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Ecophysiological strategies to overcome water deficit in herbaceous species under Mediterranean conditions

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SUMMARY – Because of the climatic characteristics of the Mediterranean Basin, most of the world's water problems can be found in this area. This fact and the future prospects of the Climate Change make it necessary for more efficient forages and grasslands to be used in order to obtain environmental quality benefits. For these reasons, the main objective of this work is to review the ecophysiological strategies of herbaceous species to overcome water deficit under Mediterranean conditions, paying special attention to their ability to survive a summer drought period and to produce biomass under restricted and unpredictable water availability.

Keywords: Mediterranean climate, drought, grasslands, ecophysiological strategies, water use efficiency, summer dormancy.

RESUME *– "Stratégies écophysiologiques pour surmonter le déficit hydrique chez les espèces herbacées en conditions méditerranéennes". Les caractéristiques climatiques du bassin méditerranéen sont telles qu'on peut y trouver la plupart des problèmes mondiaux liés à l'eau. Cette situation et les perspectives futures de changement climatique imposent une recherche de fourrages et d'herbages (gazon) plus efficaces qui permettrait de tirer des bénéfices quant à la qualité environnementale. C'est ainsi que le principal objectif de ce travail est de reconsidérer les stratégies écophysiologiques adoptées par les espèces d'herbacées pour subsister, malgré le déficit en eau, aux conditions méditerranéennes. Pour cela, une attention toute particulière est portée à leur capacité à survivre à la sécheresse estivale, et à produire une biomasse dans le cadre d'un accès restreint et imprévisible à l'eau.*

Mots-clés : *Climat méditerranéen, sécheresse, gazon, stratégies écophysiologiques, efficacité de l'utilisation de l'eau, dormance estivale.*

Introduction

The Mediterranean climate is characterized by a strong seasonal distribution of precipitation, with severe summer droughts during three or four months and cool winters. The largest concentration of rainfall is presented during the winter half of the year (from October to March). For this reason, the warmest months coincide with a low rainfall period. Besides the enhanced seasonal character, the Mediterranean region is also characterized by a strong inter-annual variability of precipitation and it is highly sensitive to variations in precipitation amount (Paredes *et al*., 2006). In the last three decades, it has been observed a decline in annual precipitation (Sarris *et al*., 2007) and the 4th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007) predicts a decrease in the annual number of precipitation days as well as an increase in the annual mean temperatures more than the global mean. Moreover, it is expected the warming in the Mediterranean area is likely to be largest in summer.

Food supply, prevention of soil degradation and rehabilitation of crop lands are the important roles in which grasses and forage species are involved, occupying a huge number of hectares around the world. Therefore, it is necessary that forages and grasslands for the future must utilise resources (nutrients and water) more efficiently and must also confer measurable benefits in terms of environmental quality (Medrano *et al*., 1998; Humphreys, 2005). In this sense, more information is required on factors that make crops more tolerant to changing conditions. In addition, a change in the management of grasslands is needed; it is necessary to drive practices towards sustainable grasslands which permit production and environmental goals (Kemp and Michalk, 2007).

Traditionally in the past, pasture production in the Mediterranean region mainly relied on annual plants that can quickly grow and reproduce during the wet season and survive the dry season as seed, thus avoiding severe drought (Fernández, 1993; Turner, 2004). By contrast, perennial plants present a different strategy which permit a dehydration tolerance and surviving the unfavourable season in a dormant form (Assuero *et al*., 2002; Volaire, 2003). Moreover, perennial plants are useful in many cases to improve the sustainability of agricultural systems and alleviate problems such as dryland salinity (Bell *et al*., 2007) and control of weed invasion (Kemp *et al*., 2000).

The main objective of this article is to review the ecophysiological strategies of herbaceous forage species to overcome water deficit under Mediterranean conditions, paying special attention to their ability to survive a summer drought period and to produce biomass under restricted and unpredictable water availability.

Biomass production under water deficit

Strategies to improve water uptake

Osmotic adjustment has been considered one of the crucial processes in plant adaptation to drought (Flexas and Medrano, 2002; Chaves *et al*., 2003), because it permits the maintenance of water absorption and leaf turgor via the net accumulation of solutes in the leaf under water deficit. The early decrease of leaf pre-dawn water potential in perennial herbs under water deficit may reflect differences between species in their ability to adjust their osmotic potential to continue extracting available water from the soil. By contrast, basal tissues of Mediterranean perennial herbs exhibit a greater osmotic adjustment that it might favour survival of grass tillers during drought (Volaire and Thomas, 1995). Consequently, Volaire (2003) showed that in annual grasses, when the aerial biomass is mostly senescent, the water in leaf bases declines abruptly and plant death occurs rapidly. By contrast, perennial plants can stay alive for long periods of severe drought since the water content in leaf bases, although dropping early, can stabilize under minimum water flows when all mature lamina have senesced, therefore contributing to the survival of immature tissues. Bell *et al*. (2007) also observed that the Mediterranean perennial legume *Dorycnium hirsutum* (L.) sacrificed stems and leaves in order to maintain water status in buds and meristems near the base of the plant during severe water stress. Thus, the strategy of some Mediterranean perennial cultivars to avoid drought period in a dormant form, although not conferring competitive dominance over a plant expressing osmotic adjustment, could be more successful to ensure plant survival under prolonged drought (Assuero *et al*., 2002). Nonetheless, a greater degree of osmotic adjustment among Mediterranean grasslands species may be useful to extract additional water from the soil and may play a role when water stress develops more slowly or in subsequent wetting and drying cycles (Bell *et al*., 2007).

A usually observed acclimatation to drought is seasonally increased fine root growth, which implies new gene expression and temporary morphologic changes (Flexas and Medrano, 2002, and references therein). In addition, large root-to-shoot ratios and large rooting depths can be cited as adaptations to drought, which means that occur in the evolutionary scale and involve important genetic differentiation and permanent morphologic changes. These characteristics would confer an advantage during water deficit since the relatively higher proportions of root biomass would facilitate water uptake to satisfy transpiration. In this sense, Volaire and Thomas (1995) showed that one of the main effects of drought-resistant varieties of cocksfoot under water deficit is early cessation of leaf elongation and a greater partitioning of dry matter into the root system. Moreover, Assuero (2002) also observed that plants of tall fescue of the Mediterranean cultivar Maris Kasba were smaller and had a higher root-to-shoot ratio than other temperate cultivars.

Strategies to reduce water consumption

Leaf elongation and new leaf formation are early reduced as a consequence to soil drying (Hsiao, 1973). Indeed, a decrease in total leaf area is one of the most important ways to reduce plant water consumption. Many reports have shown a decreased leaf elongation rate or leaf appearance rate under drought conditions in herbaceous species (Socías and Medrano, 1994; Salah and Tardieu, 1997; Volaire, 2002; Rytter, 2005). Other processes leading to leaf area reduction involve leaf loss or accelerated senescence of older leaves, leaf movement to reduce incident radiation and leaf flagging or rolling to reduce effective leaf area.

Stomatal closure is also an early response to drought, protecting plants from extensive water loss, Leaf water status interact with stomatal conductance and transpiration, although stomatal regulation respond to a complex interaction of internal and external factors, such as light intensity, CO_2 concentration in air or leaf-to-air vapour pressure deficit (Lazaridou and Noitsakis, 2005). In the late 80's, it was shown that stomata could close in response to drought before any change was detectable in leaf water potential or leaf water content, showing the important role played by abscisic acid (ABA) promoting stomatal closure (Davis and Zhang, 1991; Flexas and Medrano, 2002; Chaves *et al*., 2003). Nevertheless, since stomatal closure is usually accompanied by a consequent reduction of photosynthetic rate (Lawlor and Cornic, 2002), to maintain a positive carbon balance is difficult under severe and/or long lasting drought conditions.

Energy dissipation mechanisms, although they are adaptations to excess of light, play an important role in leaf photoprotection under drought. Under Mediterranean conditions, where light and drought stresses occur in the summer period, photoprotection has been described as an important adaptation not only for evergreen species, but also for herbaceous species (Galmés *et al*., 2007).

Water use efficiency

Without appropriate management, irrigated agriculture can be detrimental to the environment and endangers sustainability. Increasing water use efficiency within agricultural systems is an essential priority in both irrigated and rainfed agriculture regions, including the Mediterranean basin (Howell, 2001; Parry *et al*., 2005).

Sinclair (1994) cited several of the earliest scientific studies on plants measured the ratio between plant weight increase and water use, since 1699. These studies demonstrated a linkage between plant biomass accumulation (B) and plant water loss through transpiration (TR). In 1958, De Wit quantified this relationship as *water use efficiency* (WUE), WUE = B / TR.

Nowadays, water use efficiency refers to different processes and ratios in the literature, sometimes overlapping and confounded. Most researchers describe WUE as WUE = Y / ET, where Y is the yield of the crop, either in total plant biomass or harvestable biomass or marked yield. ET is the evaporation of water from soil surface, and the transpiration through the stomata, due to the difficulty in separating evaporation from transpiration (Hatfield *et al.,* 2001). The suitable yield criterion for hay and forage crops is the above ground dry matter (AGDM) (Black, 1965). Moreover, as plants are subjected to many cuttings during the growing season at different time intervals, it is better to estimate the AGDM per unit area of ground (E) at a specific time interval (Δt). This is defined as Crop Growth Rate (CGR). In this case, the formula could be: WUE = AGDM / ET or WUE = CGR / ET.

Biomass or yield with respect to transpired water at the whole plant level is called *transpiration efficiency* (W) (Tanner and Sinclair, 1983). The transpired water during growth period can be measured in pot experiments and the amount of water used during the measurements can be expressed on grams-water basis (Bolger and Turner, 1998; Byrd and May II, 2000; Impa *et al*., 2005). In field experiments, it is difficult to measure the whole plant or crop transpiration. The total transpired water from the canopy is mainly affected from the instantaneous transpiration rate (E) and plant leaf area (LA) or leaf area index (L) of the crop (Turner, 1986; Rosental *et al.,*1987; Kato *et al*., 2004). In this case, *canopy transpiration* (CT) at crop level is equal to CT = E x L. Whether this refers to plant level, the equation is modified to CT = E x LA. Canopy transpiration indicates better plant performance than E and, although it is instantaneous measurement, it provides a relative index for plant water loss. It is also a useful criterion, when species or management practices are compared. Using the CT, the formula WUE = AGDM / T for forage crops could be WUE = AGDM / CT or WUE = CGR / CT (Lazaridou and Noitsakis, 2002; Lazaridou *et al*., 2002).

With the development of modern gas exchange methodologies, transpiration efficiency can be determined at a single leaf level, as the ratio of instantaneous exchange of water for CO_2. This approach to WUE is mainly based on physiological processes, and it expresses the short- term plant performance at leaf level (Howell, 2001). The term *instantaneous water use efficiency* is defined as A/E, where A is carbon assimilation (net photosynthesis), measured as CO_2 uptake, and E is the transpiration. The term *intrinsic water use efficiency* (IWUE) has been proposed for direct comparison of intrinsic physiological considerations and it is defined as A/g, where g is stomatal conductance (Davies and Pereira, 1992; Yu *et al*., 2005, Guo *et al*., 2006).

More recently, the discrimination against the naturally occurring stable isotope discrimination (Δ), has been developed as a measure of transpiration efficiency. Δ is a measure of the $^{13}C/^{12}C$ ratio in plant tissue relative to the value of the same ratio in the air on which plants feed. The C_3 plants actively discriminate against ^{13}C during photosynthesis, while much less variation occurs among C_4 plants (Ehleringer and Vogel, 1993; Jensen *et al*., 2002; Condon *et al*., 2002). Δ is an indirect method that accurately evaluates the differences in WUE for plants growing in a particular environment (O'leary, 1993; Johnson and Yangyang, 1999; Impa *et al*., 2005) and it is correlated to plant performance under drought (Ebdon and Kopp, 2004). It has been shown to be negatively correlated with WUE in a wide range of forages, as cool season grasses (Johnson and Yangyang, 1999) and alfalfa (Johnson and Tieszen, 1994).

Plant characteristics can affect WUE through photosynthetic capacity, stomatal behaviour, and leaf characteristics, such as size, structure, and foliage orientation. Differences between species are very consistent and are clearly related to photosynthetic pathway. CAM plants have highest dry matter efficiencies, followed by C_4 plants, which are approximately twice as efficient as C_3 plants (Jones 1992). Concerning intrinsic WUE, it is approximately double for C_4 species than for C_3 species (Yu *et al.,* 2005). Moreover, higher transpiration efficiency (W) was found in grasses than in dicots (Bolger and Turner, 1998). Differences in WUE (A/E) have also been related to perenniality. In this sense. Karatassiou *et al*. (1998) have reported differences between two annuals *(Medicago minima, Avena fatua*) compared with two perennials (*Lotus aegaeus, Chrysopogon gryllus*) for the same leaf water potential, depending on the growing season.

Absolute values of WUE vary markedly from place to place and from year to year, depending on climatic, soil and plant factors. Climatic factors influence WUE through rainfall distribution, vapour pressure deficit of the air and carbon dioxide concentration (Nielsen *et al*., 2005; Da Costa and Huang, 2006). Both chemical and physical characteristics of the soil can directly or indirectly influence WUE through soil water content, infiltration rates, soil surface features, water movement, availability of soil water, impedance of root penetration, salinity and nutrient status (Power, 1983; Johnson and Asay, 1993; Yu *et al.,* 2005). Water use efficiency can be increased through proper management. Field scale experiments have shown that these changes positively affect crop yield (Pendleton, 1965; Turner, 2004; Hatfield *et al*., 2001; Jensen *et al.,* 2002). Wide differences in yield induced by differences in soil fertility or management practices may result minor differences in evapotranspiration and in high values of WUE (Black 1965; Nielsen *et al*., 2005; Cao *et al*. 2007). Forages grown in mixture presented differences in water use efficiency in relation to their monoculture (Bolger and Turner, 1998; Lazaridou and Noitsakis, 2003).

WUE changes as water supply changes. The water supply significantly modifies the growth of root in relation to above ground plant part. In other words, water influences the amount of harvestable biomass of the forages in relation to total biomass (Davies and Pereira, 1992; Lovelli *et al*. 2007). Moreover, as a plant becomes water limited, stomatal closure causes a proportionately greater reduction in transpiration than photosynthesis, and consequently, the WUE increases (Stanhill, 1986; Johnson and Asay, 1993). These parameters are directly associated to WUE values, regardless of the applied method. Generally, it is accepted that for forages and other crops water deficiency determines a more efficient water use (Jensen *et al.,* 2002; Lovelli *et al*. 2007). Metochis and Orphanos (1981), Frame *et al.* (1998) and Lazaridou and Noitsakis (2003) reported higher WUE under water stress for alfalfa, although they used different methods of estimation. Moreno *et al*. (2007) also observed higher WUE under water stress in *Dactylis glomerata*, showing important variations among cultivars. Lazaridou and Koutroubas (2004) observed higher plant water use efficiency for bersim clover subjected to drought. The water stress effect on WUE depends on species and on irrigation regime (Da Costa and Huang, 2006). The water-limited ryegrass had W (considered as the ratio of dry matter to the amount of water used from thinning to harvest) values similar to those under well-watered conditions, whereas subterranean clover and capeweed (*Arctotheca calendula*) had increased W values under water-limited conditions (Bolger and Turner, 1998). In this sense, water deficit improved WUE of two genotypes of cowpea (*Vigna unguiculata* L.) by approximately 20%, but caused moderate to huge reductions in most of genotypes (Anyia and Herzog, 2003). Transpiration efficiency of nine cultivars of switchgrass (*Panicum virgatum* L.) did not differ between water stressed and well watered conditions (Byrd and May II, 2000). Water Use Efficiency (photosynthesis/transpiration) at the single twig level of broom snakeweed (*Gutierrezia sarothrae*) remained the same for the well watered and slightly stressed treatments, but declined dramatically in severe and extremely stressed treatments. This opposite behaviour exhibited by broom snakeweed, is due to the predominance of non stomatal limitation to photosynthesis and due to the fact that stomata are less sensitive to severe water deficit (Wan *et al*., 1993). Studies on both field and glasshouse environments showed that Δ decreased with increasing drought (Johnson *et al*., 1993). Jensen *et al.* (2002) have grown cultivars of orchardgrass, perennial ryegrass, intermediate ryegrass and festulolium in four water levels. Within all water levels orchardgrass cultivars exhibited higher Δ than ryegrasses.

The effect of temporary water stress on WUE depends on the phenological stage, during which it was applied (Mastorilli *et al.,* 1999) and varies during growing season (Lazaridou and Noitsakis, 2003; Ray *et al*., 2004).

Results concerning the relationship between WUE or Δ and forage yield are limited. However, negative correlations between shoot biomass and Δ have been reported in four cool-season grasses (Johnson and Bassett, 1991). Under irrigated conditions, nine germplasms of alfalfa with lower Δ (high WUE) tended to grow and develop more slowly than germplasms exhibiting higher Δ (Ray *et al.,* 1998). Generally, under a sufficient water supply, WUE is not always linearly correlated to the biomass or economic yield (Guo *et al.,* 2006). Under dry soil conditions, dry matter and Δ were negatively correlated to orchardgrass and positively to ryegrass (Jensen *et al.,* 2002). In a rainout sheltered experiment the forage yield was positive correlated to Δ. This suggests that selection for increased WUE (low Δ) may lead to decrease in forage yield (Johnson and Asay, 1993).

WUE, irrespective of estimation way, considered to be a useful selection criterion for superior performance of plant, particularly in a dry environment (Johnson and Asay, 1993; Ray *et al.,* 1998; Ray *et al.,* 2004; Ebdon and Kopp, 2004). According to Cao *et al.* (2007), biotechnology offers another avenue for modification of genomes by transferring one or more genes relating to improve WUE.

Perenniality and summer survival

As mentioned above, annual and perennial species show different strategies to overcome summer drought period. Annual species usually germinate after the first heavy autumn rains (October-November), flower and set seed during the spring, die at the beginning of the summer and pass the unfavourable season as seeds in the soil, escaping to the severe drought. Escape strategies rely on successful reproduction before the onset of severe stress. The traditional dominance by annuals in Mediterranean grasslands has been associated with ruderal environments undergoing human disturbance and long summer drought (Fernández *et al*., 1993). This is because in some competitive environments, strategies that allow a rapid resource uptake could be more important than efficiency of use (Clary *et al*., 2004). So, annual species may rely on uptake and immediate use of resources, since they can escape harsh periods as seeds. In this sense, early vigour (fast leaf area development) has been shown to be an important adaptation of barley and durum wheat to terminal drought in Mediterranean environments because it improves the ratio T/ET (transpiration/evapotranspiration) and encourages growth when evaporative demand is low, giving higher A/E (instantaneous water use efficiency) (Condon *et al*., 2004). Moreover, genotypic variation in assimilate storage in the stem during the vegetative phase for remobilisation to the grain during grain filling has been considered an important contributor to yield under terminal drought (Turner, 2004).

On the other hand, perennials need to be able to avoid or tolerate periods of water deficit to survive. Thus, the ability to access water from the subsoil and the ability to remain dormant when water supply is limited are crucial strategies for these plants.

It is necessary to distinguish between perennial grasses that are able to avoid water stress and those that are able to tolerate certain water stress. Dormancy is defined as a temporary suspension of any visible structure containing a meristem (Volaire, 2002). Within this context, dormancy represents a form of stress evasion since active growth and reproduction are suppressed in dormant plants (Ofir and Kigel, 2003). Thus, summer dormancy enables perennial plants to evade the unfavourable hot and dry season in regions with a Mediterranean climate. In this case, the rate of growth is reduced markedly, specialized resting regeneration buds are produced and senescence of leaves takes place as dormancy sets in (Ofir and Kigel, 1998). In this sense, Volaire and Norton (2006) proposed a classification of three major groups of populations of temperate perennial grasses: (i) populations that maintain active growth under irrigation. This corresponds to populations that do not express summer dormancy, so which remains photosynthetically active with not very high rates of senescence and without forming resting organs under well watered conditions during summer; (ii) populations that cease growth completely for a minimum of four weeks during the summer. This pattern of response corresponds to completely dormant populations, as in the case of *Poa bulbosa*, which enters summer dormancy in early spring, before the end of the rainy period (Ofir and Kigel, 1999); (iii) populations that exhibit markedly reduced growth, associated with partial senescence of foliage, but no dehydration of leaf bases. This pattern could be also called incomplete dormancy, as occurs in many cultivars of *Dactylis glomerata*, *Festuca arundinacea* and *Phalaris aquatica*. An important difference between this group and group (ii) is the capacity to recover easily after an occasional summer rain. A good example was observed by Volaire *et al*. (2001) in cultivar Medly of *Dactylis glomerata*, in which its aerial surviving organs can dehydrate up to a water content to 25-30% and it regrowths easily after rewatering; in contrast with buds of *Poa bulbosa* which are able to maintain a water content around 10% and it regrowths one month later than *Dactylis*, indicating that it was fully dormant. Then, a continuous water supply, however small, is indispensable for survival of these species during the summer resting period. Moreover, it has been shown that dehydration tolerance and summer dormancy, although usually associated, are independent phenomena since dehydration tolerance is exhibited when plants are subjected to drought at any time of the year, while dormancy is exhibited only in summer. Therefore, summer dormancy appears to confer superior drought avoidance but not necessarily higher dehydration tolerance (Volaire, 2002).

However, the environmental factors and physiological processes involved in summer dormancy induction have been little studied. Ofir and Kigel (1999) showed that long days are the main factor in the induction of dormancy in *Poa bulbosa*, while elevated temperatures enhance their effect and accelerate dormancy development, with a critical day length of 11-12 hours required for the induction. Moreover, they showed that pre-exposure to short days (during autumn and early winter) and to low temperatures (during winter) enhance quantitatively dormancy induction by subsequent long days, indicating that the longer the pre-exposure the stronger is their effect. This effect has also been observed in cultivars of cocksfoot and tall fescue, where growth reduction and senescence of mature foliage under summer irrigation were much lower when plants were sown in spring than in the preceding autumn (Volaire and Norton, 2006).

This developmental and physiological processes induced by long days are concurrent with a gradual increase of ABA levels in leaf blades, as well as in the basal part of the tiller, where the bulb develops (Ofir and Kigel, 1998). This increase in ABA content occurred in plants that were adequately watered, so that water stress could not have been the cause for this change. Consequently, an increase in ABA level has a key role in the induction of summer dormancy by long days.

On the other hand, Ofir and Kigel (2007) showed that water deficit can induce summer dormancy in *P. bulbosa* in the absence of the inductive long days at moderate temperature; although experiments of Volaire *et al*. (2001, 2006) do not support this hypothesis. It is suggested that the stress resulting from water deficit induces summer dormancy through an increase in endogenous ABA. This is supported by the fact that ABA application under non-inductive short days resulted in a similar dormancy syndrome as induction by long days and the finding that ABA levels increased in the leaves and tiller bases under inductive long-day conditions. These alternative mechanisms may allow an early dormancy induction during the winter by drought stress in case of unusual dry winters; and a delay in summer dormancy inducted by daylength in years with higher water availability.

Dehydrins are proteins which typically accumulate in plants during the late stages of embryogenesis or in response to low temperature, ABA application, or any environmental influence that has a dehydration component, such as drought, salinity or extra cellular freezing (Close, 1997). Dehydrin accumulation has been found in water stressed leaf bases of *D. glomerata* and *P. bulbosa* (Volaire *et al*., 2001; Volaire 2002). It is shown that only dormant, and therefore dehydrated, genotypes of *D.glomerata* and *P.bulbosa* express dehydrins under irrigated conditions, reflecting the endogenous control of dehydration in these tissues (Volaire 2002). Nevertheless, the amount of dehydrins do not correlate with the stress tolerance of these genotypes; in fact, the dehydrin content has been found to be a function of the water status of plant tissues and to be independent to soil moisture status (Volaire *et al*., 2005).

Unfortunately, little is known about drought survival and recovery in perennial grasses. As mentioned above, the ability to develop a deep root system is basic for the delay of tissue dehydration while the dehydration tolerance and membrane stability of meristematic tissues are critical components to drought tolerance. Volaire and Lelièvre (2001) compared drought resistant cultivars of *D. glomerata* with a drought resistant cultivar of *F. arundinacea* under the same restricted conditions for root development in pots of 60 cm deep; and they observed that tall fescue exhibit the earliest mortality in spite of its high resistance in the field. So, they proposed that the drought resistance of tall fescue in the field can mainly be ascribed to its ability to develop a deep root system. By contrast, in cocksfoot, dehydration tolerance in surviving tissues and the ability of roots to extract water at low soil water potentials contribute significantly to plant survival under severe drought. In addition, it is also shown that the aerial organs of these perennial grasses could dehydrate up to a minimum water content (25-30% for *D. glomerata*; 10% for *P. bulbosa*), but mortality occurs quickly beyond this threshold (Volaire *et al*., 2001). However, the fact that neither the final level of dehydration nor the membrane stability of the surviving organs differed between drought resistant and drought sensitive cultivars of *D. glomerata* suggests that plant survival is more related to how long the surviving tissues can maintain cell integrity at a given moisture content, than on the actual minimum threshold of dehydration reached by the tissues (Volaire, 2002). Furthermore, one of the differences between desiccation tolerance and summer dormancy is the rapid recovery after rewatering of the former. Conversely, the gradual release of dormancy in dormant genotypes is mediated by relatively high temperatures at the end of the summer, while sprouting of the dormant buds is accelerated at autumn low temperature onset (Volaire and Norton, 2006).

Conclusions

Under Mediterranean conditions, plant strategies to overcome water deficit are mainly related to survive summer period and to their ability to complete their life cycle successfully. In this sense, plant adaptations to produce biomass under water deficit and those improving water use efficiency are of special interest. Moreover, agricultural management techniques have been shown to be a key point to maximize water use efficiency in forage and grain crops. Difficult and time consuming techniques to measure water use efficiency have led to explore new methodologies to estimate this parameter, like gas exchange and carbon isotope discrimination. Regrettably, the relationship between WUE, carbon isotope discrimination and gas exchange parameters is not always clear. In this sense, up to know, these rapid techniques to estimate WUE has not been useful in most of the selection programs. In addition, the relationship between WUE and crop yield also depends on genotypes, management techniques and environmental factors.

Annual and perennial species show different strategies to overcome summer drought period and also offer different opportunities in agricultural systems and restoration programs. In this sense, the interest on perennial species has increased in the last decades and important advances have been done to understand the physiological and environmental control of summer dormancy. Nevertheless, some points still remain unclear, and more effort is needed in order to achieve a better comprehension of the physiology and ecophysiology of these species allowing their incorporation in productive systems.

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