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

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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

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 “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 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

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opening, photosynthesis and growth (Chimenti et al. 2002). Proline, betaines, dimethyl sulfoxoniopropionate, mannitol, sorbitol, piitol, trehalose and fructans are some of the examples for osmoprotectants (Karmanos 1995; Smirnoff 1998).

Survival of several weeds and grasses, such as turf-type tall fescue (Festuca arundinacea), 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 (Mundere 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 sp., and Caragana korshinskii) or mesophytes (Agriophyllum squarrosum and Conispermum micromelicum) 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 viscossa, Talbotia elegans, Sporobolus stapfianus, Borya nitida and other members of families Myrothamnaceae, Scrophulariaceae, Lamiales, Poaceae, Cyperaceae, Liliaceae). These plants survive in arid environments because they are able to dehydrate, remain during long periods of water deficit, and then rehydrate 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 (Mundere et al. 2002). As a typical example of this category, we could refer to Reaunaria soongorica, a short woody shrub widely spread in semi-arid areas of China, which can survive severe desiccation of its vegetative organs. Xerophyllum 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 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 sp., and Caragana korshinskii) or mesophytes (Agriophyllum squarrosum and Conispermum micromelicum) 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).

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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 thin-walled hypodermis (hairs) cells. This particular anatomy reduces the transpiration gradient and is considered as a notable adaptation for water conservation (Metcalfe 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 (Gulisas et al. 2002). Another outstanding mechanism for maximal drought adaptation, involves stomata sunk 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 (Chenopodium 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 semi-arid 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 (Hamerlyck et al. 2000; Gibbens and Lenz 2001).

Low epidermal conductance may affect the survival of perennial grasses (e.g. Digitaria californica and Erargrostis 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 reclamations 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 conductance 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 marama (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 1997; Chachalis et al. 2001; Chachalis and Reddy 2005).

Features representing xeromorphy usually include a small leaf or leaflet area, pubescent surfaces, amphistomate 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 amphibiotic, isolarateral 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, Marantaceae and Oxalidaceae and also in the flowers of Kalancheoe (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 (Tylosoma esculentum) (Travlos et al. 2008). This species is a wild perennial legume (Fabaceae tribe Fabaeae) 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 usual, but rather drought-avoiding, which produces 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 gas exchange, with critical drought-shade 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 photo-inhibition (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 dormancy of the leaves of several indigenous plant species (Or-
shian 1964; Margaris 1975; Christodoulakis 1989). In Phlo-
minis fruticosa, significant differences are observed between
winter and summer leaves obtained from the same indivi-
duals. 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 pheno-
olics and crystals. Chloroplasts are fewer in number and less
dense in ultrastructural level that 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 photoprotec-
tive potential and higher optimum temperature for photo-
synthesis of summer compared to winter leaves (Kyparissis and Manetas 1993). Moreover, Kofidis et al. (2003) re-
ported 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 me-
chanism 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 sum-
mer leaves of Scleroptotermum spinosum possess a thick epi-
dermis composed of tannin-containing cells, large amount of
mucilage secreted through the inner periclinal walls
kwards the mesophyll and a thick cuticle on the leaf sur-
face (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 environmen-
tal conditions and especially drought throughout the year
(Aronne and de Micco 2000). Therefore, we should say that
seasonal dimorphism is a major strategy that produces
seasonally different plants from the same individual and ena-les 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

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
development of 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 environ-
mental factors such as drought (Karamanos and Papatheo-
hari 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 useful method for improving the field
drought tolerance of turf-type tall fescue (Festuca arundin-
nacea), since freshwater resources for irrigation are be-
coming 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. 1985). Moreover, several other plants are extensively
examined in pursuit of drought-related characters. 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 complicated
overall drought adaptation strategy which usually involves
several mechanisms of drought escape, tolerance and avoid-
ance. 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 phenol-
ology 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
Adekunle DO (1986) Further aspects of Sahelian drought as evident from rain-
fall regime of Nigeria. Archives for Meteorology, Geophysics, and Bioclima-
tology Series B 36, 277-295
Arnesto JJ, Vidiella PE (1993) Plant life-forms and bibliographic relations of
the flora of Lagoniillas (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 Cit-
rus incanus L. subsp. incanus. Annals of Botany 87, 789-794
Benson L, Darrow RA (1954) The Trees and Shrubs of the Southwestern Des-
erts (2 Edn), University of Arizona Press, Tucson, 437 pp
resistance in rootstocks of redvine (Brumichia ovata) and trumpet creeper
(Campsis radicans). Weed Technology 19, 141-147
Weed Science 49, 156-161
Chimenti CA, Pearson J, Hall AJ (2002) Osmotic adjustment and yield main-
tenance 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, Fassas C (1990) Leaf structural peculiarities
in Sarcopoterium spinosum, a seasonally dimorphic subshrub. Annals of Botany
65, 291-296
synthesis, and leaf anatomy in two species of Calotropis genus. Interciencia
32, 791-796
nutrition in marama bean (Tyleosema esculentum L.), a tuber-producing under-
utilized african grain legume. Symbiosis 27, 269-277
Millar AJ (Eds) Biological Rhythms and Photoperiodism in Plants, Bios,
Oxford, UK. pp 5-50
Fahn GA (1997) Leaf anatomy and its relation to the eco physiology of some
non-succulent desert plants from Egypt. Journal of Arid Environments 36,
499-526
three angiosperm resurrection plant species. Plant Ecology 151, 29 - 59
Farrant JM, Brandt W, Lindsey GG (2007) An overview of mechanisms of
desiccation tolerance in selected angiosperm resurrection plants. Plant Stress
1, 72-84
Kramer PJ (Eds) Adaptation of Plants to Water and High Temperature Stress,
Wiley, New York, pp 207-230
Journal of Arid Environments 49, 221-263
water deficit in six Mediterranean sclerophyll species: possible factors ex-
plaining the declining distribution of Rhamnus ludovicai-salvatorius, an ende-
icma Balearic species. Tree Physiology 22, 687-697
Hamelryck EP, McAffule JR, Smith SD (2000) Effects of surface and sub-
surface soil horizons on the seasonal performance of Larrea tridentate (creo-
sotebush). Functional Ecology 14, 596-606
Herppich WB, Flach BMT, Von Willert DJ, Herppich M (1996) Field inves-
tigations of photosynthetic activity, gas exchange and water potential at dif-
ferent leaf ages in Welwitschia mirabilis during a severe drought. Flora 191,
59-66
Herppich WB, Flach BMT, Von Willert DJ, Herppich M (1997) Field inves-
tigations in Welwitschia mirabilis during a severe drought. II. Influence of
leaf age, leaf temperature and irradiance on photosynthesis and photoinhibi-
tion. Flora 192, 165-174
Hesekel MS, Rigos NC (2005) Markers of selection for drought stress
tolerance and avoidance in Impatiens capensis (Balsaminaceae). American Journal of Botany 92, 37-44


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