International Journal of Plant & Soil Science



31(5): 1-8, 2019; Article no.IJPSS.52649 ISSN: 2320-7035

Adaptive Strategies of Desert Plants in Coping with the Harsh Conditions of Desert Environments: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. Author KUE is the main author, structured the write-up. Author CBE is the main internal editor. Author TNO managed the literature searches. Author GCU and all other authors read and approved the final manuscript.

Article Information

DOI: 10.9734/IJPSS/2019/v31i530224 <u>Editor(s):</u>

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(3) Danni Guo, South African National Biodiversity Institute (SANBI), South Africa. Complete Peer review History: <u>http://www.sdiarticle4.com/review-history/52649</u>

Review Article

Received 25 September 2019 Accepted 30 November 2019 Published 07 February 2020

ABSTRACT

The low and erratic precipitation of desert habitats and the resultant drought have been a huge environmental challenge to the desert flora. Because these organisms must harmonize their structures and functions to thrive in their environments, they have evolved a range of strategies to survive the drought that characterizes the desert ecosystem. Desert plants have adopted some strategies like drought tolerance, drought escape, and succulence as the means to conserve and use water. Also, to minimize the rate of transpiration, they have evolved leaf sclerophylly. All these adaptations and more, play an important role in the organisms' ability to conquer the harsh conditions of desert environments amidst the prevailing climate changes. It seems that some of these plants could potentially serve as models for understanding drought adaptation mechanisms and their potential uses. It is expected that understanding the response of plants to increasing

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drought would be important in the light of global and regional climate changes, not only to forecast population dynamics in natural ecosystems but also to adjust management processes in agronomy and vegetation management for improvement.

Keywords: Desert; plants; adaptation; drought; climate change.

1. INTRODUCTION

Shortage of water is a constraint to live that recurs more and more in many regions of the world due to global climate change [1]. Desert ecosystems have long been known for their low precipitation, and irregular and their characteristic aridity is encouraged by the progressive climate change impacts. Most deserts have an average annual precipitation of less than 400 mm [2], thus imposing harsh environmental conditions characterized by moisture deficit. Aridity is the sole factor that defines a desert and is the primary limitation to which desert organisms must adapt [3]. However, deserts are not necessarily dry. It is the high evaporation relative to the precipitation that makes a desert such hash environment [4]. According to Ward [5], four factors influence the lack of rainfall in desert: (1) the global atmospheric circulation maintains twin belts of dry, high-pressure air over the edges of the tropics, called Hadley cells (2) marine circulation patterns contribute to aridity when cold coastal waters on the west coasts of North and South America, Africa, and Australia chill the air, reducing its moisture-carrying capacity (3) rain shadows are created by mountain ranges, and (4) if the distances to the interior of a continent are too great (such as the Gobi and Taklamakan deserts of China) then water is limited.

Increasing drought has an impact on the survival of plants whose survival depends upon the ability to harmonize their structures and functions to withstand desiccation without permanent damage. Many desert species exhibit a range of strategies to survive in arid and semi-arid systems characterized by episodic precipitation and soil-moisture pulses that vary in amount and frequency [6]. Plants show structural alternations that are mainly related to water saving (e.g. water storage and reduction of water losses) and mechanical reinforcement of tissues (e.g., thickening and strengthening of cell walls) [7]. Drought tolerant typically requires the capacity to maintain physiological functions 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 [8]. One basic drought-avoiding

adaptation mechanism for many desert species is the evolution of ephemeral life cycle characterized by a short-lived growth and reproductive cycles much less than one year. The desert plants have developed strategies to adjust stomatal behaviour, rate of transportation and water potential to cope with the harsh environment of the desert [9]. The reduction of transpiration can be reached through various means including sclerophylly, seasonal dimorphism, the reflectivity of leaves, and stomatal regulation.

2. DROUGHT TOLERANCE

Drought tolerance is defined as the ability to grow, flower and display economic yield under sub-optimal water supply. Plants which can maintain productivity even when their tissues become stressed exhibit tolerance. Drought stress affects the water relations of plants at cellular, tissue and organ levels, causing specific, as well as unspecific reactions [5]. To cope with the drought, tolerant plants initiate defence mechanisms against water deficit [10]. The mechanisms of drought tolerance are the maintenance of turgor using osmoregulation (a which induces accumulation of process compatible solutes in the cell), increase in elasticity of the cell and a decrease in cell size and desiccation tolerance by protoplasmic resistance [11].

Some vascular plants, the resurrection plants, have a noticeable and impressive tolerance to almost complete desiccation of vegetative organs [12]. Apart from resurrection plants, some authors agree that the term drought resistance does not apply to many higher plants because they evolved different avoidance reactions based on the restriction of growth events into time windows when the water supply is satisfactory [13]. These plants survive in arid environments because they can dehydrate, remain quiescent during long periods of drought, and then resurrect upon rehydration.

3. DROUGHT AVOIDANCE

One fundamental drought-surviving adaptation mechanism for many species is the evolution of

ephemeral life cycle. An ephemeral life cycle is characterized by a short life and the capacity to complete their life cycle in much less than one mechanism year. This involves rapid phenological development (early flowering and developmental early maturity), plasticity (variation in the duration of growth period depending on the extent of water deficit) and remobilization of pre-anthesis assimilates [14]. For drought-escaping species, such as the weed Avena barbata, high metabolic active ity 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 [15]. There is evidence that the transition between phenophases can be affected by increasing aridity depending on speciesspecific phenotypic plasticity, which is also influenced by the environment. Matching growth duration of plants to soil moisture availability is critical to realize high seed yield [16]. Developing short duration varieties has been an effective strategy for minimizing yield loss from terminal drought, as early maturity helps the crop to avoid the period of stress [17]. This strategy is especially suitable for environments with welldefined wet and dry seasons, since it involves the completion of plant's life cycle during the wet season while water is still adequate, thus escaping the drought season [18]. This ability is found only in plants, but also in many invertebrates. Desert ephemerals are astonishingly rapid growers capable of reproducing at a remarkably high rate during the favourable season.

The drought escape strategy may partially explain the abundance of annual species thriving in the aridest habitats [19]. In the driest habitats (deserts) up to 90% of the plants are annuals, which effectively employ dormancy periods to take advantage of the very short favourable season [18].

4. SUCCULENCE

Some desert plants are adept at efficiently absorbing water during even light rainfalls, and storing the water in specialized cells in their stems, leaves or roots. This succulent, waterholding tissue provides the plants with security against extended dry spells. Succulents are plants which are adapted to withstand periods of drought by their ability to store moisture in specialized storage organs [20]. Saguaro grows slowly but may live for up to two hundred tears. The surface of the trunk is folded like a concertina, thus allowing it to expand, and a large specimen can hold eight tons of water after a good rainfall. Cacti are by far the best known of the succulents, but many other plants have also adopted this strategy including agave, aloe, elephant trees *Bursera spp.* and many members of euphorbia (Euphorbiaceae) [3], and milkweed (Asclepiadaceae) families. Acquiring water is part of the battle, keeping it is the other. Cacti and other desert plants are notorious for their spines and thorns as a deterrent to thirsty or hungry browsers. Plants may rely on toxic or bittertasting plant juices, camouflage or inaccessible growing sites as forms of protection in addition to or instead of spines and thorns [3].

5. ROOT ARCHITECTURE OF DESERT PLANTS

Root architecture of terrestrial plants can be defined as how the roots of the plants are positioned in different microenvironments that determines the efficiency of water and nutrient uptake from the soil. Roots are the key plant organ for adaptation to drought. If tolerance is defined as the ability to maintain leaf area and growth under prolonged vegetative stage stress, the main basis of variation appears to be constitutive root system architecture that allows the maintenance of more favourable plant water stress [20].

It is also commonly accepted that the distribution of roots throughout the soil is largely affected by the moisture content of the superficial layers more than that of deeper layers [21]. The presence of small diameter roots under reduced water availability is considered as a strategy aimed to maximize absorptive surfaces and nutrient uptake [22]. Evidence suggests that it is quality (i.e., the distribution and structure), and not the quantity of roots that determine the most effective strategy for extracting water during the crop-growing season. The ability of roots of common lamb's quarter 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 [23]. In some species such as in Agave deserti Engel, the root system is made of established and rain-induced roots which are produced or established within a few hours of rains and are shed when the soil dries [24]. Although representing an additional production cost for the plant, rain-induced roots confer an adaptive advantage in desert environments since they are characterized by higher hydraulic conductivity than established ones.

In semi-arid environments, both root systems characterized by shallow and deep roots coexist [25] (see Fig. 1). African rue Peganum harmala. herbaceous perennial nature of 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 [26,27]. As many of the world's invasive weeds, the root systems of mature African rue plants possess extensive lateral roots and deep tap conferring an advantage roots [26], to during established plants conditions of moisture deficit. Similarly, based on a study of many vascular plants by [28], the maximum rooting depth is significantly correlated with their sustainable growth under drought conditions.

6. ANATOMY OF ROOTS OF DESERT PLANTS

The control of water loss is also exerted by the presence of specialized tissues such as rhizodermis with thickened outer cell walls, a well-specialized suberised exodermis, often accompanied by many layers of thin- or thick-walled suberised cells [29]. The presence of suberised layers of cells, at the periphery of the root, represents an important mechanism not only in the selection of nutrient uptake but especially because it regulates the inverse flux of water that, in extreme drought conditions, could pass from the root to the soil [30]. It has been

experimentally shown that the limitation imposed on root radial hydraulic conductivity by suberised layers increases during root development and soil drying [31]. After crossing epidermis and endodermis, water has to pass through the cortical parenchyma. The reduced number of cortical layers is considered an adaptive advantage under drought conditions because it shortens the way between the soil and the stele favouring quick radial water transport [32].

7. TRANSPIRATION AND LEAF XEROMORPHY

The morphology and physiology of desert plants are variously adapted to conserve water and commonly also to store large quantities of water, during dry periods. Other species may be adapted to survive long periods of desiccation of their tissues, during which their metabolic activity may effectively shut down. Water absorbed by plant roots is lost in the atmosphere mostly through leaf transpiration. Transpiration rates vary widely among plant groups; from 10 to 0.1 g of water dm⁻²h⁻¹ in hydrophytes and xerophytes respectively [33]. Plants in arid and semi-arid environments show leaves with xeromorphic traits designed to reduce transpiration to a minimum under drought conditions. The reduction of transpiration can be reached through various means including sclerophylly, seasonal dimorphism, the reflectivity of leaves, and stomatal regulation.



Fig. 1. Root architecture of a desert tree with the characteristic coexistence of extensive lateral roots and deep roots against the soil profile



Fig. 2. Sclerophyllous leaves of a desert plant

8. SCLEROPHYLLY

Sclerophylly of plants is also considered an adaptation to drought; hard leaves do not suffer from permanent damage due to wilting and can completely recover when favourable conditions are restored. It reduces evaporation through a variety of traits including waxy coatings, thicker cell layers and recessed stomata. Sclerophylls are widely distributed in arid and semi-arid environments together with seasonally dimorphic species. Sclerophylly has been interpreted as a phenomenon linked also to other functions as a protection against pathogens or as a response to scarce nutrient availability [34]. However, there is evidence that stiff leathery leaves are widespread in species adapted to drought occurring in various environments throughout the world. Sclerophyllous leaves are characterized by reinforcing tissues (e.g. thick-walled epidermal cells, sclereids, e.t.c.), which prevent the collapse of the whole structure when water availability is scarce, thus reducing the risk for mechanical damage (see Fig. 2). Under drought conditions, a sclerophyllous leaf slightly reduces its volume through the thick cuticle and thickwalled epidermal cells, but thin-walled mesophyll cells severely shrink increasing intercellular spaces. This allows photosynthesis to remain active also in conditions of severe water stress when other leaf types wilt [35].

9. SEASONAL DIMORPHISM

Field observation demonstrated that leaf quality and structure are controlled by the moisture status of the environment [36]. Seasonal dimorphism is considered another strategy to wade off the effects of drought in desert plants. Seasonally dimorphic species are characterised by a seasonal reduction in their transpiring surface; larger winter mesomorphic leaves growing on dolichoblasts (long twigs) are shed at the beginning of the arid season and are replaced by smaller summer xeromorphic leaves on new branchyblasts (short twigs) [37,38].

10. REFLECTIVITY OF LEAF

The colour of a plant, or the waxes or hairs on its surface, may serve to reflect sunlight and reduce evaporation. Shiny leaves, light green or grey/silver in colour have high reflectivity and absorb less. Many desert shrubs including brittlebush *Encelia farinose* and white bursage *Ambrosia dumosa* use colour to stay cool [39]. The white chalky wax (epicuticular wax) coatings of *Dudleya brittonii* have the highest ultraviolet (uv) reflectivity of any known naturally occurring biological substance [40].

11. STOMATAL REGULATIONS

The rate of transpiration is greatly affected by the level of responses of stomata. Under conditions of soil water limitation and/or high atmospheric evaporative demand, partial or complete stomatal closure allows plants to maintain a favourable water balance while limiting the carbon gain [41,42]. Diffusion resistance decreases under dry air condition. Experiment on stomata responses to changes in humidity in plants growing in the desert showed that at low water stress, diffusion resistance for water vapour decreased in response to the gradual increase in temperature, and transpiration increased accordingly [43]. Adaptation to drought also involves the decrease of stomata size, while stomata density shows a more plastic response to environmental changes.

Plants of arid and semi-arid environments show sunken stomata, often covered by resinous masses and wax layers or confined in deep crypts of the lamina [32,33]. These crypts are often occluded by wax tubules or trichomes which might further reduce transpiration.

12. SUMMARY AND CONCLUSIONS

Plants adapt to and survive under the harsh environment of desert ecosystems marked by drought conditions by the evolution of various morphological, biochemical and physiological responses. These responses Drought tolerance typically requires the capacity to maintain physiological functions 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 [8]. Drought avoidance, mostly found among the annuals, involves response to imposed drought by starting and completing their short-lived phenological cycles before the arrival of the dry season, thus avoiding the growth-inhibiting drought. Succulence ensures that arid plants withstand periods of drought by their ability to store moisture in specialized storage organs. To minimize water loss, plants in arid environments show leaves with xeromorphic traits designed to minimise the effects of transpiration under drought conditions, while at the same time, the root architectures and the root anatomy are uniquely designed for efficient water and nutrient uptakes from the soil profile.

Knowledge of plants' response to increasing drought would be crucial amidst the global and regional climate changes, not only in the study of population dynamics in natural habitats but also to adjust management practices in agronomy and forestry for improvement. Thus, by the production of the most appropriate genotypes together with the adjustment of agronomic practices, drought stress effects can be managed. This is done to ensure the desired crop stages occur at the time when the likelihood of drought is minimal. Also, understanding the mechanisms of plants response to episodic drought and precipitation pulse, and the underlying mechanisms are remarkably crucial to implement vegetation management practices in the prevailing climate changes. For instance, selection for a deep and extensive root system has been advocated to increase the productivity of food legumes under moisture-deficit conditions as it can optimize the capacity to acquire water [44]. Also, selecting plants with a high root/shoot ratios 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 [45].

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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