

Drought Adaptation Strategies of Weeds and other Neglected Plants of Arid Environments

Ilias S. Travlos* • Demosthenis Chachalis

Benaki Phytopathological Institute, Department of Weed Science, 8 St. Delta street, GR-145 61 Kifissia, Athens, Greece

Corresponding author: * htravlos@yahoo.gr

ABSTRACT

Drought is the major limitation to the productivity of plants and an upcoming global threat. Many weeds, minor crops and other plants thriving in arid environments have evolved several mechanisms of drought escape, tolerance and avoidance. Consequently, the careful observation of the adaptive mechanisms of some of these wild or cultivated species could offer new choices in the exploitation of poor, arid regions, and important alternatives toward the development of drought adaptive crop strategies. Therefore, the information concerning their high competitiveness, proliferation and survival under water deficit conditions are urgently needed. In this paper we present and classify some outstanding cases of drought adaptive weeds and other neglected plants, which could be potentially useful in the future.

Keywords: drought avoidance, drought escape, drought stress, drought tolerance, plant stress

CONTENTS

INTRODUCTION.....	40
DROUGHT ADAPTATION STRATEGIES OF PLANTS IN ARID ENVIRONMENTS.....	40
Examples of drought tolerance.....	40
Mechanisms for escaping drought.....	41
Drought avoidance cases.....	41
FUTURE CHALLENGES AND PROSPECTS.....	43
REFERENCES.....	43

INTRODUCTION

Models of global climate change clearly suggest an increase in the frequency of major droughts and extreme events in many areas of the earth (IPCC 2001). Water availability is one of the most important limitations to plant growth and productivity. Nowhere is the reality of plants facing daily stressful situations more evident than in arid environments. Morphological and other adaptations that enable plant species to survive under these harsh conditions are well known and have received detailed and ongoing attention in the literature. However, in contrast to crop plants, the literature on the responses of weeds and other underutilized-neglected plants to drought is much more limited and has to be updated (van Heerden *et al.* 2007).

Neglected are the species that are grown primarily in their centres of origin or centres of diversity by traditional farmers, where they are still important for the subsistence of local communities. Although these species continue to be maintained by sociocultural preferences, they receive scarce attention from agricultural and biodiversity conservation policies and are almost ignored by scientific research and development (Padulosi and Hoeschle-Zeledon 2004). Within that point of view, this review article was written in order to highlight several cases of weeds and minor (neglected) plants that still have not been adequately studied and used, despite their outstanding mechanisms and remarkable ability to withstand or avoid drought.

DROUGHT ADAPTATION STRATEGIES OF PLANTS IN ARID ENVIRONMENTS

Several plant species adapted to arid regions are characterized by one or more strategies and mechanisms of drought adaptation, namely: tolerance, escape and avoidance (Turner 1979). Besides, many plants use more than one mechanism at a time to deal with drought (Gaff 1980), making it almost impossible to characterize them as exclusively drought “tolerators”, “escapers” or “avoiders”. A typical case is that of *Impatiens capensis* and other weeds, in which early-season drought conditions may select for drought avoidance traits (such as low water use efficiency and early reproduction), whereas later drought selects for tolerance traits (high water use efficiency and decreased stomatal conductance) (Heschel and Riginos 2005).

Examples of drought tolerance

Plants which are able to maintain productivity even when their tissues become stressed exhibit drought tolerance. The mechanisms of drought tolerance are maintenance of turgor by means of osmoregulation (a process which induces accumulation of compatible solutes in the cell), increase in elasticity of the cell and a decrease in cell size and desiccation tolerance by protoplasmic resistance (Sullivan and Ross 1979). Osmotic adjustment refers to the lowering of osmotic potential due to net accumulation of solutes in response to water deficits, and results in the maintenance of a higher turgor potential that may contribute to limiting the effects of stress on physiological functions such as stomatal

opening, photosynthesis and growth (Chimenti *et al.* 2002). Proline, betaines, dimethyl sulfoniopropionate, mannitol, sorbitol, pinitol, trehalose and fructans are some of the examples for osmoprotectants (Karamanos 1995; Smirnov 1998).

Survival of several weeds and grasses, such as turf-type tall fescue (*Festuca arundinaceae*), is associated with low osmotic potential before stress and osmotic adjustment, prolonged positive turgor maintenance, and delayed leaf rolling during stress (White *et al.* 1992). Besides, tiller and plant survival during competitive soil moisture extraction could be taken into account, since they seem to be easily assessed indicators of tall fescue germplasm drought tolerance. Moreover, several desert evergreens avoid drought by synthesising osmoprotectants for turgor maintenance in their tissues during water deficit (Mundree *et al.* 2002). *Solidago canadensis*, a highly invasive weed of many regions shows remarkable drought tolerance behaviour. Its seeds are drought tolerant, while in the summer a fraction of the energy in leaves and stems is allocated underground to increase fine root growth and water uptake during hot weather (Huang *et al.* 2007).

Furthermore, many desert species exhibit a range of strategies to survive in arid and semiarid systems characterized by episodic precipitation and soil-moisture pulses that vary in amount and frequency (Noy-Meir 1973). Drought tolerance typically requires the capacity to maintain physiological function and growth during periods of water stress, and the ability to access soil moisture from multiple depths in the soil profile often confers an advantage to desert dominants (Abbott *et al.* 2008). The distribution characteristics of proline were investigated in several desert plants, characterized as xerophytes (*Haloxylon ammodendron*, *Zygophyllum xanthoxylum*, *Artemisia sphaerocephala* and *Caragana korshinskii*) or mesophytes (*Agriophyllum squarrosum* and *Corispermum mongolicum*) and the data suggest that free proline accumulation may be one of the most effective strategies for adaptation of some of these plants to arid environments (Wang *et al.* 2004).

Some vascular plants, the resurrection plants, have a noticeable and impressive tolerance to almost complete desiccation of vegetative organs (Rascio and la Rocca 2005). Some hundreds of plants that possess this kind of desiccation-tolerance have already been identified (e.g. *Ramonda* spp., *Haberlea* spp., *Xerophyta viscosa*, *Talbotia elegans*, *Sporobolus stapfianus*, *Borya nitida* and other members of families Myrothamnaceae, Scrophulariaceae, Lamiaceae, Poaceae, Cyperaceae, Liliaceae). These plants survive in arid environments because they are able to dehydrate, remain quiescent during long periods of drought, and then resurrect upon rehydration. They use an uncommon strategy that they can lose bound-water in their vegetative tissues about to 5% during water limited conditions and can rehydrate when water becomes available (Mundree *et al.* 2002). As a typical example of this category, we could refer to *Reaumuria soongorica*, a short woody shrub widely spread in semi-arid areas of China, which can survive severe desiccation of its vegetative organs. During dehydration, mesophyll and chloroplast ultrastructures are disrupted in leaves, but not in stems, and water storage tissues are rich in osmotically active substances. Upon rewatering, osmophilic globules in stems disappear and a repair process in the phloem is observed. In resurrection plants, the mechanical stress associated with cell volume reduction is counteracted by number of different protection mechanisms. In some interesting species such as *Myrothamnus flabellifolia*, *Craterostigma wilmsii* (Farrant 2000) and *Eragrostis nindensis* (Vander Willigen *et al.* 2001), mesophyll cells show significant cell volume reduction associated with a regulated phenomenon of cell wall folding. In other resurrection plants like *Xerophyta humilis*, *Xerophyta viscosa* cells maintain their volume by multiple (small) vacuole formation (Farrant 2000). Malate and proline, which accumulated in stems during water loss, may play a major role in osmoregulation, too (Liu *et al.* 2007). Moreover, the mechanisms

of cell wall folding were recently described for the above mentioned resurrection plants *Craterostigma wilmsii* and *Myrothamnus flabellifolia* (Farrant *et al.* 2007). It was found that the antioxidant systems of these plants effectively deal with radical oxygen species generated by other metabolic processes, while polyphenols, seed-associated antioxidants and sucrose are also accumulated (Farrant *et al.* 2007).

Mechanisms for escaping drought

One functional strategy that plants employ to cope with decreasing water availability is drought escape. This mechanism involves rapid phenological development (early flowering and early maturity), developmental plasticity (variation in duration of growth period depending on the extent of water-deficit) and remobilization of preanthesis assimilates to grain (Turner 1979). For drought-escaping species, such as the weed *Avena barbata*, high metabolic activity and rapid growth are hypothesized to confer a fitness advantage, because this enables a plant to complete its life cycle before the most intense period of drought (Sherrard and Maherali 2006). This strategy is especially suitable for environments with well-defined wet and dry seasons, since it involves the completion of the plant's life cycle during the wet season while water is still adequate; thus escaping the drought season. Therefore, the introduction of several drought-escaping plants is highly suggested as a permanent solution to the drought perennial problems of several regions worldwide (Adefolalu 1986). By completing their life-cycle in much less than one year, some annual plants (called ephemerals) allow more than one generation of the plant to set seed in one growing season. This is a good explanation of the fact that many invasive weeds, such as hairy bittercress (*Cardamine hirsuta*), are ephemerals. Several annual weeds that belong to this group (e.g. *Avena* spp., *Poa* spp.) show a high metabolic activity and rapid growth, in order to complete their short life cycle before drought arrives (Sherrard and Maherali 2006). In addition, other weeds like *Stellaria media* and *Arabidopsis thaliana* are ephemerals since they can mature and produce seeds at only 4 to 6 weeks after their emergence. By existing only as dormant seeds during the dry season, weeds and other ephemerals protect their protoplasm from being subjected to very low water potentials (Salisbury and Ross 1992).

The drought escape strategy may partially explain the abundance of annual species thriving in the most arid habitats (Arnesto and Vidiella 1993). In the driest habitats (deserts) up to 90% of the plants are annuals, which effectively employ dormancy periods in order to take advantage of the very short favourable seasons. Additionally, some indigenous plants of Greece and the broader Mediterranean region can shed their leaves, slow down their growth or stay viable using their below-ground organs (tubers, rhizomes, etc.) and consequently escape drought. Apart from changing their leaf shape, size and position, some species have evolved their whole structure to reduce water loss. Typical species of this kind are Greek spiny spurge (*Euphorbia acanthothamnus*) and thorny burnet (*Sarcopoterium spinosum*). These plants down-regulate their annual growth rate in order to save energy to endure dry periods (Margaris 1976).

We have also to note that several ecotypes of some weeds display differential drought-adaptive strategies when subjected to a progressive drought stress. Thus, an ecotype of *Arabidopsis* spp. exhibits a clear escape strategy (early flowering and bolting, high sensitivity of the rosette leaves to water deficit leading to leaf senescence), whereas another ecotype withstands water stress by drought tolerance (e.g. higher biomass allocation to vegetative organs and water-use efficiency) (Meyre *et al.* 2001).

Drought avoidance cases

Drought avoidance entails increasing water acquisition and reducing water loss, thereby avoiding drought that would

otherwise occur. The leaf shedding option, the tight stomatal control, the midday depression of photosynthesis and the development of a prolific root system are several components of the same strategy.

The leaves of *Nerium oleander* are broad and flat, hence, adapted to optimize photosynthesis, whereas their stomata are arranged in crypts. Stomatal crypts are large concave chambers formed by invaginations of the lower epidermal layer that contain trichomes (hairs) projecting into the crypt. This particular anatomy reduces the transpiration gradient and is considered as a notable adaptation for water conservation (Metcalf and Chalk 1979). Besides, several widely distributed Mediterranean species (*Quercus ilex*, *Q. humilis*, *Pistacia terebinthus*, *P. lentiscus*, etc.) can avoid desiccation by rapidly adjusting their stomatal conductance at the onset of drought, and maintaining constant leaf relative water content (Gulias *et al.* 2002). Another outstanding mechanism for maximal drought adaptation, involves stomata sunken deeply into the cuticle, reducing ease of water loss, or they might only be on the inner surface of a tightly rolled leaf. The dune grass, *Ammophila* sp., which in addition possesses sunken stomata, is a great example of this strategy (Huiskes 1979).

The ability of the roots of common lambsquarters (*Cenopodium album*) to penetrate deeply into the soil and its large fraction of fine roots enable it to survive periods of summer drought better than other species (Maganti *et al.* 2005). African rue (*Peganum harmala*), a herbaceous perennial native to arid and semiarid regions of Africa and Asia, is an invasive rangeland weed that has spread into parts of North America, South Australia and elsewhere (Michelmore 1997; Abbott *et al.* 2007). As many of the world's invasive weeds, the root system of mature African rue plants possess extensive lateral roots and deep taproots (Michelmore 1997), conferring an advantage to established plants during conditions of moisture deficit. Similarly, based on a study of many vascular plants by Reader *et al.* (1992), the maximum rooting depth is significantly correlated with their sustainable growth under drought conditions. Caper bush (*Capparis spinosa*), a summer perennial shrub growing in the Mediterranean and semiarid ecosystems shows an exceptional photosynthetic performance under drought conditions accommodated by its ability to sufficient access to water resources (Levizou *et al.* 2004). The later is owed to its deep root system (Sozzi 2001) and xylem vessel anatomical characteristics which favour high hydraulic conductivity (Psaras and Sofroniou 1999). This efficient system for water supply disengages caper bush from tight stomatal control allowing high transpiration and photosynthetic rates (Levizou *et al.* 2004). Creosotebush (*Larrea tridentata*), an evergreen shrub that dominates many sites in the hot deserts of southwestern United States and Mexico (Benson and Darrow 1954), thrives in arid environments potentially due in part to its ability to access water from both shallow and deep regions of the soil profile (Hamerlynck *et al.* 2000; Gibbens and Lenz 2001).

Low epidermal conductance may affect the survival of perennial grasses (e.g. *Digitaria californica* and *Eragrostis lehmanniana*), while the success of invasive grasses may also be associated with this reduced conductance compared to non-invasive competitors (Smith *et al.* 2006). *Quercus coccifera* and other Mediterranean plants could be potentially used as suitable candidates for reclamation of degraded areas, since they manage to maintain high relative water content by reducing their stomatal conductance and preventing leaf water potential to drop to critical values (Saccali and Ozturk 2004). The success of the above-mentioned African rue in arid environments is due in part to the ability of seedlings to tolerate and recover from water deficit (Abbott *et al.* 2008), since the rapid change in conductance rate and slower response in leaf water potential indicates that stomatal control is an important component of seedling response to water deficit. In addition to stomatal control of photosynthesis, the maintenance of low levels of photosynthesis and its early recovery relative to conduc-

tance and water potential suggest that nonstomatal control of photosynthesis is an important component of African rue seedling response to water deficit. African rue has green stems, similar to European spotted knapweed (*Centaurea biebersteinii*), an invasive herbaceous perennial that relies on stem photosynthesis, a specialization that helps maintain physiological function and efficiency under drought conditions (Hill and Germino 2005). Many other invasive weeds, such as trumpet creeper (*Campsis radicans*) have vigorous growth, waxes in the leaves and several other morphological and physiological traits in order to avoid drought (Wen Jun and Jansen 1995; Chachalis *et al.* 2001; Chachalis and Reddy 2005).

Features representing xeromorphy usually include a small leaf or leaflet area, pubescent surfaces, amphistomatic and a multilayered palisade of two to four layers and are common among several weeds of arid regions, such as *Chrozophora* spp. (Fahmy 1997). Additionally, the weeds *Calotropis procera* and *C. gigantea* are characterized by a marked adaptation to drought. Leaves of both species show an amphistomatic, isolateral mesophyll structure with high pubescence, while stomatal conductance of *C. procera* significantly decreases during drought, suggesting an even higher water use efficiency of this drought avoidant species (Colombo *et al.* 2007).

Although plant movements are rather uncommon, some plants are known to open and close their leaves diurnally, in order to save water and improve their photosynthetic capacity. This phenomenon has been of great interest to scientists from ancient times (described by Androstenes in the 4th century BC), while in the 19th century, Charles Darwin investigated these movements in more than 300 plant species (Darwin 1880). Leaf and leaflet movements are controlled by specialized organs called pulvinus, primarily in the families Fabaceae, Maranthaceae and Oxalidaceae and also in the flowers of *Kalanchoë* (Engelmann and Johnson 1998). A typical example of improvement of water use efficiency of a weed by means of its solar-tracking leaf movements is velvetleaf (*Abutilon theophrasti*) (Jurik and Akey 1994). Leaf senescence is also common among several neglected plants or genotypes, which have limited capacity for osmotic adjustment, but they can adapt to drought mainly by regulating transpiration. This is primarily achieved by a moderate reduction of leaf area (e.g. *Solanum villosum* and *S. sarrachoides*) until a critical point (Masinde *et al.* 2006).

A typical example of a plant showing a complex of drought adaptation mechanisms is marama bean (*Tylosema esculentum*) (Travlos *et al.* 2008). This species is a wild perennial legume indigenous in southern Africa, which produces protein- and oil-rich seed (comparable to soybean and groundnut respectively) and tubers of relatively high protein and carbohydrate content. Therefore, it has been characterized of great potential for use as human food and animal fodder (Dakora *et al.* 1999; Travlos *et al.* 2007a). Several studies showed that marama is not particularly drought tolerant in the sense of being able to grow undiminished as the soil dries, but rather a drought-avoiding species using its tubers as water reservoirs and its stomata and leaflet closure to save water (Travlos *et al.* 2007a, 2007b, 2008; Travlos and Karamanos 2008).

Talking about indigenous plants of Africa, we should not omit the case of *Welwitschia mirabilis*. This species is a desert plant indigenous to the west coast deserts of southern Africa. During drought *W. mirabilis* exhibits a two-peaked pattern of diurnal CO₂ exchange, while leaf conductance for water vapour and water potentials are high only during the cooler, humid morning and decline thereafter (Herppich *et al.* 1997). In this species, the reduction of photosynthetic efficiency during drought stress is preceded by photoinhibition (Herppich *et al.* 1997).

Another remarkable and common adaptive strategy to the long-lasting, hot and arid summer of the regions with Mediterranean climatic conditions is the seasonal dimorphism of the leaves of several indigenous plant species (Or-

shan 1964; Margaris 1975; Christodoulakis 1989). In *Phlomis fruticosa*, significant differences are observed between winter and summer leaves obtained from the same individuals. Winter leaves are thick, amphistomatic with a large number of chloroplasts in the cells of the loose mesophyll. The thinner summer leaves are hairier and hypostomatic, with compact mesophyll and cells that accumulate phenolics and crystals. Chloroplasts are fewer in number and less developed, and at the ultrastructural level they present pronounced differences from those of the winter leaves (Christodoulakis 1989). Leaf functional adaptations include higher light reflectance, higher diffusive resistance to water vapour, lower light harvesting but comparable photoprotective potential and higher optimum temperature for photosynthesis of summer compared to winter leaves (Kyparissis and Manetas 1993). Moreover, Kofidis *et al.* (2003) reported that the observed seasonal difference in leaf blade thickness in *Origanum vulgare* was due to an increase of the size of the mesophyll cells, reflecting an adaptation mechanism involved in higher rates of photosynthesis as well as in storage of water in leaf tissues, in poor soils with low water-holding capacity. Besides, it was also found that summer leaves of *Scleropoterium spinosum* possess a thick epidermis composed of tannin-containing cells, large amount of mucilage secreted through the inner periclinal walls towards the mesophyll and a thick cuticle on the leaf surface (Christodoulakis *et al.* 1990). Similarly, *Cistus incanus* has evolved two different habits, one more mesophytic, the other more xerophytic (leaf area reduction, leaf rolling with a folded lamina, stomata in crypts, more trichomes), to optimize adaptation to the seasonal fluctuation of environmental conditions and especially drought throughout the year (Aronne and de Micco 2001). Therefore, we should say that seasonal dimorphism is a major strategy that produces seasonally different plants from the same individual and enables the survival of several weeds and other plants under the unfavourable conditions of Mediterranean-type ecosystems. It is also remarkable that several native shrubs and trees of Mediterranean region have also been increasingly studied; due to their drought adaptation and their potential use for the rehabilitation of degraded lands (Lo Gullo and Salleo 1988; Nardini *et al.* 1999; Travlos and Economou 2006; Travlos and Karamanos 2007; Travlos *et al.* 2007c).

FUTURE CHALLENGES AND PROSPECTS

Nowadays, scientists are researching ways to improve a plant's ability to cope with drought. The development of drought adapted cultivars will be of great value, while the desirable goal is not only to create new crops of high yield or high drought resistance, but rather plant species and genotypes with high relative adaptability, meaning an ideal balance between yield and adaptation to several environmental factors such as drought (Karamanos and Papatheohari 1999). Selecting germplasm based on several features indicative of drought management could be very important. For example, selecting plants with a high root/shoot ratio in the greenhouse is a viable method for improving the field drought tolerance of turf-type tall fescue (*Festuca arundinaceae*), since freshwater resources for irrigation are becoming limited (Karcher *et al.* 2008). The example of *Phaseolus* is indicative, as long as among several *Phaseolus* species, the highest levels of drought resistance are found in the tepary bean (*Phaseolus acutifolius* A. Gray) (Thomas *et al.* 1983). Moreover, several other plants are extensively examined in pursue of drought-related characteristics. Among them, some resurrection plants, which are able to survive long periods without water and remarkably resume their full metabolic functions rapidly after rain (Farrant 2000).

Many weeds, minor crops and other non-cultivated plants growing naturally have evolved a more complicate overall drought adaptation strategy which usually involves several mechanisms of drought escape, tolerance and avoidance. In this mini review we have focused on a small frac-

tion of the thousands of weeds and other underexploited and underutilized members of the plant kingdom, which show noticeable strategies of drought management. Our main aims were to highlight some of these cases, characterize their noticeable drought adaptation mechanisms and update the literature on this topic. And it seems that some of these plants could potentially serve as models for understanding the plethora of drought adaptation mechanisms and their potential uses.

REFERENCES

- Abbott LB, Lepak D, Daniel DL (2007) Vegetative and reproductive phenology of African rue (*Peganum harmala*) in the northern Chihuahuan Desert. *Southwestern Naturalist* **52**, 209-218
- Abbott LB, Bettmann GT, Streling TM (2008) Physiology and recovery of African rue (*Peganum harmala*) seedlings under water-deficit stress. *Weed Science* **56**, 52-57
- Adefolalu DO (1986) Further aspects of Sahelian drought as evident from rainfall regime of Nigeria. *Archives for Meteorology, Geophysics, and Bioclimatology Series B* **36**, 277-295
- Arnesto JJ, Vidiella PE (1993) Plant life-forms and bibliographic relations of the flora of Lagunillas (30°S) in the fog-free Pacific Coastal Desert. *Annals of the Missouri Botanical Garden* **80**, 499-511
- Aronne G, de Micco V (2001) Seasonal dimorphism in the Mediterranean *Cistus incanus* L. subsp. *incanus*. *Annals of Botany* **87**, 789-794
- Benson L, Darrow RA (1954) *The Trees and Shrubs of the Southwestern Deserts* (2nd Edn), University of Arizona Press, Tucson, 437 pp
- Chachalis D, Reddy KN (2005) Factors affecting sprouting and glyphosate translocation in rootstocks of redbine (*Brunnichia ovata*) and trumpetcreeper (*Campsis radicans*). *Weed Technology* **19**, 141-147
- Chachalis D, Reddy KN, Elmore CD (2001) Characterization of leaf surface, wax composition, and control of redbine and trumpetcreeper with glyphosate. *Weed Science* **49**, 156-163
- Chimenti CA, Pearson J, Hall AJ (2002) Osmotic adjustment and yield maintenance under drought in sunflower. *Field Crops Research* **75**, 235-246
- Christodoulakis NS (1989) An anatomical study of seasonal dimorphism in the leaves of *Phlomis fruticosa*. *Annals of Botany* **63**, 389-394
- Christodoulakis NS, Tsimbani H, Fasseas C (1990) Leaf structural peculiarities in *Scleropoterium spinosum*, a seasonally dimorphic shrub. *Annals of Botany* **65**, 291-296
- Colombo R, Marin O, Irazabal S, Tezara W (2007) Water relations, photosynthesis, and leaf anatomy in two species of *Calotropis* genus. *Interciencia* **32**, 791-796
- Dakora FD, Lawlor DW, Sibuga KP (1999) Assessment of symbiotic nitrogen nutrition in marama bean (*Tylosema esculentum* L.), a tuber-producing underutilized african grain legume. *Symbiosis* **27**, 269-277
- Darwin C (1880) *The Power of Movement in Plants*, John Murray, London, 592 pp
- Engelmann W, Johnson A (1998) Rhythms in organ movement. In: Lumsden PJ, Millar AJ (Eds) *Biological Rhythms and Photoperiodism in Plants*, Bios, Oxford, UK, pp 5-50
- Fahmy GA (1997) Leaf anatomy and its relation to the ecophysiology of some non-succulent desert plants from Egypt. *Journal of Arid Environments* **36**, 499-526
- Farrant JM (2000) A comparison of mechanisms of desiccation tolerance among three angiosperm resurrection plant species. *Plant Ecology* **151**, 29-39
- Farrant JM, Brandt W, Lindsey GG (2007) An overview of mechanisms of desiccation tolerance in selected angiosperm resurrection plants. *Plant Stress* **1**, 72-84
- Gaff DF (1980) Protoplasmic tolerance of extreme water stress. In: Turner NC, Kramer PJ (Eds) *Adaptation of Plants to Water and High Temperature Stress*, Wiley, New York, pp 207-230
- Gibbens RP, Lenz JM (2001) Root systems of some Chihuahuan Desert plants. *Journal of Arid Environments* **49**, 221-263
- Gulías J, Flexas J, Abadía A, Madrano H (2002) Photosynthetic responses to water deficit in six Mediterranean sclerophyll species: possible factors explaining the declining distribution of *Rhamnus ludovici-salvatoris*, an endemic Balearic species. *Tree Physiology* **22**, 687-697
- Hamerlynek EP, McAuliffe JR, Smith SD (2000) Effects of surface and sub-surface soil horizons on the seasonal performance of *Larrea tridentate* (creosotebush). *Functional Ecology* **14**, 596-606
- Herppich WB, Flach BMT, Von Willert DJ, Herppich M (1996) Field investigations of photosynthetic activity, gas exchange and water potential at different leaf ages in *Welwitschia mirabilis* during a severe drought. *Flora* **191**, 59-66
- Herppich WB, Flach BMT, Von Willert DJ, Herppich M (1997) Field investigations in *Welwitschia mirabilis* during a severe drought. II. Influence of leaf age, leaf temperature and irradiance on photosynthesis and photoinhibition. *Flora* **192**, 165-174
- Heschel MS, Riginos C (2005) Mechanisms of selection for drought stress

- tolerance and avoidance in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany* **92**, 37-44
- Hill JP, Germino MJ (2005) Coordinated variation in ecophysiological properties among life stages and tissue types in an invasive perennial forb of semi-arid shrub steppe. *Canadian Journal of Botany* **83**, 1488-1495
- Huang H, Guo S, Chen G (2007) Reproductive biology in an invasive plant *Solidago canadensis*. *Frontiers of Biology in China* **2**, 196-204
- Huiskes AHL (1979) Biological flora of the British Isles: *Ammophila arenaria* (L.) Link. *Journal of Ecology* **67**, 363-382
- IPCC (2001) Climate change 2001: the scientific basis. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D (Eds) *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (IPCC), Cambridge University Press Cambridge, UK, 944 pp
- Jurik TW, Akey WC (1994) Solar-tracking leaf movements in velvetleaf (*Abutilon theophrasti*). *Vegetatio* **112**, 93-99
- Karamanos AJ (1995) The involvement of proline and some metabolites in water stress and their importance as drought resistance indicators. *Bulgarian Journal of Plant Physiology* **21**, 98-110
- Karamanos AJ, Papatheohari AY (1999) Assessment of drought resistance of crop genotypes by means of the water potential index. *Crop Science* **39**, 1792-1797
- Karcher DE, Richardson MD, Hignight K, Rush D (2008) Drought tolerance of tall fescue populations selected for high root/shoot ratios and summer survival. *Crop Science* **48**, 771-777
- Kofidis G, Bosabalidis AM, Moustakas M (2003) Contemporary seasonal and altitudinal variations of leaf structural features in Oregano (*Origanum vulgare* L.). *Annals of Botany* **92**, 635-645
- Kyparissis A, Manetas Y (1993) Seasonal leaf dimorphism in a semi-deciduous Mediterranean shrub: ecophysiological comparisons between winter and summer leaves. *Acta Oecologica* **14**, 23-32
- Levizou E, Drilias P, Kyparissis A (2004) Exceptional photosynthetic performance of *Capparis spinosa* L. under adverse conditions of Mediterranean summer. *Photosynthetica* **42**, 229-235
- Liu YB, Wang G, Liu J, Zhao X, Tan HJ, Li XR (2007) Anatomical, morphological and metabolic acclimation in the resurrection plant *Reaumuria soongorica* during dehydration and rehydration. *Journal of Arid Environments* **70**, 183-194
- Lo Gullo MA, Salleo S (1988) Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *The New Phytologist* **108**, 267-276
- Maganti M, Weaver S, Downs M (2005) Response of spreading orach (*Atriplex patula*) and common lambsquarters (*Chenopodium album*) to soil compaction, drought, and waterlogging. *Weed Science* **53**, 90-96
- Margaris NS (1975) Effect of photoperiod on seasonal dimorphism of some Mediterranean plants. *Bericht der Schweizerischen Botanischen Gesellschaft* **85**, 96-102
- Margaris NS (1976) Structure and dynamics in a phryganean (East Mediterranean) ecosystem. *Journal of Biogeography* **3**, 249-259
- Masinde PW, Stützel H, Agong SG, Fricke A (2006) Plant growth, water relations and transpiration of two species of African nightshade (*Solanum villosum* Mill. ssp. *miniatum* (Bernh. ex Willd.) Edmonds and *S. sarrachoides* Sendtn.) under water-limited conditions. *Scientia Horticulturae* **110**, 7-15
- Metcalfe CR, Chalk L (1979) *Anatomy of the Dicotyledons. Systematic Anatomy of Leaf and Stem, with a Brief History of the Subject*, Clarendon Press, Oxford, 276 pp
- Meyre D, Leonardi A, Brisson G, Vertanian N (2001) Drought-adaptive mechanisms involved in the escape/tolerance strategies of *Arabidopsis* Landsberg erecta and Columbia ecotypes and their F1 reciprocal progeny. *Journal of Plant Physiology* **158**, 1145-1152
- Michelmore M (1997) *African Rue Management-Distribution, Biology, Impact and Control Strategies for Peganum harmala L. (Zygophyllaceae) in South Australia*. Primary Industries South Australia, Port Augusta, Australia, 34 pp
- Mundree SG, Baker B, Mowla S, Peters S, Marais S, Willigen CV, Govender K, Maredza A, Muyanga S, Farrant JM, Thomson JA (2002) Physiological and molecular insights into drought tolerance. *African Journal of Biotechnology* **1**, 23-38
- Nardini A, Lo Gullo MA, Salleo S (1999) Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant, Cell and Environment* **22**, 109-116
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**, 25-51
- Orshan G (1964) Seasonal dimorphism of desert and Mediterranean chamaephytes and its significance as a factor in their water economy. In: Rutter AJ, Whitehead FH (Eds) *The Water Relations of Plants*, Blackwell Scientific, Oxford, pp 206-222
- Padulosi S, Hoeschle-Zeledon I (2004) Underutilized plant species: what are they? *LEISA Magazine* **20**, 5-6
- Psaras GK, Sofroniou I (1999) Wood anatomy of *Capparis spinosa* from an ecological perspective. *IAWA Journal* **20**, 419-429
- Rascio N, la Rocca N (2005) Resurrection plants: the puzzle of surviving under extreme vegetative desiccation. *Critical Reviews in Plant Sciences* **24**, 209-225
- Reader RJ, Jalili A, Grime JP, Spencer RE, Matthew N (1992) A comparative study of plasticity in seedling rooting depth in drying soil. *Journal of Ecology* **81**, 543-550
- Saccali MS, Ozturk M (2004) Eco-physiological behaviour of some Mediterranean plants as suitable candidates for reclamation of degraded areas. *Journal of Arid Environments* **57**, 141-153
- Salisbury FB, Ross CW (1992) *Plant Physiology*, Wadsworth Publishing Company, Belmont, California, pp 408-437
- Sherrard ME, Maherali H (2006) The adaptive significance of drought escape in *Avena barbata*, an annual grass. *Evolution* **60**, 2478-2489
- Smirnov N (1998) Plant resistance to environmental stresses. *Current Opinion in Biotechnology* **9**, 214-219
- Smith SE, Fendenheim DM, Halbrook K (2006) Epidermal conductance as a component of dehydration avoidance in *Digitaria californica* and *Eragrostis lehmanniana*, two perennial desert grasses. *Journal of Arid Environments* **64**, 238-250
- Sozzi GO (2001) Caper bush: Botany and horticulture. *Horticultural Reviews* **27**, 125-188
- Sullivan CY, Ross WM (1979) Selecting for drought and heat resistance in grain sorghum. In: Mussel H, Staples RC (Eds) *Stress Physiology in Crop Plants*, Wiley, New York, pp 263-281
- Thomas CV, Manshardt RM, Waines JG (1983) Teparies as a source of useful traits for improving common beans (*Phaseolus acutifolius* hybridization with *Phaseolus vulgaris*). *Desert Plants* **5**, 43-48
- Travlos IS, Economou G (2006) Optimization of seed germination and seedling emergence of *Medicago arborea* L. *International Journal of Botany* **2**, 415-420
- Travlos IS, Karamanos AJ (2007) Influence of heat on seed germination and seedling emergence of chaste tree (*Vitex agnus castus* L.). *Journal of Agronomy* **6**, 25-28
- Travlos IS, Economou G, Karamanos AI (2007a) Germination and emergence of the hard seed coated *Tylosema esculentum* (Burch) A. Schreb in response to different pre-sowing seed treatments. *Journal of Arid Environments* **68**, 501-507
- Travlos IS, Economou G, Karamanos AJ (2007b) Effects of heat and soil texture on seed germination and seedling emergence of marama bean, *Tylosema esculentum* (Burch) A. Schreb. *Journal of Food, Agriculture and Environment* **5**, 153-156
- Travlos IS, Economou G, Karamanos AJ (2007c) Seed germination and seedling emergence of *Spartium junceum* L. in response to heat and other pre-sowing treatments. *Journal of Agronomy* **6**, 152-156
- Travlos IS, Karamanos AJ (2008) Growth responses of marama bean (*Tylosema esculentum*) to water deficit conditions. *International Journal of Agricultural Research* **3**, 155-160
- Travlos IS, Liakopoulos G, Karabourniotis G, Fasseas C, Karamanos AJ (2008) Circadian leaflet movements of *Tylosema esculentum* (Burch) A. Schreb, and the abolishment of these diurnal movements by potassium deficiency. *Journal of Arid Environments* in press
- Turner NC (1979) Drought resistance and adaptations to water deficits in crop plants. In: Mussel H, Staples RC (Eds) *Stress Physiology in Crop Plants*, Wiley-Interscience, New York, pp 343-373
- van Heerden PDR, Swanepoel JW, Krüger GHJ (2007) Modulation of photosynthesis by drought in two desert scrubs species exhibiting C₃-mode CO₂ assimilation. *Environmental and Experimental Botany* **61**, 124-136
- van der Willigen C, Pammenter NW, Mundree SG, Farrant JM (2001) Some physiological comparisons between the resurrection grass, *Eragrostis nindensis*, and the related desiccation-sensitive species, *Eragrostis curvula*. *Plant Growth Regulators* **35**, 121-129
- Wang S, Wan C, Wang Y, Chen H, Zhou Z, Fu H, Sosebee RE (2004) The characteristics of Na⁺, K⁺ and free proline distribution in several drought-resistant plants of the Alxa Desert, China. *Journal of Arid Environments* **56**, 525-539
- Wen Jun, Jansen RK (1995) Morphological and molecular comparisons of *Campsis grandiflora* and *C. radicans* (Bignoniaceae), an eastern Asian and eastern North American vicariad species pair. *Plant Systematics and Evolution* **196**, 173-183
- White RH, Engelke MC, Morton SJ, Ruemmele BA (1992) Competitive turgor maintenance in tall fescue. *Crop Science* **32**, 251-256