with the slope value of the regression line, a measure of WUE_E (Baldocchi et al. 2001). Ecosystem differences in CO_2 and H_2O fluxes have important management implications including primary productivity, carbon sequestration, and rangeland health (Emmerich 2007).

6.4 Selection and Breeding Programs to Improve WUE

Breeding for drought resistance has long been part of the breeding practice in most crops that have been grown under dryland conditions (Blum 2011). Plant breeders use a step-wise selection procedure to identify the best performing genotypes in early generations (Bänzinger et al. 2000; Atlin 2003). First, many genotypes are evaluated with few replicates and at few sites. Later, the most successful genotypes or their descendants are evaluated with more replicates and at more sites. Finally, the breeder reduces both the number of genotypes and the variation among genotypes, mainly by eliminating the poor-performing fraction. According to Bänzinger et al. (2000), the key to breeding for drought tolerance is to manage stress. This is done by conducting experiments partly or entirely in the dry season and managing the stress through irrigation.

In the past, breeding efforts to improve drought tolerance have been hindered by its quantitative genetic basis and our poor understanding of the physiological basis of yield in water-limited conditions (Blum 1998; Passioura 2002). Breeders and physiologists addressed the question of how physiological approaches in plant breeding could have greater impact, namely through (Jackson et al. 1996; Reynolds et al. 2001):

- Focusing physiological work on a suitable range of germplasm;
- working with larger populations to enable extrapolation of findings to breeding processes;

- identifying traits for use as indirect selection criteria, in addition to those already used in core breeding programs;
- identifying traits for use as selection criteria in introgression programs;
- conducting selection trials in more representative environments;
- developing tools that could be quickly and easily applied to large numbers of segregating lines.

According to Tuberosa and Salvi (2006), drought is the most devastating stress and the most recalcitrant to breeder's efforts of all the abiotic stresses that curtail crop productivity. Moreover, breeding for specific physiological traits that are expected to impart a yield advantage in dry environments has been notoriously difficult and unsuccessful (Richards et al. 2001). In fact, breeding for drought tolerance is further complicated by the fact that several types of environmental stresses can challenge plants simultaneously. High temperatures, high irradiance, scarcity of water, and nutrient deficiencies are commonly encountered under normal growing conditions but may not be amenable to management through traditional farm practices (Mittler 2006; Fleury et al. 2010). In general, it is crucially important, according to Bacon (2004), to select genotypes able to optimize water harvest and WUE. Flexas et al. (2010) suggested the enhancement of WUE by biotechnology and genetic engineering in grapevine, mainly by: (1) increasing CO₂ diffusion to the sites of carboxylation without increasing stomatal conductance, thanks to increase in mesophyll conductance to CO₂, which partly depends on aquaporins; and (2) improving the carboxylation efficiency of Rubisco that could be achieved by replacing Rubisco from grapevine with Rubiscos from other C₃ species with higher specificity for CO₂.

On the other hand, indiscriminant selection for higher WUE with the assumption that it equates with improved drought resistance or improved yield under stress might bring about serious negative consequences (Blum 2005). If low water use is the breeder's target it is highly probable that selection for this end can be achieved by directly selecting simple traits, such as reduced leaf area, without measuring WUE. Therefore, Blum (2009) recommended that plant breeders targeting water-limited environments should consider skipping the use and reference to WUE and consider plant constitutive and adaptive traits which drive the effective use of water (EUW) and the resultant dehydration avoidance as major traits for yield improvement in drought prone environments.

At the molecular level, pathways and gene networks between abiotic stresses overlap (Shinozaki and Yamaguchi-Shinozaki 2007). Moreover, some biochemical mechanisms may have opposing effects under different stresses; therefore tackling tolerance to one stress may lead to sensitivity to another (Fleury et al. 2010). Although the reductionist approach of studying isolated stress has considerably increased our knowledge of tolerance mechanisms, interaction between multiple stresses and stress combinations should be studied so as to make progress relevant to field conditions (Fleury et al. 2010). In addition to these confounding environmental factors, a drought research program should also consider plant phenology (Fukai and Cooper 1995; Fleury et al. 2010). For example, breeding for a

shortened crop life cycle has been a very successful strategy in C_3 cereals in Mediterranean conditions (Araus et al. 2002). However, in well-developed agricultural regions, crop flowering time has already been optimized by breeders so that the plant's phenology matches its environment (Passioura 2007).

Pang et al. (2011) found evidences for the development of new perennial legume forages for a wide range of drought prone agricultural regions in breeding/selection programs. The inter- and intraspecific variability of responses to drought stress in the plants examined by those authors suggests a wide range of strategies in perennial herbaceous legumes to cope with drying conditions. For example, leaf osmotic adjustment was observed in *Bituminaria bituminosa* var. *albomarginata* accessions 6 and 10, both accessions of *Cullen australasicum* and *Kennedia prostrata* and leaf water potential was maintained at a high level in *B. bituminosa* var. *albomarginata* accessions 6 and 10 and *Macroptilium atropurpureum*.

Campos et al. (2004) refereed that the association between genotype and phenotype must be better understood and quantified to improve the ability to predict phenotypic performance based on genetic information. Tinker (2002) specifies that genomics and high throughput laboratory-based analysis of DNA are indispensable to comprehending gene-phenotype associations. This will be critically important for drought tolerance, where performance is regulated by many loci and subject to multiple genotype x environment and gene x gene interactions (epistasis) (Campos et al. 2004). Also, crop simulation models can assist investigation of the physiological and genetic basis of genotype variation (Shorter et al. 1991) and help selection decisions in plant breeding (Cooper et al. 1993).

6.5 Improving WUE by Agricultural Management Techniques

It is widely accepted that water is the most universally limiting factor in agricultural production systems (Centritto 2005). Natural factors related with the environment and genetic characteristics are basically responsible by the definition of the plant water requirements and, in the last circumstance, by their WUE. However, the farmer's decision, through the crop managements that ensure a better equilibrium between plants and environment, cannot be minimized. This role is much crucial as the local aridity index is higher. Improving of WUE_C is essential for agricultural sustainability under higher potential ET- associated soil moisture deficits exacerbated by the global climatic change (Flexas et al. 2010). To achieve higher WUE_C the increment/validation of scientific monitoring tools is necessary, such as infrared thermometry (Grant et al. 2007), trunk diameter sensors (Conejero et al. 2007), passive chlorophyll fluorescence (Flexas et al. 2002), hyperspectral reflectance indices (Rodríguez-Pérez et al. 2007), or sap flow meters (Fernández et al. 2008). The impact of agricultural management tools on WUE_C has been studied by many researchers. From the social and economic points of view, this

subject is of crucial importance for many world regions where the lack of food is a direct consequence of the insufficient and unreliable rainfall and changing rainfall patterns (FAO 2010). This section intends to refer some management techniques, either at soil or plant level, that can optimize crop water use efficiency and crop yield and its quality attributes.

6.5.1 At Soil Level

In those arid and semi-arid areas where the highest crop water requirements coincide with periods without rain, some soil properties such as texture, effective depth, and organic matter content are important to ensure both a high soil water-holding capacity and a good root development. The soil volume that can be explored by the roots is a key factor that affects the plant–water relations and mineral nutrition and therefore its vigor and yield (Keller 2005). Generally, plants are less affected by severe drought when the root system is deeper. This situation should be enhanced by greater soil depth and adequate fertility (Rodrigues et al. 2011).

Soil texture affects the erodibility and the availability of water, air, and mineral nutrients (Northcote 1988). In general, sandy soils show poor water availability while more argillaceous textures lead to soils more compact and oxygen-poor, impairing the development of the root system. In an increasingly mechanized agriculture, this negative aspect is exacerbated by excessive traffic of heavy farm machinery.

Soil management has great influence on crop–water relations. Cover crops keep the soil protected against erosion, reduce soil compaction, increase water infiltration, introduce organic carbon, and may prevent nitrate leaching. In periods of greater water scarcity, however, this practice affects crops in a manner comparable to deficit irrigation, because the covers use water and reduce nutrient availability for the crops (Lipecki and Berbeć 1997; Rodrigues et al. 2011). Conversely, the critical situation of water resources in most arid regions makes the soil surface management one of the most critical aspects of the agriculture practices applied to rainfed crops (Rodrigues et al. 2005). Thus, it is desirable that cover vegetation dries out naturally (using species that employ a drought escape strategy) or artificially before the drought period, creating a mulch of dead material on the ground. Therefore, the soil rest permanently protected, the water infiltration increases, and the root system develops freely close to the soil surface. In addition, the mulch reduces soil temperature and water losses by evaporation in summer (Van Huyssteen et al. 1984; Possingham 1992; Rodrigues et al. 2011).

The mycorrhizal associations have been studied due to their advantages in arid environments. These associations vary widely in structure and functions, but arbuscular mycorrhizas (AM) are by far the most prevalent of all mycorrhizal categories. It is estimated that 80 % of all terrestrial plants form this type of association, including many agriculturally and horticulturally important crop species (Peterson 2004; Mohammadi Goltapeh et al. 2008). Inoculate soils with appropriate AM fungi may

directly enhance root water uptake, contributing to preserve physiological activity in plants under severe drought conditions. Mycorrhizal fungi improved WUE in species such as safflower and wheat (Bryla and Duniway 1997) and watermelon (Kaya et al. 2003). Among the mechanisms involved, many are related to the physiology of the host plant, but some are related to the extraradical mycelia (Liu et al. 2007).

6.5.2 At Plant Level

At plant level, assuming that the plant breeding programs already took into account the greater intrinsic water use capacity, there are numerous cultural practices that can be implemented from the beginning of crop cycle to adult stage, to improve this attribute. Normally, these cultural strategies have in common the achievement of high environmental resources efficiency (light, temperature, CO₂, water and nutrients), with significant benefit to crop water economy. First, the management of the crop training system has a fundamental role to reach this goal (Smart 1974). This subject includes a set of cultural techniques selected by the farmers to train and guide the structure of the plant to its best performance. Some of these cultural practices have permanent effects for the crop life, such as the plantation density, the row orientation, and the plant shape, while others are susceptible to annual changes, e.g., all operations performed on the size of the branches and total leaf area during dormancy and the growing season (Carbonneau et al. 1981; Huglin and Schneider 1998). The row orientation has an important influence on WUE_C, both because of the light and thermal canopy microclimate and the thermal soil microclimate effects. Specifically for vineyards in dry and hot regions, some authors (Carbonneau et al. 1981; Intrieri et al. 1998) have proposed an N-S orientation rather than an E-W one, to improve light interception early in the morning (east side) and late in the afternoon (west side). This leads to higher photosynthetic rates, mostly in the morning, when the environmental conditions are relatively more favorable. On the other hand, at midday, the total leaf surface exposed to light is reduced (just the top receives sunlight), which may be helpful in reducing transpiration and preventing the leaf water potential dropping below the threshold values for runaway embolism (Moutinho-Pereira et al. 2001).

As refereed, the plant density has a crucial role for soil moisture exploitation. Usually, for rainfed fruit tree orchards and vineyards grown in the driest areas, the plant density must be lowered for each plant to have a greater rootzone and thus increasing the available water for each plant. However, it may increase the water loss by ET because the total leaf area and the soil area exposed to direct solar radiation are higher (Yuste 2007).

Pruning and removal of shaded leaves influence plant vigor, affecting the ratio between the total leaf area and sun exposed leaf area (Baeza et al. 2005). When this ratio increases, WUE decreases. In very hot and dry regions, given the weak vigor that plants usually present, the maintenance of the leaf surface in good health guarantees greater photosynthetic productivity and allows lower water loss

because the integrity of protective tissues, the epidermis and cuticle, is better safeguarded.

In arid regions, irrigation is undoubtedly a cultural practice with enormous benefits for the plant growth and development (Feres and Evans 2006). However, under limited water resources, the technical, economic, and cultural irrigation managements require careful decisions. The efficient management of limited water resources requires irrigation scheduling techniques based on deficit supplies with respect to crop water needs (Tognetti et al. 2005). Deficit irrigation, defined as the application of water below full crop water requirements, is an important tool to achieve the goal of reducing irrigation water use (Feres and Soriano 2007). Techniques such as RDI, where a water deficit is applied in a closely controlled way in low water stress sensitivity periods (Chalmers et al. 1981; Kriedemann and Goodwin 2003), and Partial Root-zone Drying (PRD), in which half of the root-zone is irrigated alternatively in scheduled irrigation events (Dry and Loveys 1998), are being increasingly valued because they allow to reconcile the advantages of a moderate water stress for a more efficient water use and an adequate development of the plants (Santos et al. 2007). In Australia, PRD has resulted in water savings of up to 50 % compared with the conventional irrigation of grapevines. An additional response of crops to PRD appears to be a shift of root growth to deeper soil layers, whereas under standard drip irrigation roots are often concentrated in the surface soil, which makes crops less drought resistant (Keller 2005).

Without disregarding the importance that irrigation can have for improving crop performance, it is crucial to develop mitigation alternatives, not only in economic terms but also in terms of environmental sustainability. Among these mitigation alternatives, there has been a major effort by the scientific community to study the effect of inorganic substances on the improvement of light microclimate and water relations of leaves. Reflective antitranspirants (e.g., kaolin, Bordeaux mixture), have interesting properties because they can lower leaf temperature by increasing reflection of infrared radiation (Moutinho-Pereira et al. 2001) (Fig. 6.1). Lowered leaf temperature reduces the vapor pressure gradient between the leaf and the bulk air. Since this is the driving force behind transpiration, the plant water consumption is reduced (Glenn and Puterka 2005). Jifon and Syvertsen (2003) found that midday WUE of grapefruit kaolin-sprayed leaves was 25 % higher than that of control leaves, indicating improved WUE under high light intensity. However, the results of kaolin application require further demonstration since they have often been contradictory, ranging from increased to decreased yields and photosynthetic rates.

6.6 Water Use Strategies of Native and Invasive Plants

In xeric environments, WUE is likely to be a target of natural selection (Heschel et al. 2002). As previously discussed in this chapter, plants under natural conditions need to greatly improve their WUE to increase their chances of survival in



Fig. 6.1 Kaolin and Bordeaux mixture application in grapevine: **a** and **b** field trials in the Douro Demarcated Region; treatments: **c** control; **d** kaolin and **e** Bordeaux mixture

water -scarce environments. Due to climate change, biological invasions may become a serious problem under natural conditions. Competitive strategies are important for the successful establishment and persistence of invasive plants (Vilá and Weiner 2004). Tolerance strategies may also help in the successful

establishment or dominance of invasive species (Allred et al. 2010). An important trait is the ability of seedlings to develop root systems quickly, before the dry summer begins (Roché et al. 1994). Greater competitive ability could include greater use of limiting resources, such as water, thereby inhibiting establishment, survival, and reproduction of native species (Blicker et al. 2003). According to McDowell (2002) invasive species increase the efficiency of resource capture by maintaining a high rate of photosynthesis per unit water loss.

To identify the factors that make some plant species troublesome invaders, many studies have compared native and invasive plant performance (Daehler 2003). Hill et al. (2006) found that invasive species had lower diurnal variation in leaf water potential than native ones despite the high transpiration. This capacity may be due to the ability of water uptake through deeper roots (Hill et al. 2006).

Increased WUE may also be an important contribution to the success of invasive species in areas where water is limiting (Hill et al. 2006). The efficiency of water use can be caused by variations in the environment or leaf functional traits (Seibt et al. 2008). Invasive *Rubus* plants had higher instantaneous WUE than native ones, probably due to their thicker leaves (McDowell 2002). However, Hill et al. (2006) found that WUE was higher in invasive species than in natives only under the most unusually dry conditions. Leaf carbon isotope composition allowed McAlpine et al. (2008) to conclude that the higher WUE of invasive plants/species resulted from increased carbon gain and not from strategies that limit water loss. Blicker et al. (2003) found that mature invasive plants may prolong their growing season by increasing WUE during mid- and late summer, when neighboring semi-arid plants are quiescent. On the other hand, Funk and Vitousek (2007) and Cavaleri and Sack (2010) reported similar values of WUE among invasive and native species.

Some studies support the hypothesis that high photosynthetic rate is an important strategy of invasive ability (Kloeppel and Abrams 1995; Baruch and Goldstein 1999; McDowell 2002; Hill et al. 2006; Jiang et al. 2009; Allred et al. 2010). Invasive species can maintain higher photosynthetic rates by modifying leaf anatomy and structure. Specific leaf area (SLA) represents light-capturing area deployed per dry mass allocated (Hamilton et al. 2005). A high SLA is a trait often associated with invasiveness (Baruch and Goldstein 1999; Lake and Leishman 2004; Hamilton et al. 2005; Burns and Winn 2006; Grotkopp and Rajmánek 2007; Feng et al. 2008; Allred et al. 2010). A high SLA reflects the occurrence of thinner leaves, which are less costly to produce and to maintain (Lee and Graham 1986) and, due to the associated rapid leaf production, allows an opportunistic capture of solar energy to invasive plants (Grotkopp and Rajmánek 2007). Thus, species with a high SLA have a shorter investment return rate and greater potential for fast growth (Lake and Leishman 2004). However, some authors defend that a high SLA favors invasive species only under some conditions, such as when in new environments with non-limiting resources (Burns 2006; Burns and Winn 2006; Leishman et al. 2007).

In general, invasive species had greater WUE and adaptations at root level that allow a more efficient water uptake. The most relevant attributes that favor the

invaders are the greater photosynthetic rates associated to a high SLA. However, these attributes may vary according to the species and the environment in which they are established. This subject is still controversial, and the problem of what makes a species invasive is far from solved.

6.7 Conclusions

The available freshwater is limited in many parts of the planet due to multiple factors, such as climate change, population increase, and rapid economic development. The greatest potential savings can be made in agriculture. In fact, small improvements in WUE by human manipulation such as breeding and agricultural management techniques can have a significant effect on water availability. However, the concept of WUE is of limited application when discussing the fitness of plants for water-limited environments (Jones 2004). Intrinsic WUE_{leaf} presents substantial intra- and interspecific variation, and depends on environmental conditions. Moreover, improving WUE_{leaf} may not necessarily result in improved WUE_{WP} , WUE_C and WUE_Y . For natural ecosystems, improvements in WUE are only valuable if there is little competition. In fact is not useful for a species to have a conservative water use, with a high WUE, if the competitors will use all the water available first.

References

- Alamillo J, Almoguera C, Bartels D, Jordano J (1995) Constitutive expression of small heat shock proteins in vegetative tissues of the resurrection plant *C. plantagineum*. *Plant Mol Biol* 29(5):1093–1099
- Allred BW, Fuhlendorf SD, Monaco TA, Will RE (2010) Morphological and physiological traits in the success of the invasive plant *Lespedeza cuneata*. *Biol Invasions* 12:739–749
- Alpert P, Oliver MJ (2002) Drying without dying. In: Black M, Pritchard H (eds) *Desiccation and survival in plants: drying without dying*. CAB International, Wallingford, pp 4–31
- Amthor JS (2000) The mccree-de wit-penning de vries-thornley respiration paradigms: 30 years later. *Ann Botany* 86:1–20
- Araus JL, Slafer GA, Reynolds MP, Royo C (2002) Plant breeding and drought in C3 cereals: what should we breed for? *Ann Botany* 89:925–940
- Arndt SK (2000) Mechanisms of drought resistance in the tropical fruit tree *Ziziphus*. PhD Thesis, Vienna
- Aroca R, Porcel R, Ruiz-Lozano JM (2012) Regulation of root water uptake under abiotic stress conditions. *J Exp Bot* 63(1):43–57
- Asada K (1999) The water–water cycle in chloroplasts scavenging of active oxygens and dissipation of excess photons. *Annu Rev Plant Physiol Plant Mol Biol* 50:601–639
- Ashraf M, Harris PJC (2004) Potential biochemical indicators of salinity tolerance in plants. *Plant Sci* 166:3–16

- Atlin G (2003) Improving drought tolerance by selecting for yield. In: Fischer KS, Lafitte R, Fukai S, Atlin G, Hardy B (eds) Breeding rice for drought-prone environments. International Rice Research Institute, Los Baños (Philippines), pp 14–22
- Bacelar EA, Correia CM, Moutinho-Pereira JM, Gonçalves B, Lopes JI, Torres-Pereira JM (2004) Sclerophylly and leaf anatomical traits of five field-grown olive cultivars growing under drought conditions. *Tree Physiol* 24:233–239
- Bacelar EA, Moutinho-Pereira JM, Gonçalves BC, Ferreira HF, Correia CM (2007a) Changes in growth, gas exchange, xylem hydraulic properties and water use efficiency of three olive cultivars under contrasting water availability regimes. *Environ Exp Bot* 60:183–192
- Bacelar EA, Moutinho-Pereira JM, Gonçalves BC, Lopes JI, Correia CM (2009) Physiological responses of different olive genotypes to drought conditions. *Acta Physiol Plant* 31(3):611–621
- Bacelar EA, Santos DL, Moutinho-Pereira JM, Gonçalves BC, Ferreira HF, Correia CM (2006) Immediate responses and adaptative strategies of three olive cultivars under contrasting water availability regimes: changes on structure and chemical composition of foliage and oxidative damage. *Plant Sci* 170(3):596–605
- Bacelar EA, Santos DL, Moutinho-Pereira JM, Lopes JI, Gonçalves BC, Ferreira TC, Correia CM (2007b) Physiological behavior, oxidative damage and antioxidative protection of olive trees grown under different irrigation regimes. *Plant Soil* 292:1–12
- Bacon MA (2004) Water use efficiency in plant biology. Blackwell Publishing CRC Press, Oxford
- Baeza P, Ruiz C, Cuevas E, Sotés V, Lissarrague J (2005) Ecophysiological and agronomic response of Tempranillo grapevines to four training systems. *Am J Enol Viticul* 56:129–138
- Baldocchi D, Falge E, Gu L, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer Ch, Davis K, Evans R, Fuentes J, Goldstein A, Katul G, Law B, Lee X, Malhi Y, Meyers T, Munger W, Oechel W, Paw KT, Pilegaard K, Schmid HP, Valentini R, Verma S, Vesala T, Willson K, Wofsy S (2001) Fluxnet: a tool to study the temporal and spatial variability of ecosystem scale carbon dioxide, water vapor, and energy flux densities. *B Am Meteorol Soc* 82:2415–2434
- Bänzinger M, Edmeades GO, Beck D, Bellon M (2000) Breeding for drought and nitrogen stress tolerance in maize: from theory to practice. D.F., Cimmyt, Mexico
- Bartels D, Schneider K, Terstappen G, Piatkowski D, Salamini F (1990) Molecular cloning of abscisic acid-modulated genes which are induced during desiccation of the resurrection plant *C. plantagineum*. *Planta* 181:27–34
- Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia* 121:183–192
- Blicker PS, Olson BE, Wraith JM (2003) Water use and water-use efficiency of the invasive *Centaurea maculosa* and three native grasses. *Plant Soil* 254:371–381
- Bloom AJ, Zwieniecki MA, Passioura JB, Randall LB, Holbrook NM, St.Crair DA (2004) Water relations under root chilling in a sensitive and tolerant tomato species. *Plant, Cell Environ* 27:971–979
- Blum A (1998) Plant breeding for stress environments. CRC Press, Boca Raton
- Blum A (2005) Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive? *Aust J Agr Res* 56:1159–1168
- Blum A (2009) Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crop Res* 112:119–123
- Blum A (2011) Plant breeding for water-limited environments. Springer Science+Business Media, New York
- Bohnert HJ, Nelson DE, Jensen RG (1995) Adaptations to environmental stresses. *Plant Cell* 7:1099–1111
- Bongi G, Mencuccini M, Fontanazza G (1987) Photosynthesis of olive leaves: effect of light flux density, leaf age, temperature, peltates and H₂O vapour pressure deficit on gas exchange. *J Am Soc Hortic Sci* 112:143–148

- Bota J, Flexas J, Medrano H (2001) Genetic variability of photosynthesis and water use in Balearic grapevine cultivars. *Ann Appl Biol* 138:353–365
- Bray EA, Bailey-Serres J, Weretilnyk E (2000) Response to abiotic stresses. In: Buchanan BB, Gruissem W, Jones RL (eds) *Biochemistry and molecular biology of plants*. American Society of Plant Physiologists Press, Rockville, pp 1158–1203
- Bruce WB, Edmeades GO, Barker TC (2002) Molecular and physiological approaches to maize improvement for drought tolerance. *J Exp Bot* 53:13–25
- Bryla DR, Duniway JM (1997) Effects of mycorrhizal infection on drought tolerance and recovery in safflower and wheat. *Plant Soil* 197:95–103
- Burns JH (2006) Relatedness and environment affect traits associated with invasive and noninvasive introduced Commelinaceae. *Ecol Appl* 16(4):1367–1376
- Burns JH, Winn AA (2006) A comparison of plastic responses to competition by invasive and non-invasive congeners in the Commelinaceae. *Biol Invasions* 8:797–807
- Campos H, Cooper M, Habben JE, Edmeades GO, Schussler JR (2004) Improving drought tolerance in maize: a view from industry. *Field Crop Res* 90:19–34
- Carbonneau A, Casteran P, Leclair Ph (1981) Principes de choix de systèmes de conduite pour des vignobles temperes et definitions pratiques utilisables en reglementation. *Connaiss Vigne Vin* 15(2):97–124
- Cavaleri MA, Sack L (2010) Comparative water use of native and invasive plants at multiple scales: a global meta-analysis. *Ecology* 91(9):2705–2715
- Cellier F, Conejero G, Casse F (2000) Dehydrin transcript fluctuations during a day/night cycle in drought-stressed sunflower. *J Exp Bot* 51:299–304
- Centritto M (2005) Photosynthetic limitations and carbon partitioning in cherry in response to water deficit and elevated [CO₂]. *Agricult Ecosys Environ* 106:233–242
- Cernusak LA, Winter K, Aranda J, Turner BL (2008) Conifers, angiosperm trees, and lianas: growth, whole-plant water and nitrogen use efficiency, and stable isotope composition ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of seedlings grown in a tropical environment. *Plant Physiol* 148:642–659
- Chalmers DJ, Mitchell PD, van Heek L (1981) Control of peach tree growth and productivity by regulated water supply, tree density, and summer pruning. *J Am Soc Hort Sci* 106:307–312
- Chaves MM (1991) Effects of water deficits on carbon assimilation. *J Exp Bot* 42:1–16
- Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant response to drought: from genes to the whole plant. *Funct Plant Biol* 30:239–264
- Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CP, Osório ML, Carvalho I, Faria T, Pinheiro C (2002) How plants cope with water stress in the field. *Photosynthesis and growth*. *Ann Bot* 89:907–916
- Chen THH, Murata N (2002) Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. *Curr Opin Plant Biol* 5:250–257
- Chrispeels MJ, Agre P (1994) Aquaporins: water channel proteins of plant and animal cells. *Trends Biochem Sci* 19:421–425
- Close T (1996) Dehydrins: emergence of a biochemical role of a family of plant dehydration proteins. *Physiol Plantarum* 97:795–803
- Conde A, Silva P, Agasse A, Conde C, Gerós H (2011) Mannitol transport and mannitol dehydrogenase activities are coordinated in *Olea europaea* under salt and osmotic stresses. *Plant Cell Physiol* 52(10):1766–1775
- Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2004) Breeding for high water-use efficiency. *J Exp Botany* 55:2447–2460
- Conejero W, Alarcón JJ, García-Orellana Y, Nicolás E, Torrecillas A (2007) Evaluation of sap flow and trunk diameter sensors used for irrigation scheduling in early maturing peach trees. *Tree Physiol* 27:1753–1759
- Connor DJ (2005) Adaptation of olive (*Olea europaea* L.) to water-limited environments. *Aust J Agric Res* 56:1181–1189
- Cooper M, Delacy IH, Eisemann RL (1993) Recent advances in the study of genotype \times environment interactions and their application to plant breeding. In: Imrie BC, Hacker JB (eds) *Focused plant improvement: towards responsible and sustainable agriculture*. In: Proceedings

- tenth Australian plant breeding conference, Vol 1. Organising Committee, Australian Convention and Travel Service, Canberra, pp 116–131
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu Rev Ecol Evol Syst* 34:183–211
- Dry PR, Loveys BR (1998) Factors influencing grapevine vigour and the potential for control with partial rootzone drying. *Aust J Grape Wine Res* 4:140–148
- Emmerich WE (2007) Ecosystem water use efficiency in a semiarid shrubland and grassland community. *Rangeland Ecol Manage* 60:464–470
- Fahn A, Werker E, Baas P (1986) Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. *Isr Acad Sci Hum*, Jerusalem
- FAO (2010) Climate change implications for food security and natural resources management in Africa. Twenty-sixth regional conferences for Africa. Luanda, Angola
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537
- Feng Y-L, Fu G-L, Zheng Y-L (2008) Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners. *Planta* 228:383–390
- Fereres E, Evans RG (2006) Irrigation of fruit trees and vines: an introduction. *Irrigation Sci* 24:55–57
- Fereres MA Soriano (2007) Deficit irrigation for reducing agricultural water use. *J Exp Bot* 58:147–159
- Fernández JE, Green SR, Caspari HW, Diaz-Espejo A, Cuevas MV (2008) The use of sap flow measurements for scheduling irrigation in olive, apple and Asian pear trees and in grapevines. *Plant Soil* 305:91–104
- Fleury D, Jefferies S, Kuchel H, Langridge P (2010) Genetic and genomic tools to improve drought tolerance in wheat. *J Exp Bot* 61(12):3211–3222
- Flexas J, Bota J, Escalona JM, Sampol B, Medrano H (2002) Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Funct Plant Biol* 29:461–471
- Flexas J, Galmes J, Galle A, Gulias J, Pou A, Ribas-Carbo M, Tomas M, Medrano H (2010) Improving water use efficiency in grapevines: potential physiological targets for biotechnological improvement. *Aust J Grape Wine Res* 16:106–121
- Fukai S, Cooper M (1995) Development of drought-resistant cultivars using physiological traits in rice. *Field Crop Res* 40:67–86
- Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081
- Garay-Arroyo A, Colmenero-Flores JM, Garciarubio A, Covarrubias AA (2000) Highly hydrophilic proteins in prokaryotes and eukaryotes are common during conditions of water deficit. *J Biol Chem* 275:5668–5674
- Glenn DM, Puterka GJ (2005) Particle films: a new technology for agriculture. *Hortic Rev* 31:1–45
- Grant OM, Tronina L, Jones HG, Chaves MM (2007) Exploring thermal imaging variables for the detection of stress responses in grapevine under different irrigation regimes. *J Exp Bot* 58:815–825
- Grotkopp E, Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *Am J Bot* 94(4):526–532
- Halliwell B, Gutteridge JMC (1999) Free radicals in biology and medicine, 3rd edn. Oxford University Press, Oxford
- Hamilton EW, Heckathorn SA (2001) Mitochondrial adaptations to sodium chloride: complex I is protected by anti-oxidants and small heat-shock proteins, while complex II is protected by proline and betaine. *Plant Physiol* 126:166–1274

- Hamilton MA, Murray BR, Cadotte M, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecol Lett* 8:1066–1074
- Hendrick JP, Hartl FU (1995) The role of molecular chaperones in protein folding. *Faseb J* 9:1559–1569
- Heschel MS, Donohue K, Hausmann N, Schmitt J (2002) Population differentiation and natural selection for water-use efficiency in *Impatiens capensis* (Balsaminaceae). *Int J Plant Sci* 163(6):907–912
- Hill JP, Germino MJ, Wraith JM, Olson BE, Swan MB (2006) Advantages in water relations contribute to greater photosynthesis in *C. maculosa* compared with established grasses. *Int J Plant Sci* 167(2):269–277
- Hong S-W, Vierling E (2000) Mutants of *Arabidopsis thaliana* defective in the acquisition of tolerance to high temperature stress. *P Natl Acad Sci U S A* 97:4392–4397
- Huglin P, Schneider C (1998) *Biologie et écologie de la vigne*. Technique and Documentation, 2e éd. Paris
- Ingram J, Bartels D (1996) The molecular basis of dehydration tolerance in plants. *Annu Rev Plant Physiol Plant Mol Biol* 47:377–403
- Intrieri C, Poni S, Rebucci B, Magnanini E (1998) Row orientation effects on whole-canopy gas exchange of potted and field-grown grapevines. *Vitis* 37(4):147–154
- Ionenko IF, Anisimov AV, Dautova NR (2010) Effect of temperature on water transport through aquaporins. *Biol Plant* 54:488–494
- IPCC (2011) The special report on managing the risks of extreme events and disasters to advance climate change adaptation. <http://www.ipcc.ch/> Cited 1 Dez 2011
- Jackson P, Robertson M, Cooper M, Hammer G (1996) The role of physiological understanding in plant breeding: from a breeding perspective. *Field Crop Res* 49:11–37
- Jiang L-F, Luo Y-Q, Chen J-K, Li B (2009) Ecophysiological characteristics of invasive *Spartina alterniflora* and native species in salt marshes of Yangtze River estuary, China. *Est Coast Shelf Sci* 81:74–82
- Jifon JL, Syvertsen JP (2003) Kaolin particle film applications can increase photosynthesis and water use efficiency of ‘Ruby red’ grapefruit leaves. *J Am Soc Hortic Sci* 128:107–111
- Jones H (2004) What is water use efficiency? In: Bacon MA (ed) *Water use efficiency in plant biology*. Blackwell Publishing CRC Press, Oxford, pp 27–41
- Jones HG (1992) *Plants and microclimate: a quantitative approach to environmental plant physiology*, 2nd edn. Cambridge University Press, Cambridge
- Karabourniotis G, Bormann J (1999) Penetration of UV-A, UV-B and blue light through the leaf trichome layers of two xeromorphic plants, olive and oak, measured by optical fibre microprobes. *Physiol Plantarum* 105:655–661
- Karl TR, Melillo JM, Peterson TC (eds) (2009) *Global climate change impacts in the United States*. Cambridge University Press, Cambridge
- Kaya C, Higgs D, Kirnak H, Tas I (2003) Mycorrhizal colonisation improves fruit yield and water use efficiency in watermelon (*Citrullus lanatus* Thunb.) grown under well-watered and water-stressed conditions. *Plant Soil* 253:287–292
- Keller M (2005) Deficit irrigation and vine mineral nutrition. *Am J Enol Vitic* 56(3):267–283
- Kloppel BD, Abrams MD (1995) Ecophysiological attributes of the native *Acer saccharum* and the exotic *Acer platanoides* in urban oak forests in Pennsylvania, U S A. *Tree Physiol* 15:739–746
- Kozłowski TT, Kramer PJ, Pallardy SG (1991) *The physiological ecology of woody plants*. Academic, San Diego
- Kozłowski TT, Pallardy SG (1997) *Physiology of woody plants*, 2nd edn. Academic, San Diego
- Kriedemann PE, Goodwin I (2003) Regulated deficit irrigation and partial root-zone drying. Irrigation insights No.3. In: Currey A (ed) *Land and water Australia*, Canberra, p 102
- Lake JC, Leishman MR (2004) Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117:215–226
- Larcher W (1995) *Physiological plant ecology*, 3rd edn. Springer, Berlin

- Lee D, Graham R (1986) Leaf optical properties of rainforest sun and extreme shade plants. *Am J Bot* 73:1100–1108
- Leishman MR, Haslehurst T, Ares A, Baruch Z (2007) Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytol* 176:635–643
- Leon J, Bukovac M (1978) Cuticle development and surface morphology of olive leaves with reference to penetration of foliar-applied chemicals. *J Am Soc Hortic Sci* 103:465–472
- Levitt J (1972) Responses of plants to environmental stresses. Academic, New York
- Liakoura V, Stavrianakou S, Liakopoulos G, Karabourniotis G, Manetas Y (1999) Effects of UV-B radiation on *Olea europaea*: comparisons between a greenhouse and a field experiment. *Tree Physiol* 19:905–908
- Lipecki J, Berbeć S (1997) Soil management in perennial crops: orchards and hop gardens. *Soil Till Res* 43:169–184
- Liu A, Plenchette C, Hamel C (2007) Soil nutrient and water providers: how arbuscular mycorrhizal mycelia support plant performance in a resource limited world. In: Hamel C, Plenchette C (eds) *Mycorrhizae in crop production*, Haworth Press, Inc, Philadelphia, pp 37–66
- Lovisolo C, Schubert A (1998) Effects of water stress on vessel size and xylem hydraulic conductivity in *Vitis vinifera* L. *J Exp Bot* 49:693–700
- Ludlow MM (1980) Adaptive significance of stomatal responses to water stress. In: Turner NC, Kramer PJ (eds) *Adaptations of plants to water and high temperature stress*. Wiley Interscience, New York, pp 123–138
- Ludlow MM (1989) Strategies of response to water stress. In: Kreeb KH, Richter H, Hinckley TM (eds) *Structural and functional responses to environmental stresses*. SPB Academic Publishing, The Hague, pp 269–281
- Maroco JP, Pereira JS, Chaves MM (2000) Growth, photosynthesis and water use efficiency of two C₄ Sahelian grasses subjected to water deficits. *J Arid Environ* 45:119–137
- Masle J, Gilmore SR, Farquhar GD (2005) The ERECTA gene regulates plant transpiration efficiency in *Arabidopsis*. *Nature* 436:866–870
- McAlpine KG, Jesson LK, Kubien DS (2008) Photosynthesis and water-use efficiency: a comparison between invasive (exotic) and non-invasive (native) species. *Austral Ecol* 33:10–19
- McDowell SCL (2002) Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). *Am J Bot* 89(9):1431–1438
- McNeil SD, Nuccio ML, Hanson AD (1999) Betaines and related osmoprotectants. Targets for metabolic engineering of stress resistance. *Plant Physiol* 120:945–949
- Mediavilla S, Escudero A, Heilmeyer H (2001) Internal leaf anatomy and photosynthetic resource-use efficiency: interspecific and intraspecific comparisons. *Tree Physiol* 21:251–259
- Mittler R (2006) Abiotic stress, the field environment and stress combination. *Trends Plant Sci* 11(1):15–19
- Mohammadi Goltapeh E, Rezaee Danesh Y, Prasad R, Varma A (2008) Mycorrhizal fungi: what we know and what should we know? In: Varma A (ed) *Mycorrhiza*. Springer, Berlin, pp 3–27
- Møller IM (2001) Plant mitochondria and oxidative stress: electron transport, NADPH turnover, and metabolism of reactive oxygen species. *Annu Rev Plant Physiol Plant Mol Biol* 52:561–591
- Moran JF, Becana M, Iturbe-Ormaetxe I, Frechilla S, Klucas RV, Aparicio-Tejo P (1994) Drought induces oxidative stress in pea plants. *Planta* 194:346–352
- Morison JI, Baker NR, Mullineaux PM, Davies WJ (2008) Improving water use in crop production. *Philos T Roy Soc B* 363:639–665
- Moutinho-Pereira JM, Correia CM, Gonçalves B, Bacelar E, Torres-Pereira JM (2004) Leaf gas-exchange and water relations of grapevines grown in three different conditions. *Photosynthetica* 42(1):81–86
- Moutinho-Pereira JM, Magalhães N, Gonçalves B, Bacelar E, Brito M, Correia C (2007) Gas exchange and water relations of three *Vitis vinifera* L. cultivars growing under Mediterranean climate. *Photosynthetica* 45(2):202–207

- Moutinho-Pereira JM, Magalhães N, de Torres Castro LF, Chaves MM, Torres-Pereira JM (2001) Physiological responses of grapevine leaves to Bordeaux mixture under light stress conditions. *Vitis* 40(3):117–121
- Murai-Hatano M, Kuwagata T, Sakurai J, Nonami H, Ahamed A, Nagasuga K, Matsunami T, Fukushi K, Maeshima M, Okada M (2008) Effect of low root temperature on hydraulic conductivity of rice plants and the possible role of aquaporins. *Plant Cell Physiol* 49:1294–1305
- Nelson DE, Repetti PP, Adams TR, Creelman RA, Wu J, Warner DC, Anstrom DC, Bensen RJ, Castiglioni PP, Donnarummo MG, Hinchey BS, Kumimoto RW, Maszle DR, Canales RD, Krolowski KA, Dotson SB, Gutterson N, Ratcliffe OJ, Heard JE (2007) Plant nuclear factor Y (NF-Y) B subunits confer drought tolerance and lead to improved corn yields on water-limited acres. *P Nat Acad Sci U S A* 104:16450–16455
- Noiraud N, Delrot S, Lemoine R (2000) The sucrose transporter of celery: identification and expression during salt stress. *Plant Physiol* 122:1447–1455
- Northcote KH (1988) Soils and Australian viticulture. In: Coombe BG, Dry PR (eds) *Viticulture*, vol 1. Winetitles, Australia, pp 61–90
- Pang J, Yang J, Ward P, Siddique Kadambot HM, Lambers H, Tibbett M, Ryan M (2011) Contrasting responses to drought stress in herbaceous perennial legumes. *Plant Soil* 348(1–2):299–314
- Papageorgiou GC, Murata N (1995) The unusually strong stabilizing effects of glycine betaine on the structure and function of the oxygen evolving photosystem II complex. *Photosynth Res* 44:243–252
- Passioura J (2002) Environmental biology and crop improvement. *Funct Plant Biol* 29:537–546
- Passioura J (2007) The drought environment: physical, biological and agricultural perspectives. *J Exp Bot* 58(2):113–117
- Passioura JB (1983) Roots and drought resistance. *Agr Water Manage* 7:265–280
- Passioura JB (1982) Water in the soil-plant-atmosphere continuum. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Physiological plant ecology II*. Encyclopedia of plant physiology, vol 12 B. Springer, Berlin, pp 5–33
- Patakas A, Noitsakis B (1999) Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. *J Plant Physiol* 154:767–774
- Peterson RL, Massicotte HB, Melville LH (2004) *Mycorrhizas: anatomy and cell biology*. NRC Research Press Ottawa/CABI Publishing, Wallingford
- Possigham JV (1992) Factors affecting growth, flowering and fruit ripening in *Vitis vinifera*. In: Proceedings of the IV international symposium on grapevine physiology, Torino (Italia)
- Rajendrakumar CSV, Reddy BDB, Reddy AR (1994) Proline-protein interactions: protection of structural and functional integrity of M4 lactate dehydrogenase. *Biochem Biophys Res Commun* 201:957–963
- Rathinasabapathi B, Fouad WM, Sigua CA (2001) β -Alanine betaine synthesis in the Plumbaginaceae: purification and characterization of a trifunctional, S-adenosyl-L-methionine-dependent N-methyltransferase from *Limonium latifolium* leaves. *Plant Physiol* 126:1241–1249
- Reynolds MP, Ortiz-Monasterio JI, McNab A (2001) Application of physiology in wheat breeding. CIMMYT, Mexico
- Rhodes D, Hanson AD (1993) Quaternary ammonium and tertiary sulfonium compounds in higher plants. *Annu Rev Plant Physiol Plant Mol Biol* 44:357–384
- Richards RA, Condon AG, Rebetzke GJ (2001) Traits to improve yield in dry environments. In: Reynolds MP, Ortiz-Monasterio JI, McNab A (eds) *Application of physiology in wheat breeding*. CIMMYT, Mexico, pp 88–100
- Richardson A, Berlyn G (2002) Changes in foliar spectral reflectance and chlorophyll fluorescence of four temperate species following branch cutting. *Tree Physiol* 22:499–506
- Rivero RM, Kojima M, Gepstein A, Sakakibara H, Mittler R, Gepstein S, Blumwald E (2007) Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *P Nat Acad Sci U S A* 104:19631–19636

- Roché BF, Roché CT, Chapman RC (1994) Impacts of grassland habitat on yellow starthistle (*Centaurea solstitialis* L.) invasion. *Northwest Sci* 68(2):86–96
- Rodrigues MA, Arrobas M, Bonifácio N (2005) Análise de terras em olivais tradicionais de sequeiro. O efeito da aplicação localizada de fertilizantes. *Revista de Ciências Agrárias* 28:167–176
- Rodrigues MA, Pavão F, Lopes JI, Gomes V, Arrobas M, Moutinho-Pereira JM, Ruivo S, Cabanas J, Correia CM (2011) Olive yields and tree nutritional status during a four-year period without nitrogen and boron fertilization. *Communin Soil Sci Plant Anal* 42:803–814
- Rodríguez-Pérez JR, Riaño D, Carlisle E, Ustin S, Smart DR (2007) Evaluation of hyperspectral reflectance indexes to detect grapevine water status in vineyards. *Am J Enol Viticult* 58:302–317
- Samuel D, Kumar TKS, Ganesh G, Jayaraman G, Yang P-W, Chang M-M, Trivedi VD, Wang S-L, Hwang K-C, Chang D-K, Yu C (2000) Proline inhibits aggregation during protein refolding. *Protein Sci* 9:344–352
- Santos TP, Lopes CM, Rodrigues ML, Souza CR, Ricardo-da-Silva JM, Marococ JP, Pereira JS, Chaves MM (2007) Effects of deficit irrigation strategies on cluster microclimate for improving fruit composition of Moscatel field-grown grapevines. *Sci Hortic* 112(3):321–330
- Schulte PJ (1993) Tissue hydraulic properties and the water relations of desert shrubs. In: Smith JAC, Griffith H (eds) *Water deficits, plant responses from cell to community*. BIOS, Oxford, pp 177–192
- Schultz HR, Matthews MA (1988) Resistance to water transport in shoots of *Vitis vinifera* L. *Plant Physiol* 88:718–724
- Schwabe W, Lionakis S (1996) Leaf attitude in olive in relation to drought resistance. *J Hortic Sci* 71:157–166
- Seibt U, Rajabi A, Griffiths H, Berry JA (2008) Carbon isotopes and water use efficiency: sense and sensitivity. *Oecologia* 155:441–454
- Shinozaki K, Yamaguchi-Shinozaki K (2007) Gene networks involved in drought stress response and tolerance. *J Exp Bot* 58:221–227
- Shorter R, Lawn RJ, Hammer GL (1991) Improving genotypic adaptation in crops—a role for breeders, physiologists and modellers. *Exp Agr* 27:155–175
- Smart RE (1974) Photosynthesis by grapevine canopies. *J Appl Ecol* 11:997–1006
- Smirnoff N (1998) Plant resistance to environmental stress. *Curr Opin Biotech* 9:214–219
- Sperry JS (2003) Evolution of water transport and xylem structure. *Int J Plant Sci (Suppl.)* 164:S115–S127
- Sun W, Van Montagu M, Verbruggen N (2002) Small heat shock proteins and stress tolerance in plants. *Biochim Biophys Acta* 1577:1–9
- Taiz L, Zieger E (1998) *Plant Physiology*, 2nd edn. Sinauer Associates Inc., Sunderland
- Tinker NA (2002) Why quantitative geneticists should care about bioinformatics. In: Kang MS (ed) *Quantitative genetics, genomics and plant breeding*. CABI, Wallingford, pp 33–44
- Tognetti R, d'Andria R, Morelli G, Alvino A (2005) The effect of deficit irrigation on seasonal variations of plant water use in *Olea europaea* L. *Plant Soil* 273:139–155
- Tognetti R, Raschi A, Béres C, Fenyvesi A, Ridder HW (1996) Comparison of sap flow, cavitation and water status of *Quercus petraea* and *Quercus cerris* trees with special reference to computer tomography. *Plant, Cell Environ* 19:928–938
- Tuberosa R, Salvi S (2006) Genomics approaches to improve drought tolerance in crops. *Trends Plant Sci* 11(8):405–412
- Tubiello FN, Lin G, Druitt JW, Marino BEV (1990) Ecosystem-level evapotranspiration and water-use efficiency in the desert biome of Biosphere 2. *Ecol Eng* 13:263–271
- Turner NC (1986) Crop water deficits: a decade of progress. *Adv Agron* 39:1–51
- Tyerman SD, Niemietz CM, Bramley H (2002) Plant aquaporins: multifunctional water and solute channels with expanding roles. *Plant, Cell Environ* 25:173–194
- Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. *New Phytol* 119:345–360

- Tyree MT, Sperry S (1989) Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Physiol Mol Biol* 40:19–38
- Van Huyssteen E, Van Zyl JL, Koen AP (1984) The effect of cover crop management on soil conditions and weed control in a Colombarid vineyard in Oudtshoorn S Afr. *J Enol Vitic* 5:7–17
- Vijn I, Smeekens S (1999) Fructan: more than a reserve carbohydrate? *Plant Physiol* 120:351–360
- Vilá M, Weiner J (2004) Are invasive plant species better competitors than native plant species?—evidence from pair-wise experiments. *Oikos* 105:229–238
- Wan XC, Zwiazek JJ (2001) Root water flow and leaf stomatal conductance in aspen (*Populus tremuloides*) seedlings treated with abscisic acid. *Planta* 213:741–747
- Wehmeyer N, Hernandez LD, Finkelstein RR, Vierling E (1996) Synthesis of small heat-shock proteins is part of the development program of late seed maturation. *Plant Physiol* 112:747–757
- Yuste J (2007) Efectos de la forma de conducción del viñedo en el régimen hídrico y en la respuesta agronómica. Fundamentos, aplicación y consecuencias del riego en la vid, Editorial Agrícola Española S.A., Madrid