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University of Kashan

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The Biology of Deserts Plants Defense Mechanisms against Extreme Conditions

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Sokhanvaran pub.

سرشناسه : رنجبرفردوئی، ابوالفضل، ۱۳۳۹- AbolfazlRanjbar Fordoei ,
عنوان و نام پدیدآور : The biology of deserts plants defense mechanisms against extreme conditions[Book]/ Abolfazl Ranjbar-Fordoei.
مشخصات نشر : تهران : سخنوران، ۱۳۹۹= ۲۰۲۰م.
مشخصات ظاهری : ۲۸۸ص.
شابک : 978-622-215739-5
وضعیت فهرست نویسی : فیپا
یادداشت : انگلیسی.
آوانویسی عنوان : بیولاجی...
موضوع : گیاهان کویری -- سازگاری
موضوع : Desert plants -- Adaptation
رده بندی کنگره : QK۹۹۲۲گ/
رده بندی دیویی : ۵۲۶۵۲/۵۸۱
شماره کتابشناسی ملی : ۶۱۴۶۸۰۰

۶۵۴

The Biology of Deserts Plants Defense Mechanisms against Extreme Conditions

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ناشر: سخنوران - دانشگاه کاشان
طراح جلد: سخنوران
سال و نوبت چاپ: ۱۳۹۹ - اول
شمارگان: ۱۰۰۰ نسخه
شابک: ۹۸۷-۶۲۲-۲۱۵-۷۳۹-۵
قیمت: ۵۵۰۰۰ تومان
انتشارات دانشگاه کاشان - کیلومتر شش بلوار قطب راوندی - صندوق پستی: ۸۷۳۱۷-۵۳۱۵۳

انتشارات سخنوران: کارگر شمالی، بعد از ادوارد براون، شماره ۱۴۰۷، طبقه اول، تلفن: ۶۶۴۷۶۳۰۶

To, Imam Ali (peace be upon him) for inspiring human to learn.
Indeed, knowledge is the lifeblood of the hearts, enlightening the
blinds and empowered bodies of the disabled.

Preface

Deserts are defined by their arid conditions. However, deserts are not necessarily dry. It is the high evaporation relative to the precipitation that makes a desert as a harsh environment. Such evaporation occurs because deserts are often hot, and because precipitation is low.

A result of this aridity is that most of the area occupied by deserts is barren and tedious. However, biologists perceive deserts to be laboratories of nature, where natural selection is exposed at its most extreme. Scientists have long considered the many unique adaptations of plants and animals for surviving the harsh desert environment. More recently, researchers have focused on the biotic interactions among organisms.

Thus, the harsh abiotic environment defines the desert and imposes the strong selection pressures on organisms that live there. However, it is the relative simplicity of desert ecosystems that makes them frequently more tractable for study than more complex environments such as forests. Several studies have confirmed that, most deserts have an average annual precipitation of less than 400 mm. A common definition distinguishes between true deserts, which receive less than 250 mm of average annual precipitation, and semi-deserts or steppes, which receive between 250 mm and 400 to 500 mm.

Four factors influence the lack of rainfall in deserts:

(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.

(4) If the distances to the interior of a continent are too great (such as in the Gobi and Taklimakan deserts), then water is limited.

Many of these four factors act in tandem. An additional type of desert is the polar desert, which occurs in Antarctica region. This desert has extremely low humidity and no snow cover.

Descending winds, which occur when cold and dense air is pulled down by gravity, heat as they descend and evaporate all moisture (Doran et al. 2002). These winds can reach speeds in excess of 300 km per hour. Here too, rain shadows are created by mountain ranges that are sufficiently high that the seaward-flowing ice is blocked from reaching the sea, thereby reducing humidity.

Drought, salt and extreme temperature, are major problems for plant development because these adverse environmental factors prevent plants to realize their full genetic potential. Salt stress is one of the main environmental constraints that decrease plant growth. Compared to salt stress, the problem of drought is even more penetrating and damaging (Vahdati and Lotfi, 2013).

Drought stress signaling certainly merits separate treatment. Nevertheless, most studies on water stress signaling have focused on salt stress, primarily because plant responses to salt and drought are closely related and the mechanisms overlap.

Salinity is detrimental to plant growth, causing nutritional constraints by decreasing uptake of phosphorus, potassium, nitrate and calcium, ion cytotoxicity and osmotic stress.

To avoid the risk of ion toxicity associated with this strategy, Na+ and Cl- are generally compartmentalized in the vacuole and in less sensitive tissues (Mark and Romola, 2003). In parallel, adjustment of the cytoplasmic compartment is achieved via production of compatible osmolytes such as, proline, mannitol, sorbitol, and glycine betaine (GB).

Glycine betaine also acts as an antioxidant and thus detoxifies reactive oxygen species (ROS) (Slama et al., 2015). Ionic toxicity, osmotic stress, and nutritional defects under salinity lead to metabolic imbalances and oxidative stress.

Also, drought, salinity, extreme temperatures and oxidative stress are often interconnected, and may induce similar cellular damage. For example, drought and/or salinization are manifested primarily as osmotic stress, resulting in the disruption of homeostasis and ion distribution in the cell. Oxidative stress, which frequently accompanies high temperature, salinity, or drought stress, may cause denaturation of functional and structural proteins (Smirnoff N., 1998).

As a consequence, these diverse environmental stresses often activate similar cell signaling pathways and cellular responses, such as production of stress proteins, up-regulation of anti-oxidants and accumulation of compatible solutes. Compatible solutes are small organic metabolites that are very soluble in water and are non-toxic at high concentrations (Cushman and Bohnert, 2000).

With respect to the abovementioned constrains, harsh environment like deserts support living organisms. A place where in animals and plants can survive and flourish. It shows that organisms are adapted to their environment in a great variety of ways: in their structure, physiology, and genetics, in their locomotion or dispersal, in their means of defense and attack, in their reproduction and development, and in other respects.

For instance, plant adaptations may exhibit through the following aspects:

1. Increased absorption of water, to compensate the water lost and to maintain a positive water balance. This is achieved by adaptations of the root system, as well as by the high osmotic pressure of the cell sap.
2. Control and reduction of the water lost during transpiration through:

a) Reduction of the transpiring surface, or at least of the exposed surface, e. g. by leaf orientation or rolling.

b) Control of transpiration through the evolution of stoma, which allow a plant's transpiration rate to be related to its water status.

c) Communal reduction of water loss; either by losing of individual plants or by a decrease in the green foliage biomass.

3. Tolerance and/or resistance to drought through the biochemical characteristics of the cytoplasm. Tolerance can be through the anatomical features. Desiccation tolerance by resurrection plants, desert lichens and algae, is an extreme example.
4. Evasion and escape from drought.

An anatomical feature in desert plants is leaf trichosome. The trichomes help in reducing water loss and that protects the photosynthesizing plant organs. Hairs or scales, wax and resin, may play a role in reducing insolation and in reflecting light.

The well-known adaptations of roots to desert conditions include the succulence of the root system.

Two interesting features have been seen in the primary roots of desert plants include: (1) a reduced number of cortical layers and (2) wide casparian strips, which imply greater efficiency of the endodermis.

Desiccation tolerance is another feature of plants in desert system. These plants experience protoplasmic dehydration without permanent injury and known also as poikilohydrous plants. They can benefit from: (1) extreme desiccation tolerance; (2) utilization of dew or water vapour for hydration; and (3) rapid emergence from the quiescent state.

One of the most important adaptation features in desert plants is seed dispersal strategies. The escape strategy occurs when plants produce large numbers of small seeds with long viability. The protection strategy occurs when mature seeds remain attached to the mother plant and must be dispersed by wind, animals, or rain. In addition, seed structures and characters (seed mass and seed shape) affect the effectiveness of seed dispersal. Hence, species with different structures form different dispersal syndromes, including anemochory, zoochory, autochory, ombrohydrochory, and barochory.

This volume describes the ways in which the desert plants cope with harsh and unpredictable environmental conditions and plant dispersal mechanisms to ensure the survival of the species.

I hope that the information compiled in this volume will be beneficial to the academics such as graduate students and researchers, mostly from desert remediation, soil conservation, plant science including botany and agriculture. It will also be of interest to environmental scientists. Professionals working in arid lands crop growers, arid lands and desert managers will also be among the benefited.

Overall, the author has effectively used his experience and knowledge to incorporate experiences from more than 50 books, many book chapters and more than 200 papers to write a collection covering important aspects of plant defense mechanisms against extreme conditions.

The author wishes to express his gratitude to the authorities of University of Kashan.

Abolfazl Ranjbar-Fordoei, PhD

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Chapter 1

A General Introduction to Desert Environment

Deserts are defined by their arid conditions. A consequence of this aridity is that most of the area occupied by desert is barren and tedious, leading many people to view it as a wasteland. In contrast, biologists have long seen deserts as laboratories of nature, where natural selection is exposed at its most extreme.

In the other word, dry lands / deserts and are regions where precipitation is counterbalanced by evaporation from surfaces and transpiration by plants (evapotranspiration). The Drylands can be further classified into four subtypes: dry sub-humid lands, semi-arid lands, arid lands, and hyperarid lands. Usually, hyperarid lands and even arid lands are not considered dry lands (Stafford and Cribb, 2009).

1.1. Why precipitation is too low in the desert?

The desert formation is a complicated process. The causes of desert formation are not less controversial. The vast geomorphic and climatic processes – the same forces which have made other regions wet have made the deserts dry. In the formation of any two deserts not all of these factors have been needed in every case, nor have they ever combined in exactly the same way.

Causes of desert formation can mainly be attributed to the following factors:

Natural Situation

The regions that are desert have suffered geographically or climatically or both due to their natural situation. Perhaps the most significant natural situation leading to desert formation is a by-product of the movement of air masses over the surface of the earth. As the globe turns on its axis 40,000 kilometers per 24 hours at the equator, zero speed at the poles, its atmosphere tends to circulate in a well-defined pattern of gigantic air swirls.

At the equator air tends to be hot, and the air movement is generally upward; this creates an equatorial zone of low atmospheric pressure. The rising air flows away on both sides of the equator to descend earthwards in the two subtropical zones, which are characterized by high pressure. Farther to the north and south are two more broad belts of ascending air with low pressure. The Polar Regions have descending air and high pressure where deserts are located (Persson 2006).

Air Circulation Pattern:

Within high pressure belts air has tendency to descend from high altitudes toward surface. During descent its temperature is greatly increased through compressional heating, warming at the adiabatic rate of 10°C per 1000 meters. Consequently, it arrives at the surface of earth as very hot, very dry air and totally incapable of producing precipitation. It causes aridity (Stone, 2013).

Oceanic Currents:

Cold currents from the Polar Regions flow towards the equator and, in places, come up against the edges of continents. Additional masses of cold water are added to them by upwelling from the frigid ocean depths. Winds blowing landwards over this cold water become cold and can carry little moisture; they may bring fog and mist but it rarely condensed into rain (Figure 1).

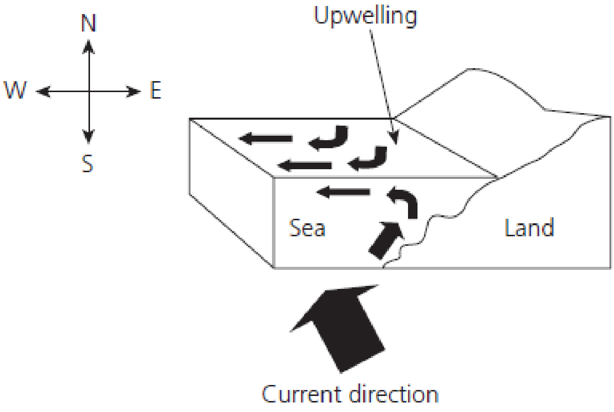

Figure 1.1 Wind and currents running parallel to the coast toward the equator are deflected westwards by the rotational movement of the Earth (the Coriolis Effect). As the top layer of ocean water moves away from the coast, cold, nutrient-rich water from the bottom is brought to the surface. These Waters generate immensely fertile

ocean coasts but also create a cool and stable coastal atmosphere with very low rainfall (Ezcurra, 2006).

Remote Situation from Oceanic Moisture:

The sheer remoteness from an oceanic moisture source may cause aridity. Winds reaching the Gobi and the interior of the Sahara have travelled over vast expanses of land, and most of their water has been squeezed out of them along the way. Mountain barriers accomplish the water extraction over much shorter distances.

Rainless:

Rainfall normally does not occur because of several factors:
1. The air aloft is devoid of moisture,
2. Convectional developments are prevented by the layer of cold air near the surface and
3. The moist surface air is too small in volume to provide an adequate moisture source. The rainless condition accelerates aridity and thereby creates desert.

Temperature:

The clarity of the dry air permits the rapid penetration of solar insolation with minimum alteration, selection, or diffusion of the various wavelengths of radiant energy. The receipt of solar energy by the ground is very great and very high ground temperature results. The very hot ground gives off much heat in the form of terrestrial radiation. Thus the high temperatures are indirectly produced in desert lands. This accelerates the formation of desert (Peel et al., 2007).

Mountain Barrier:

The mountain system forces the winds to discharge rain on the wind ward-side and create desert in the lee or ‘rain shadow’ of the mountains. A striking aspect of the rain-shadow effect is the fact that the entire desiccation process from the wet mountain side to the dry desert side often occurs over a horizontal distance of less than 200 km. Thus some of the world’s wettest and driest spots lie, but a short distance apart, separated by a mountain wall that traps of the incoming moisture (Fig.1.2). The unidirectional persistence of the trade winds produces conditions of heavy precipitation on the windward side and rainfall deficiencies on the leeward side of all mountains (Gooseff et al., 2003).

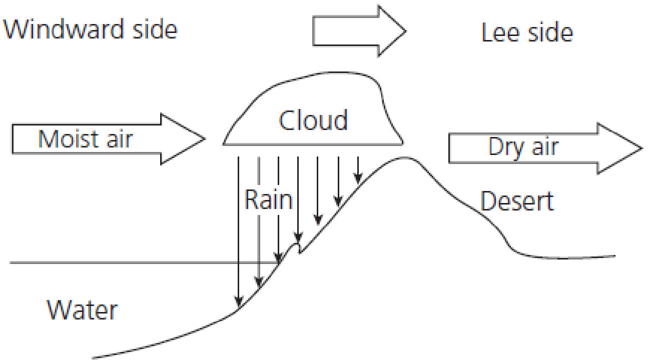

Figure 1.2 a schematic diagram of a rain shadow desert

Man in Desert Making:

The role of man in desert making has been no more than marginal. Many semi-arid steppes and grasslands bordering deserts are unstable and subject to rapid erosional change because their delicate cover of vegetation is disturbed or destroyed. Some destruction is inevitable.

1.2. Precipitation variability and water resource scarcity in deserts

Deserts are considered both as resource-poor environments and as places where there are enormous variations in environmental quality in space and time. In these environments, there is a strong negative correlation between the coefficient of variation in annual rainfall and its median value. For instance in the north of the Sahara, the coefficient of variation of annual rainfall increased from 25–30% in the 400- to 500-mm zone to 70–80% in the 100-mm belt. In a study it has shown that this trend is generally true as well. Coefficients of variation of mean annual rainfall in specific places may be as much as five times higher than in mesic places. An outstanding feature of desert rainfall is the occurrence of sudden, localized cloudbursts, which bring torrential rains (Ward et al., 2000b).

The scanty rainfall and its spatial and temporal variability have a considerable effect on plant life. As a consequence, the soil moisture available to plants is very scarce and highly variable. The surface soil is almost dry throughout the year except for a few days in winter and spring. Subsurface layers of deeper soils may comprise a permanently wet layer. This represents a permanent source of moisture for the deeply penetrating roots of perennials.

1.3. Lack of precipitation creates deserts, not temperature

The location of each biome is determined by the regional climate. Deserts are dry areas that experience extremely small amounts of rainfall. Many people assume falsely that all deserts are hot. This is not the case as deserts can be either hot or cold. The determining factor for considering a biome to be a desert is the lack of precipitation, which can be in various forms. A desert is classified according to its location, temperature, and amount of precipitation. The extreme dry condition of the desert biome makes it difficult for plant and animal life to thrive. Organisms that make their home in the desert have specific adaptations to deal with the harsh environmental conditions. Deserts are determined by low amounts of precipitation, not temperature. They typically receive less than 30 cm of rain per year. The driest deserts often receive less than a half an inch or 2 cm of rain per year. Temperatures in the desert are extreme. Because of the lack of moisture in the air, heat quickly dissipates as the sun sets. In hot deserts, the temperatures can range from above 37°C in the day to below 0°C at night.

Most deserts lie in two belts between the Equator and the tropics of Cancer and Capricorn. In the Northern Hemisphere, the arid belt includes the Sahara, Arabian, and Iranian deserts, the Gobi and central Asian deserts, and the deserts of the North American Southwest (Fig.1.3).

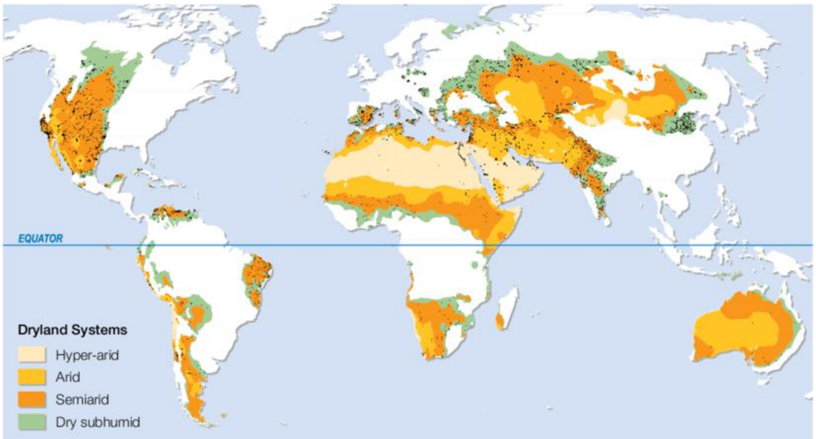

Figure 1.3 Map of the global deserts. The world's deserts are largely subtropical in distribution (Jeffrey and Susan, 2015).

In the Southern Hemisphere, the arid belt includes the Namib and Kalahari deserts, the deserts of Peru and Chile, and the Australian deserts.

1.4 Aridity indices

An aridity index (AI) is a numerical indicator of the degree of dryness of the climate at a given location. A number of aridity indices have been proposed (see below); these indicators serve to identify, locate or delimit regions that suffer from a deficit of available water, a condition that can severely affect organisms' life.

At the beginning of the 20th century, Wladimir Koppen and Rudolf Geiger developed the concept of a rainfall accumulation where arid regions were defined as those places where the annual rainfall accumulation (in cm) is less than R/2, where:

$R = 2 \times T$ if rainfall is in the cold season,

$R = 2 \times T + 14$ if rainfall occurs throughout the year, and

$R = 2 \times T + 28$ if rainfall occurs in summer

with T = mean annual temperature (in °C).

A number of other aridity indices have since been developed. The United Nations Environment Programme (1992) defined aridity as AI = P/PET, where P refers to precipitation and PET refers to potential evapotranspiration. PET and P must be expressed using the same unit (e.g. in mm), and the resulting index is therefore dimensionless.

Aridity indices were also reviewed by Walton (1969) and Stadler (2005). There is a lack of agreement over the approaches used to delineate the exact boundaries between lands having different levels of aridity, although there is an agreement over the general location of arid regions (Agnew and Anderson 1992). Aridity indices inherently include an element of circularity in that they are calibrated against known aridity patterns. For example, the Atacama Desert of northern Chile is widely recognized to be the driest desert in the world. Hence, the numerical thresholds for the extremely arid or hyperaridity category for aridity indices are based on the values of the indices for the Atacama Desert and similar areas.

Several commonly used aridity indices are discussed herein to illustrate basic concepts. From a practical water management perspective, aridity indices do not have much relevance. It is typically self-evident that an arid region under investigation is indeed arid. Nor is there a strong reason to prefer one index to another with respect to water management. Aridity indices have greater value for the tracking the effects of climate change on local water resources, if sufficiently accurate data are available for mapping local changes in the values of the indices over time.

The simplest aridity index is based solely on precipitation. A commonly used rainfall-based definition is that an arid region receives less than 10-in or 250 mm of precipitation per year. This criterion for aridity was used by the Intergovernmental Panel on Climate Change (IPCC 2007). Semiarid regions are commonly defined by annual rainfalls between 10 and 20-in (250 and 500 mm).

The UNESCO (1979) aridity index (AI) is based on the ratio of annual precipitation (P) and potential evapotranspiration rates as follows:

$$\mathrm{AI} = \frac{\mathrm{P}}{\mathrm{PETp}}$$

Where; ETp is calculated using the Penman (1948) formula. The UNESCO system is attractive in that it is conceptually and operationally simple and is based solely on the two main parameters that define aridity. Warm arid regions have low P and high PETp rates and thus very low AI values. UNESCO (1979) proposed a classification of climate zones based on AI index, in which arid regions are defined by an index of less than 0.20 (Table 1.1). Alternative versions of the classification use an AI value for 0.05 for the boundary between hyperarid and arid regions.

Table 1.1 Aridity classifications, UNESCO (1979)

Classification	Aridity index
Hyperarid	Al<0.03
Arid	0.03<AI<0.20
Semiarid	0.2<AI<0.05
Dry subhumid	0.0<AL<0.65

Data on local ETp rates may not be available, which constrains the use of the UNESCO index. The De Martonne aridity index (Am) instead uses temperature as a proxy for ETp as follows:

$$\text{Am} = \frac{P}{T+10}$$

Where, P (cm) is the annual precipitation and T (°C) the annual mean temperature.

The equation is appropriate for temperatures greater than -9.9 °C. The De Martonne aridity index decreases (approaches zero) with increasing aridity.

The Thornthwaite (1948) classification scheme, and variations thereof, is also commonly used to map the distribution of non-polar dry lands. Meigs prepared a map of the distribution of non-polar arid regions for UNESCO based on the Thornthwaite classification, which still widely cited. Thornthwaite defined indices of humidity (I_h) and aridity (I_a) as follows:

$$I_h = \frac{100\,s}{n}$$

$$I_a = \frac{100\,d}{n}$$

where,

s = surplus water, which is defined as the sum of the monthly difference between precipitation (*P*) and ETp for those months when P exceeds ETP (cm)
d = water deficiency, which is defined as the sum of the monthly difference between
ETP and precipitation (P) and for those months when ETp exceeds P (cm)
n = water need, which is the sum of monthly values of potential evapotranspiration for the surplus or deficiency months (cm).
Thornthwaite then defined the moisture index (I_m) as follows:

$$I_m = \frac{100s - 60d}{n}$$

Thornthwaite considered the semiarid climate type to have a moisture index between -20 and -40 and the arid climate type to have a moisture index between -40 and -60.

It must be emphasized that the exact numerical cut-offs between the different climate classes are arbitrary lines drawn in a climatic continuum and that they do not represent a fundamental climatic change. For example, the climatic difference between areas with UNESCO aridity indices of 0.19 and 0.21 would not be significant yet they would be assigned to different classifications (arid and semiarid, respectively) (Fig. 1.4).

Figure 1.4 World maps of the Köppen-Geiger climate classification. Black = extremely arid; Grey = arid to semi-arid (Beck et al., 2018)

References

Agnew C., Anderson E. (1992) Water in the arid realm, Routledge: London and New York. Routledge. 326 pp.

Beck H.E., Zimmermann N.E., McVicar T.R., Vergopolan N., Berg A., Wood E.F. 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data, DOI: 10.1038/sdata.2018.214
Collingwood, Australia.

Cushman J.C., Bohnert H.J., (2000) Genomic approaches to plant stress tolerance. Current Opinion in Plant Biology 3: 117–124.

Doran P.T., Priscu J.P., Lyons J.B. (2002) Antarctic climate cooling and terrestrial ecosystem response. Nature 415: 517-20. DOI: 10.1038/nature710.

Ezcurra, E. (ed.), (2006). Global Deserts Outlook. United Nations Environment Program,
Geiger climate classification. Hydrology and Earth System Sciences, 11: 1633-44.

Gooseff, M.N., Barrett, J.E., Doran, P.T., et al., (2003) Snow-patch influence on soil biogeochemical processes and invertebrate distribution in the McMurdo dry valleys, Antarctica. Arctic, Antarctic, and Alpine Research, 35: 91–9.

IPCC. (2007). Climate changes (2007) Impacts, adaptation and vulnerability. In M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson (Eds.), Contribution of working group II to the fourth assessment, report of the intergovernmental panel on climate change. Cambridge, UK: Cambridge University Press.

Jeffrey A.M., Susan A.M. (2015) Conservation for a New Era.

Louw Gideon N., Mary K. Seely. (1982) Ecology of desert organisms. London: Longmans.

Mark T., Romola D. (2003) Na^+ Tolerance and Na^+ Transport in Higher Plants. Annals of Botani, 91(5): 503-527. DOI: 10.1093/aob/msg058.
Nairobi.

Peel, M.C., Finlayson, B.L., and McMahon, T.A. (2007). Updated world map of the Koppen-
Penman H. (1948) Natural evaporation from open water, bare soil and grass, Proceedings of the

Persson, A.O. (2006). Hadley’s principle: understanding and misunderstanding the trade winds. History of Meteorology, 3: 17-42.

Slama I., Abdelly C., Bouchereau A., Flowers T., Savoure A., (2015) Diversity, distribution and roles of osmoprotective compounds accumulated in halophytes under abiotic stress. Annals Bottany 115(3): 433-447. DOI:10.1039/aob/mucu239 227

Smirnoff N., (1998) Plant resistance to environmental stresses: Current Opinion in Biotechnology, 9: 214-219.

Stone, A.E.C. (2013) Age and dynamics of the Namib Sand Sea: a review of chronological evidence and possible landscape development models. Journal of African Earth Sciences, 82: 70–87.

Thornthwaite C.W. (1948) An approach toward a rational classification of climate. Geographical Review, 38(1): 55–94.

UNEP (1992) World Atlas of Desertification

United Nations Educational, Scientific and Cultural Organization (UNESCO), 1979. Map of the world distribution of arid regions: Map at scale 1:25,000,000 with explanatory note. MAB

Vahdati K., Lotfi N. (2013) Abiotic stress tolerance in plants with emphasizing on drought and salinity stress in walnut, DOI: 10.5772/56078.

Walton K., (1969) The arid zone. Chicago, I.L.: Aldine Publishing Co.

Ward D., Ngairorue B.T., Apollus A., Tjiveze H. (2000b) Perceptions and realities of land degradation in arid Otjimbingwe, Namibia. Journal of Arid Environments, 45: 337–56.

Chapter 2

Abiotic factors

Introduction

Abiotic factors are the primary reason for the differentiation of deserts from other ecosystems. Fundamentally, it is the low rainfall that deserts experience that differentiates them from other habitats. Furthermore, deserts are broadly classified into hot and cold deserts. Frequently cold deserts occur at high altitudes, such as the Tibetan Plateau. Similarly, there are areas of the Arctic and the Antarctic that receive very little rainfall and are very cold. In some researches the role of geology has been considered, particularly in terms of the effects on soils, which in turn is important for plant life and to a certain extent animal life (e.g. those animals living in burrows).

2.1. Rainfall

Depending on your definition of desert, rainfall events there are more or less very rare occurrences: in some places so rare that there are intervening rainless periods of years or decades. The rainfall is often scattered and isolated in the sense that there generally are not large convective complexes or other storm systems that have widespread effects. When rainfall does reach the ground without first evaporating, it can appear to be very intense. And, of course, the rainfall is scarce, sometimes only occurring in a particular season, and sometimes being so scarce that there is no identifiable season.

Rainfall is characteristically scanty in most of the deserts. Irregularity is not only apparent from year to year, but there is also a wide variation between the corresponding months of different years. Irregularity and variability of rainfall are not only temporal, but also spatial. Consequently, rainfall is extremely unpredictable. The amount of rainfall during the growing season, extends from September to

August, and exhibits considerable variation. Spatial variations in rainfall become even more significant when the monthly data are also considered. The patchiness of the desert rainfall is a feature affecting to a large extent the distribution of plant growth.

A prominent feature of desert rainfall is the occurrence of sudden, localized cloudbursts, which bring torrential rains. These sporadic storms are usually of the thunderstorm type. They have a significant effect on both the soil and on plant life. It is noteworthy that the rainfall on one day may exceed the average annual rainfall. The scanty rainfall and its spatial and temporal variability have a considerable effect on plant life. As a consequence, the soil moisture available to plants is very scarce and highly variable. The surface soil (surface deposits) is almost dry throughout the year except for a few days in winter and spring.

The deeper layer of ground may contain a permanently wet layer. This represents a permanent source of moisture for the deeply penetrating roots of perennials (e.g. *Halloxylon* and *Prosopis* genus). There is a prolonged dry season in the deserts. This may extends in some areas to 9 months per year. The seasonal distribution of the rainfall varies from place to place. For example in Iran, the rainy season in desert regions extends from late autumn to early spring. Winter is simultaneous the rainy season. The flash floods are a common hydrological feature in deserts. This phenomenon happens and destroys everything in their way. Soon after such storms the ground surface is covered by ephemerals. The dry season extends throughout the second half of the spring, summer and early autumn. The difference in the seasonality of rainfall in the deserts is appeared in the kind of ephemeral species growing after the rains.

2.2. Air Temperature

The air temperature is another main limiting factor of outstanding importance in the life of desert plants. The main property of air temperature in the deserts is its wide variation, both daily and seasonal. Several studies have shown that the plants in the deserts are subjected to both drastic temperature conditions during summer and wide seasonal and daily fluctuations in air temperature.

Large areas of the deserts, particularly the desert in the Middle East, such as Iranian desert experience extreme maximum air temperatures of over 50°C. In such temperatures readings are "shade" temperatures in a meteorological station. There is rarely any shade in the desert and these readings are therefore not indicator of actual temperatures experienced under direct sun radiation. Also, due to the absence of vegetation and soil moisture in vast areas, the ground temperature is very much higher. At the other extreme, some desert places experience air temperatures below freezing point. Almost all parts of the desert have a clear seasonal rhythm of temperature, which is highest during the months of June to August and lowest during December to February. The wide amplitude of air temperatures, both seasonal and daily, evince the fact that plants, especially perennials, are subjected to severe fluctuations in air temperature.

2.2.1. Hot deserts

The hot desert or Sahara type of climate is located between the latitudinal of 15°-35° in both the hemispheres on the western parts of the continents. This type of desert climate is found in:

(1) Africa - the Namib and Kalahari deserts of coastal Angola and southwest Africa, interior Botswana and South Africa, and Sahara desert;
(2) Asia - Thar deserts of India and Pakistan, Arabian deserts, Iranian desert;
(3) South America - Acatama desert of coastal Peru and Chile;
(4) Mojave and Arizona deserts of south-western USA;
(5) Australia - Great Sandy Desert, Great Victoria Desert and Tanami Desert (Fig. 2.1).

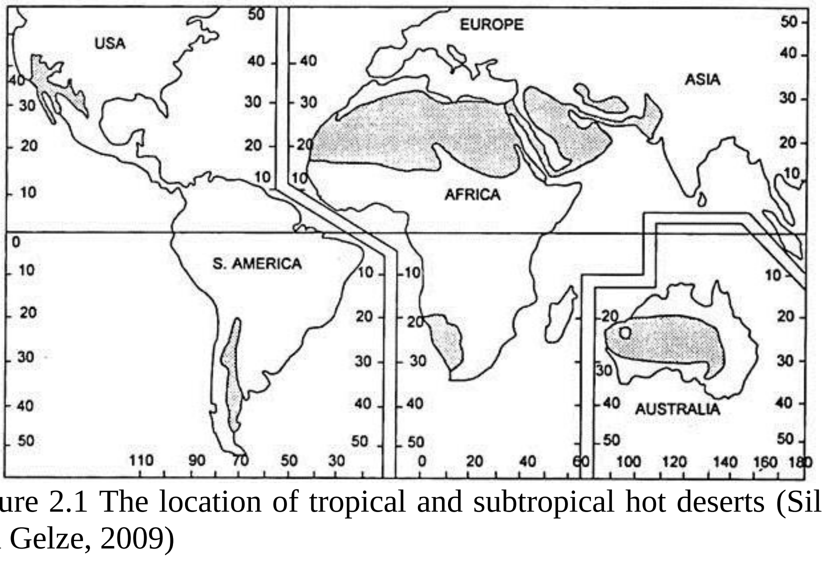

Figure 2.1 The location of tropical and subtropical hot deserts (Silvio and Gelze, 2009)

This climate is characterized by annual aridity, and subsiding warm air masses of the subtropical anticyclones.

The following reasons are held responsible for the genesis of perpetual aridity of the tropical-subtropical hot desert climate:

(1) Temperate cyclones do not reach these areas.

(2) Intertropical Convergence (ITC) also does not influence these areas because of their distant location from the equator.

(3) The trade winds spend most of their moisture through rainfall in the eastern margins of the continents and as they reach the western margins of the continents they become dry and hence are unable to give rainfall.

(4) Due to anticyclonic conditions winds descend from above and hence they are warmed adiabatically with the result their moisture retaining capacity increases resulting into marked decrease in relative humidity.

(v) Subtropical high pressure system causes divergence of surface winds which is antagonistic to rainfall.

(5) The ground temperature is so high that raindrops, if formed at all, are evaporated before they reach the ground surface.

2.2.2. Cold deserts

Cold deserts have hot summers counterbalanced by relatively or extremely cold winters. For example, for half the year, the Gobi Desert lies below 0 °C. In the arid parts of Antarctica, mean winter temperatures may be as low as -30 °C, while, in summer, diurnal temperatures will exceed 5 °C for only a few weeks (McKay et al. 2009). Nearly most cold deserts lie in the Northern Hemisphere and away from the tropics, because only great distances from the ocean make them both hot in the summer and cold in the winter. The Patagonian Desert is the exception here because it does not occur far from the ocean. Rather, it is the fact that it is in a rain shadow and because it is relatively close to Antarctica that makes it so cold. Cold deserts include the Great Basin, Patagonian, Turkestan, and Gobi deserts. In Central Asia, the cold deserts extend from northern Iran through Central Asia to Mongolia, covering an area of 2.5 million square kilometres. Deserts such as the Gobi, Taklamakan, Karakum, Kyzylkum and Muyunkum are important areas for migration, among others for hoofed animals, and host a unique array of flora and fauna, perform a range of ecosystem services including serving as grazing grounds, and are an important carbon sink. However, these deserts are under threat from excessive timber extraction and overgrazing, and are increasingly unable to fulfill key ecosystem functions. In addition, there have not been adequate efforts to establish protected areas and place larger areas under nature conservation in the countries of this region. Some famous cold deserts are: Atacama, Gobi, Great Basin, Namib, Iranian, Takla Makan, and Turkestan. Antarctica is the largest cold desert of the earth (Peel et al., 2000).

2.3. Increase and decrease in pan evaporation, a paradox

Not only annual rainfall makes deserts arid but also effect of the ratio of evaporation to rainfall is important. The process of transferring water from the land surface to the atmosphere is the link between the global water cycle, energy cycle, and carbon cycle and is of critical importance for agriculture, hydrology, ecology, and the climate system. Changes in this process will also change the energy partitioning between sensible and latent heat, altering atmospheric dynamics and influencing weather and climate (Trenberth, 2009). Pan evaporation (Epan) is the most universal and simplest way to measure evapotranspiration, which is often used to indicate the humidity level of a given regional climate (Lim et al., 2012).

As the global temperature rises, Epan should theoretically gradually increase. However, in reality, only certain regions in the world have an Epan value that is consistent with theoretical expectations, and the majority of the world's regions have been found to have declining Epan values. This phenomenon is called the "*pan evaporation paradox*" [Roderick and Farquhar, 2002]. Specifically, countries such as Spain, Iran (Tabari and Marofi, 2011), and Brazil (Silva, 2004) have been found to have increasing Epan values, and countries such as New Zealand (Roderick and Farquhar, 2005), China (Zuo et al., 2005), Thailand, India (Jhajharia, 2009), Nigeria (Oguntunde et al., 201), and Australia (Jovanovic et al., 2008) have been found to have declining Epan values. Correctly interpreting the overall declining trend of Epan in the context of rising global temperatures and uncovering the main meteorological factors that affect the reduction of Epan is of great importance to accurately predict future hydrological cycles.

Several researchers have studied the temporal and spatial changes of Epan at global and regional scales, as well as the causes of such

changes. According to their findings, the causes of Epan reduction can be categorized as follows:
(1) An increase in humidity in the surrounding environment of the evaporation pan: Brutsaert and Parlange ascertained that the decrease in Epan value was due to an increase in the volume of evaporation from the land surface, considering the difference between evaporation from the land surface and the evaporation volume observed through the evaporation pan (Brutsaert and Parlange, 1998).

(2) Changes in precipitation: Tebakari et al. (2005) analyzed the temporal and spatial variation of Epan in Thailand from 1982 to 2000 and concluded that both Epan and precipitation showed a declining trend. This conclusion was inconsistent with findings from the United States, where Epan was found to be decreasing while precipitation was increasing. Jaswal et al. utilized evaporation and rainfall data from 1971 to 2000 from 58 stations that were evenly distributed in India to analyze the overall correlation between evaporation and rainfall in a year, as well as their correlation in winter, summer, monsoon season, and post-monsoon season. The results showed that, in southern India, the evaporation trend had a complementary relationship with rainfall during the same period (Brutsaert and Parlange, 1998).

(3) A decrease in the diurnal temperature range: Peterson et al (1995) compared data from both the United States and the former Soviet Union from 1950 to 1990 and found a steady decline in Epan values in all investigated regions (except Central Asia), as well as a decline in diurnal temperature range. Epan and diurnal temperature range were thus clearly correlated. Therefore, the researchers concluded that the reduction in the diurnal temperature range, caused by an increase in cloud cover, consequently caused the reduction in Epan.
(4) A reduction in solar radiation: Roderick and Farquhar found that Epan values observed in many parts of the world over the past 50 years showed a clear downward trend and asserted that such a decline was caused by the reduction in overall solar radiation resulting from an increase in cloud cover and aerosol concentrations (Roderick and Farquhar, 2002).

(5) A reduction in wind speed:
Burn and Hesch conducted a trend analysis on the evaporation data of 48 sites in the Canadian
Prairies over three analysis periods and concluded that wind speed has a substantial influence on the decreasing trend of evaporation, while vapor-pressure deficit has a significant influence on the increasing trend of evaporation (Burn and Hesch, 2007).

(6) The comprehensive impact of meteorological elements: Roderick and Farquhar analyzed data from Australia for 1970 to 2002 and found that Epan values showed a downward trend.
The results showed that such a change might be related to a decrease in solar radiation, wind speed, and diurnal temperature range (Roderick and Farquhar, 2002). Sheng examined Epan data and other meteorological factors from 468 meteorological stations in China, measured simultaneously from 1957 to 2001, and found that the main influential factors of Epan were solar radiation, diurnal temperature range, and wind speed, while the influence of humidity was the weakest factor (Sheng, 2006).

Based on the aforementioned studies, the causes of the reduction of Epan appear to be very complicated. Owing to the location, climate, atmospheric differences, and even the differences in the length of the data series, the conclusions of these studies are inconsistent. Therefore, identifying the impact of various meteorological variables on Epan trends is critical to quantifying the impact of global warming.

Analysis of global pan evaporation data has mostly recorded declines in evaporation (Hoffman et al. 2011) despite the trend of rising global air temperatures. This is known as the ‘pan evaporation paradox’ (Roderick and Farquhar 2002), because declines in evaporation occurred at the same time as global warming. Not all sites experienced declines in pan evaporation, however. For example, in the U.S.A., only 64% of sites with this type of pan evaporimeter experienced declines (Hobbins et al. 2004) while others experienced no change or increases. In semi-arid Israel, there was an increase in evaporation during the boreal summer months (Cohen et al. 2002) and no change in winter, ascribed in part to decreases in global irradiance and increases in water vapour pressure deficit and wind speed, the last-mentioned being associated with changes in wind direction.

However, Roderick and Farquhar (2002) ascribed declines (not increases) in pan evaporation to declines in global irradiance.

2.4. Geology and soil nutrient availability

Many deserts have very high spatial variation in geological substrates and, consequently, soil type. Deserts can also have shifting habitats created by dune systems, which leads to the formation of unique vegetation forms and their associated fauna (Goudie and Seely 2011). Saline desert are the main geological features in arid and semiarid regions. Limestone deserts may support high densities of organisms, such as snails, otherwise associated with mesic ecosystems (Shachak et al. 1991).

In desert ecosystems, plant growth and nutrient uptake are restricted by availability of soil nitrogen (N) and phosphorus (P). The effects of both climate and soil nutrient conditions on N and P concentrations among desert plant life forms (annual, perennial and shrub) remain unclear. Phosphorus is widely considered to be the most limiting nutrient in Australian deserts (Orians and Milewski 2007), while nitrogen, phosphorus, and potassium are limiting in sand dune communities in Africa's Namib and Kalahari deserts (Aranibar et al., 2004).

In desert ecosystems, low soil moisture coupled with high soil alkalinity acts to decrease both soil N and P availability (Schleninger, 1997). Infrequent and low precipitation limits soil weathering, organic matter production, and mineralization, leading to slow P release from primary material, low soil organic matter content, and N bound in organic matter (Drenovsky et al., 2004).

In general, soil nutrients and organic matter tend to be concentrated in the upper 2-5 cm of the soil with the greatest amounts underneath the canopies of individual desert shrubs in 'islands of fertility. These resource islands harbor greater concentrations of water, soil nutrients, and micro-organisms than adjacent soils. Moreover, the distribution of soil nitrogen, phosphorus, and potassium is strongly associated with the presence of shrubs in desert habitats because organic matter from the plants accumulates there (Aranibar et al., 2004). The inter-shrub spaces are barren and comparatively devoid of biotic activity (Ravi et al., 2010).

Desert animals such as rodents, isopods and other insects build their burrows in soil, and change the chemical and physical qualities of the soil (including porosity, water-holding capacity, infiltration rates, redistribution of nutrients, and organic matter) and they can affect soil erosion (Whittington-Jones et al. 2011). Thus, this variability in substrate type, along with rainfall and temperature, may play a key role in determining where desert organisms can live in a particular area of a desert.

2.4.1 Desert landscapes

Aeolian depositional features

When sand grains transported by saltation are deposited, they form sand dunes as the wind slows down. Wind can slow for a number of reasons, but it is usually vegetation, rocks or other sand dunes creating an obstacle. Sand dunes form in a number of shapes and layouts dependent upon a number of factors:

-The direction and speed of the wind
-The quantity of sand being transported
-The nature of the desert surface
-The presence of vegetation

2.4.1.1. Star dunes: If the sand is confined to a basin, and the wind periodically radically changes its direction, the resulting dunes will become complex in shape and may be called star dunes.

Figure 2.2 Star dunes are the dominant dune type in Lut Desert, Kerman province (Malekaba) Southern Iran. These pyramid-shaped star dunes form because the winds blow from multiple directions.

2.4.1.2. Seif dunes: these are longitudinal dunes (named after an Arab curved sword) that are long ridges of sand which form parallel to the prevailing wind. They are much larger and more common than barchans dunes. Seif (linear) dunes can reach 200m in height and over 100km in length. They form from linked barchans dunes when a temporary – but repeated - change in wind direction occurs. This causes one of the horns or 'arms' of a barchans dune to elongate and merge with its neighboring dune to form a series of connected dunes. These dunes are dominant in South East Libya and South West Algeria.

2.4.1.3. Barchan dunes: The barchans is a crescent-shaped dune that can reach 30m high and is moved by the wind. Saltation and surface creep take place on the gentle upwind-facing slope of the dune (stoss face) as the wind pushes material upslope. Sediment then continually avalanches over the ridge and down the steeper lee (slip face) of the sand dune, moving the entire sand dune forward at a rate of up to 30 m/yr. Swirling wind currents (eddies) help to keep the lee slope steep. The horns (edges of the dune) move faster than the center of the dune as there is less sand to move.

2.4.1.4. Erg: A large area of sand dunes is known as an erg (sand sea). These features can stretch for hundreds of kilometres and cover approximately one quarter of all arid regions. Ergs are mainly confined to the Arabian and Sahara Deserts. Sand seas are an apt name for a large area of sand dunes due to the way that sand dunes appear like a slow-moving wave as they migrate with the wind. Five basic dune shapes have been recognized: *crescentic*, linear, star, dome and parabolic.

2.4.1.5. Salinization

Soils that form in desert climates are predominantly mineral soils with low organic matter content. However, the repeated accumulation of water in certain soils causes salts to precipitate out.

A distinction can be made between *primary* and *secondary* salinization processes:

− Primary salinization involves accumulation of salts through natural processes such as physical or chemical weathering and transport from saline geological deposits or groundwater.

− Secondary salinization is caused by human interventions such as inappropriate irrigation practices, use of salt-rich irrigation water and/or poor drainage conditions. Most of saline soils in deserts are attributed to primary salinization. The causes of soil salinization are commonly associated to:

2.4.1.5.1. Soluble salts

In arid and semiarid climates, there is not enough water to leach soluble salts from the soil. Consequently, the soluble salts accumulate, resulting in (leading to) salt-affected soils.

The major cations of concern in saline soils are Na^{+}, $Ca^{2+,}$ Mg^{2+} and K^{+} and the primary anions are Cl^{-}, $SO4^{2-,}$ $HCO3^{-}$, $CO3^{2+}$ and $NO3^{2-}$. In hyper-saline waters or brines B, Sr, Li, SiO2, Rb, F, Mo, Mn, Ba and Al may also be present.

Bicarbonate ions result from the reaction of carbon dioxide in water. The source of the carbon dioxide is either the atmosphere or respiration from plant roots or other soil organisms. Carbonate ions are normally found only at $pH > 9.5$.

When soluble salts accumulate, Na^{+} often becomes the dominant ion on the soil exchanger phase, causing the soil to become dispersed. This results in a number of physical problems such as poor drainage. The predominance of Na+ on the exchanger phase may occur due to replacing most of exchangeable Ca^{2+} and Mg^{2+} that precipitate as CaSO4, CaCO3 and CaMg(CO3)2.

2.4.1.5.2. Evapotranspiration

An additional factor in causing salt-affected soils is the high potential evapotranspiration in arid and semi-arid areas, which increases the concentration of salts in both soils and surface waters.

2.4.1.5.3. Poor drainage

Poor drainage can also cause salinity and may be due to a *high water table* or to *low soil permeability* caused by sodicity (high sodium content) of water. Soil permeability is "the ease with which gases, liquids or plant roots penetrate or pass through a bulk mass of soil or a layer of soil".

2.4.1.5.4. Water quality

An important factor affecting soil salinity is the quality of irrigation water. If the irrigation water contains high levels of soluble salts, Na, B and trace elements, serious effects on plants and animals can result.

2.4.1.5.5. Rising of water table

When the water table rises to within about 2 m of the ground level, water may begin to rise to the surface by capillary action. When a rising water table intersects with salts that were previously held below the root zone, the salt will dissolve and be carried up to the surface, concentrating in the upper layers of the soil as water is evaporated. Most playa lakes will consequently be highly saline (Yechieli and Wood, 2002).

2.4.1.6 Saline–Sodic Soils

Saline–sodic soils have an EC_e >4 dS m^{-1} and an ESP >15. Thus, both soluble salts and exchangeable Na^+ are high in these soils. Since electrolyte concentration is high, the soil pH is usually <8.5 and the soil is flocculated. However, if the soluble salts are leached out, usually Na^+ becomes an even greater problem and the soil pH rises to >8.5 and the soil can become dispersed (Richards, 1954).

In Saline–sodic soils reclamation involves the addition of good-quality water to remove excess soluble salts and the use of a Ca^{2+} source ($CaSO_4$ $2H_2O$ or $CaCl_2$) to exchange Na^+ from the soil as a soluble salt, Na_2SO_4. In Saline–sodic soils a saltwater-dilution method is usually effective in reclamation. In this method the soil is rapidly leached with water that has a high electrolyte concentration with large quantities of Ca^{2+} and Mg^{2+}. After leaching, and the removal of Na^+ from the exchanger phase of the soil, the soil is leached with water of lower electrolyte concentration to remove the excess salts.

2.4.1.7 Desert pavement

A desert pavement, also called reg (in the western Sahara), serir (eastern Sahara), gibber (in Australia), or saï (central Asia) is a desert surface covered with closely packed, interlocking angular or rounded rock fragments of pebble and cobble size. They typically top alluvial. Desert varnish collects on the exposed surface rocks over time.

Several theories have been proposed for the formation of desert pavements. A common theory suggests they form through the gradual removal of sand, dust and other fine-grained material by the wind and intermittent rain, leaving the larger fragments behind. The larger fragments are shaken into place through the forces of rain, running water, wind, gravity, creep, thermal expansion and contraction, wetting and drying, frost heaving, animal traffic, and the Earth's constant microseismic vibrations. The removal of small particles by wind does not continue indefinitely, because once the pavement forms, it acts as a barrier to resist further erosion. The small particles collect underneath the pavement surface, forming a vesicular A soil horrizon (Mc Faddaneh, 1987).

A second theory supposes that desert pavements form from the shrink/swell properties of the clay underneath the pavement; when precipitation is absorbed by clay it causes it to expand, and when it dries it cracks along planes of weakness. Over time, this geomorphic action transports small pebbles to the surface, where they stay through lack of precipitation that would otherwise destroy the pavement by transport of the clasts or excessive vegetative growth.

A newer theory of pavement formation comes from studies of places such as Cima Dome, in the Mojave Desert of California, by Stephen Wells and his coworkers. At Cima Dome, geologically recent lava flows are covered by younger soil layers, with desert pavement on top of them, made of rubble from the same lava. The soil has been built up, not blown away, yet the stones remain on top. There are no stones in the soil, not even gravel (Dron and Oberlander).

Figure 2.3 Desert pavement: Khara Desert, Isfahan Province, Iran. *Source*: Photo by Javad Moeini, Contributing to Wikipedia, 2015.

Desert pavement is frequently coated with desert patina (also known as *desert varnish*), which is a black or brown coating on the outer surface of the rocks (Fig. 2.3).

This gives a similar veneer to the rocks of various different compositions, created by oxides of iron and manganese and deposited by wind and water from rain and dew. This process takes thousands of years. In the Sinai Desert, thousands of square kilometers are covered with reg.

2.4.1.8. Playa

Playas occupy the flat central basins of desert plains. They require interior drainage to a zone where evaporation greatly exceeds inflow. When flooded, a playa lake forms where fine-grained sediment and salts concentrate. Terminology is quite confused for playas because of many local names. A saline playa may be called a salt flat, salt marsh, *salada*, *salar*, salt pan, alkali flat, or *salina*. A salt-free playa may be termed a clay pan, hardpan, dry lake bed, or alkali flat. Enclosed basins of salt and clay accumulation may originate from numerous causes. Tectonic causes include faulting, as in many deserts.

In Iran, playa is characterized as flat area at or near the lowest point in the desert basin and many playas flood from time to time. The main geomorphologic facies and types of Iran Playas are Kavir, Sabkha, alluvial fans, salty lake and clay pans. While the landscape and drainage in playa catchments provide a qualitative assessment of climatic and hydrological regime in the past, playa sediments preserve a wealth of Palaeo-environmental information. Iran includes more than 60 playas. Rosen (1994) defined playa as an intercontinental basin where the water budget of the playa lake is negative involving precipitation, surface and ground waters flows and evapotranspiration has been adopted (Sepehr and Almodaresi, 2013). Based on the sediment grain size, playas are classified in three classes comprising coarse and fine grained playas.

Figure 2.4 A salt playa in Maranjbab, Kashan, Iran

2.4.1.9. Plain

Geographically, a plain is a flat, sweeping landmass that generally does not change much in elevation. Plains occur as lowlands along valley or on the doorsteps of mountains, as coastal plain, and as plateaus or uplands.

Plains are one of the major landforms on earth, where they are present on all continents, and would cover more than one-third of the world's land area (Geoff et al., 1993). Plains may have been formed from flowing lava, deposited by water, ice, wind, or formed by erosion by these agents from hills and mountains. Plains would generally be under the grasslands, steppe, savannah or tundra biomes. In a few instances, deserts can also be plains (Gornitz, 2009). Plains in many areas are important for agriculture because where the soils were deposited as sediments they may be deep and fertile, and the flatness facilitates mechanization of crop production; or because they support rangelands which provide good grazing for grazing animals (Powell., 2009). Plains are classified in diffent types include: Depositional, erosional and structural plains.

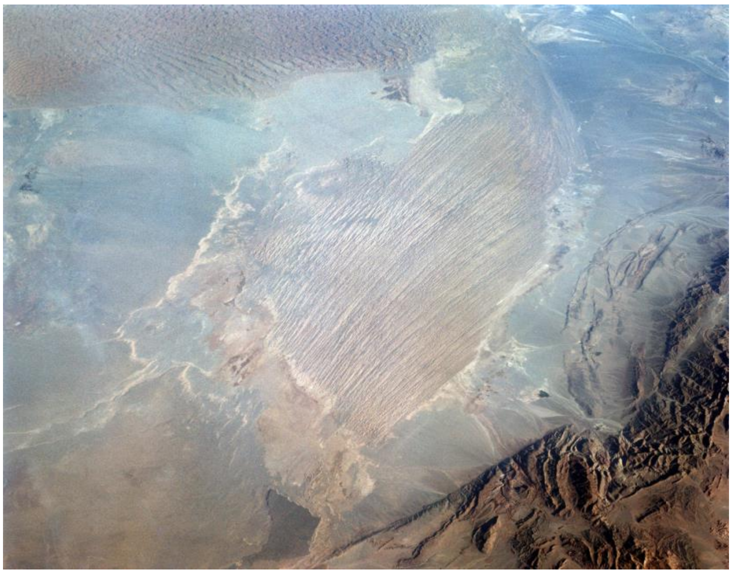

Figure 2.5 Plain of Lut from space (Iran) (UNESCO World Heritage Centre, 2016)

References

Aranibar J.N., Otter L., Macko S.A., et al., (2004) Nitrogen cycling in the soil-plant system along a precipitation gradient in the Kalahari sands. Global Change Biology, 10: 359–73.

Brutsaert W., Parlange M.B. (1998) Hydrologic cycle explains the evaporation paradox. Nature, 396, P.30.

Burn D.H., Hesch N.M., (200**7)** Trends in evaporation for the Canadian prairies. J. Hydrol., 336: 61–73.

Dorn R. I., Oberlander T. M., (1981) "Microbial Origin of Desert Varnish," *Science* 213:1245-1247.

Drenovsky R. E., ichards J. H. (2004) Critical N: P values: Predicting nutrient deficiencies in desert shrublands. Plant Soil 259: 59–69.

Geoff C.B., Hawkesworth C.J., Wilson R.C.L. (1992) Understanding the Earth (2nd ed.). Cambridge University Press, ISBN 978-0-521-42740-1.

Gornitz V., (ed.). (2009) Encyclopedia of Paleoclimatology And Ancient Environments. Springer: Dordrecht, p. 665.

Goudie A., Seely M. (2011). World Heritage Desert Landscapes: Potential Priorities for the recognition of desert landscapes and geomorphological sites on the World Heritage List

He M., Dijkstra F.A,, Zhange K., Li X., Tan H., Gao Y., Li G., (2014) Leaf nitrogen and phosphorus of temperate desert plants in response to climate and soil nutrient availability. Scientific reports, 4: 6932. DOI: 10.1038/srep06932.

Jhajharia D., Shrivastava S.K., Sarkar D., Sarkar S. (2009) Temporal characteristics of pan evaporation trends under the humid conditions of northeast India. Agric. For. Meteorol., 149: 763–770.

Jovanovic B., Jones D.A., Collins D. (2008) A high-quality monthly pan evaporation data set for Australia. Clim. Chang., 87: 517–535.

Lim W.H., Roderick M.L., Hobbins M.T., Wong S.C., Groeneveld P.J., Sun F.B.,Farquhar G.D., (2012) The aerodynamics of pan evaporation. Agric. Forest Meteorol, 152: 31–43, doi.org/10.1016/j.agrformet.2011.08.006.

McFadden L.D., Wells S.G., Jercinovich M.J. (1987) "Influences of aeolian and pedogenic processes on the origin and evolution of desert pavements", Geology 15(6):504-508.

McKay C.P., Molaro J.L., Marinova M.M. (2009) High-frequency rock temperature data from hyper-arid desert environments in the Atacama and the Antarctic dry valleys and implications for rock weathering. *Geomorphology,* 110: 182–7.

Oguntunde P.G., Abiodun B.J., Olukunle O.J., Olufayoa A.A., (2012) Trends and variability in pan evaporation and other climatic variables at Ibadan, Nigeria, 1973–2008. Meteorol. Appl., 19: 464–472.

Orians G.H., Milewski A.V. (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biological Reviews, 82: 393–423.

Powell W.G. (2009) Identifying Land Use/Land Cover (LULC) Using National Agriculture Imagery Program (NAIP) Data as a Hydrologic Model Input for Local Flood Plain Management. Applied Research Project, Texas State University.

Peel M.C., Finlayson B.L., McMahon, T.A. (2007) Updated world map of the Koppen- Geiger climate classification. Hydrology and Earth System Sciences, 11: 1633-44.

Peterson T.C., Golubev V.S., Groisman P.Y. 1995. Evaporation losing its strength. Nature 1995, 377: 687–688.

Ravi S., D’Odorico P., Huxman T.E., Collins S.L. (2010) Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. Rangeland Ecology and Management, 63: 267–74.

Trenberth K.E., Fasullo J.T., Kiehl J., (2009) Recognition of Desert Landscapes and Geomorphological Sites on the World Heritage List. “Earth's global energy budget,” Bulletin of the American Meteorological Society, 90(3): 311–323.

Roderick M.L., Farquhar G.D. 2005. Changes in New Zealand pan evaporation since the 1970s. Int. J. Climatol., 25: 2031–2039.

Roderick M.L., Farquhar G.D., (2002) The cause of decreased pan evaporation over the past 50 years. Science, 298:1410–1411.

Rosen M.R. (1994) The importance of groundwater in playas: A review of playa classifications and the sedimentology and hydrology of playas, in: M.R. Rosen (Ed.), Palaeoclimate and Basin Evolution of Playa Systems, Geological Society of America, USA, pp. 1-18.

Schlesinger W. H. Biogeochemistry: an analysis of global change (Academic Press, San Diego, (1997).

Sepehr A., Almodaresi S.A. (2013) Geotop of Lut Playa: Quaternary Geomorphologic Evidence and Civilization. Journal of Earth Science and Engineering 3:168-179.

Shachak M., Brand S., Gutterman Y. (1991) Porcupine disturbances and vegetation pattern along a resource gradient in a desert. *Oecologia*, 88: 141–7.

Sheng Q. (2006) The Variation and Causes of Small Pan Evaporation over the Past 45 Years in China. Master’s Thesis, Nanjing University of Information Science and Technology, Nanjing, China, May 2006. (In Chinese)

Silva V.D.P.R.D. (2004) On climate variability in Northeast of Brazil. J. Arid Environ. 2004: 58: 575-596.

Silvio Carlos Rodrigues, Gelze Serrat de Souza Campos Rodrigues Tropical biology and Conservation Management – Vol. IX - Geomorphology and Biogeography of Tropical Deserts - (2009)

Tabari H., Marofi S. (2011) Changes of pan evaporation in the west of Iran. Water Resource Management, 2011: 25: 97–111.

Tebakari T., Yoshitani J., Suvanpimol C. (2005) Time-space trend analysis in pan evaporation over Kingdom of Thailand. J. Hydrol. Eng., 10: 205–215.

UNESCO World Heritage Centre (2016) United Nations Educational, Scientific and Cultural Organization, "Lut Desert".

Ward D. (2016) The Biology of Deserts, second edition, Oxford University Press. United Kingdom.

Whittington-Jones, B.M. (2011) The dispersal of African wild dogs Lycaon pictus from protected areas in the northern Kwa Zulu-Natal province, South Africa. MSc. thesis, Rhodes University, Grahamstown.

Yechieli Y., Wood W.W., 2002. Hydrogeologic processes in saline systems: playas, sabkhas, and saline lakes. Earth-Science Reviews 58: 343–365.

Zuo H.C., Li D.L, Hu Y.Q., Bao Y., Lv S.H. (2005) The relationship between climate change trends and its changes in evaporation observed by evaporating dishes in the past 40 years in China. Chin. Sci. Bull.11: 1125-1130. (In Chinese)

Chapter 3

Adaptation

Introduction

In biology, adaptation is the process by which a species becomes fit to its environment. It is the result of natural selection's acting upon heritable variation over several generations. Organisms are adapted to their environment in a great variety of ways: in their structure, physiology, and genetics, in their locomotion or dispersal, in their means of defense and attack, in their reproduction and development, and in other aspects.

The word *adaptation* does not stem from its current usage in evolutionary biology but rather dates back to the early 17th century, when it indicated a relation between design and function or how something fits into something else. In biology this general idea has been coopted so that *adaptation* has three meanings. First, in a physiological sense, an animal or plant can adapt by adjusting to its immediate environment, for instance, by changing its temperature or metabolism with an increase in altitude. Second, and more commonly, the word *adaptation* refers either to the process of becoming adapted or to the features of organisms that promote reproductive success relative to other possible features. Here the process of adaptation is driven by genetic variations among individuals that become adapted to that is, have greater success in a specific environmental context (Amundson (1994).

3.1. Adaptation versus Acclimation

All living organisms need to have an environment where they can survive and flourish. Scientists refer to this place as the natural habitat. But since all species of plants and animals are connected with each other in the so-called food web, trespassing territories is unavoidable. As a result of this intrusion, any organism crossing boundaries either needs to adapt or acclimate itself to its new surroundings.

Adaptation and acclimation are two terms commonly used to describe the adjustment done by either a plant or animal when it goes beyond its normal habitat. It also applies to changes that may occur inside its own environment which can render it unsuitable for survival if they fail to adjust. While they may often refer to changes in the habitat, there are differences between how they should be used properly.

Adaptation is centered on an organism's ability to change its physical and chemical make up to adjust to its habitat. This takes a long time to achieve and usually affects the whole group to which it belongs. It is part of the evolution process, which all living things must undergo in order to cope with the ever changing planet. For instance, one of the adaptatins allows camel to withstand arid environments is the ability of this animal to survive for long periods of time with very little water.

Acclimation is a form of adaptation that an organism undergoes when transferred to a different habitat. It doesn't take as long as evolutionary adaptation and it doesn't affect the body composition of the entire species. Adjustment is made by modifying physical reactions to environmental changes, like shivering when exposed to cold weather.

Transformations that occur in adaptation tend to be permanent until new changes are needed again. The rule 'survival of the fittest' best describe how the process works. When changes in the environment occur, like a rise in temperature, animals and plants that can't cope, eventually die leaving the stronger ones to survive and proliferate. These remaining members have adapted accordingly.

Acclimation, on the other hand, is temporary adaptation to gradual changes in the natural habitat. It only occurs in the lifespan of the organism and doesn't affect evolution patterns of its species. Adaptation is a natural process that occurs for every type of organism. This is to ensure continuity and survival of species. Acclimation may or may not occur in a habitat and if it does, it only takes a short time until an adjustment is made by animals and plants. Ultimately, both terms deal with how living things cope with changes in their environment (Pigliucci, 2005).

3.2. Why do plants deal with extreme external conditions?

Most of the plants are rooted in the ground and cannot escape from the conditions into which they have been born. They are therefore continuously exposed to the full impact of extreme external conditions and consequently must adapt to them (Basu et al., 2016). The desert environment imposes severe stresses on the plants growing in it. These stresses include:

l. Water stress due to the low, variable and irregular rainfall and to the high evaporative power of the atmosphere and low atmospheric humidity.

2. Heat stress due to high temperatures (in the hot deserts) during summer, or frost stress (in the cold deserts), as well as wide diurnal and seasonal changes in the air and soil surface temperatures.

3. High solar radiation on most of the days of the year.

4. High wind velocity causing burial of the shoot systems of plants or eroding the soil and thereby exposing the root system. Such exposure can also be due to the infrequent torrents from thunderstorms. The velocity of dry wind greatly increases the evaporative power of the air, thus impairing the water balance of plants through its effect on transpiration.

5. Salinity, and in particular saline habitats, both coastal and inland.

Desert plants, especially perennials, grow under the impact of the combined effect of the above-mentioned stresses. The main problem confronting these plants is water balance. In view of the water deficit in the soil, they would be expected to have acquired several traits helping them to absorb water under desert conditions. At the same time, these plants live under a severe deficit of atmospheric humidity, which causes excessive water loss through transpiration. This indicates that the desert plants must be endowed with characteristic adaptations and traits that help them to carry out a variety of different processes.

Plants, particularly, desert plants have evolved several different types of drought resistance strategies which allow them to adapt to specific habitats for the benefit of their growth and development. Drought resistance is defined as the integrated capability of plants in response and adaption to the harsh environment caused by drought stress conditions. This capability is a sophisticated trait and is related to the adaptations at different levels, ranging from plant morphology and anatomical structures to physiological and biochemical reactions (Blum, 2002).

The mechanisms of drought resistance and/or tolerance in one species may not be the same as in another, even one growing under the same environmental conditions. Every species has its own potentialities for enduring or resisting drought.

Ecologists usually regard the terms resistance and tolerance as interchangeable. Though both have more or less the same function, the words have different meanings. Resistance can be can be defined as withstanding the impact of particular conditions and, at the same time, remaining unharmed. The plant's ability to do so arise from the adaptations acquired during its evolution. In other words, resistance arises from genetically fixed traits or adaptations. On the other hand, tolerance means the quality of being able to suffer the hardships of the severe conditions without being damaged. It is to be noted that this is a negative response. The tolerance of a plant comes from its characteristics and responses (Batanouny, 2001).

3.3. What adaptations have to be performed?

Water is a limiting factor for survival and growth of desert plants. The flow of water in the soil–plant–atmosphere continuum is a passive process driven by water potential differences and enabled by the continuity of the liquid phase of water between the soil and the leaf mesophyll (Steudle, 2001). To adapt to the arid environment, plants formed multiple morphologic and physiologic adaptation strategies to resist the drought stress environment, including plant morphology and structure, growth rate, water use efficiency, antioxidant system, and developed root system (Li et al., 2009).

Adaptation should perform for the following aspects:

1. Increased absorption of water, to at least compensate for the water lost by the plant in its attempts to maintain a positive water balance. This is achieved by adaptations of the root system, as well as by the high osmotic pressure of the cell sap.

2. Control and reduction of the water lost during transpiration. This is achieved by:

a) Reduction of the transpiring surface, or at least of the exposed surface, e. g. by leaf orientation or rolling. Orientation of the leaves is a measure by which leafy plants reduce exposure to direct solar radiation.

b) Reduction of the transpiration rate under dry conditions, both daily and seasonal. Adaptations relating to the control of transpiration are important. In particular the evolution of stoma, which allow a plant's transpiration rate to be related to its water status, has been among the most important evolutionary steps in successful colonization of the land.

c) Communal reduction of water loss; either by the disappearance of individual plants or by a decrease in the green foliage and biomass of the transpiring surface. The simultaneous occurrence of different life forms with different water requirements within the community assures an ecologically balanced distribution of water, as well as of water output of the community, all year-round (Basu et al., 2016).

3. Tolerance and/or resistance to drought through the biochemical characteristics of the cytoplasm or by the production of amino acids that protect the protoplasm. Tolerance can be partially achieved through the particular anatomical features of desert plants. Desiccation tolerance by resurrection plants, desert lichens and algae, is an extreme example (Shao et al., 2009).

4. Evasion and escape from drought. This occurs either through the complete drying out or death of above-ground parts of perennial geophytes in summer, or the disappearance of annual plants with the advent of the dry season. Partial death for the sake of survival is a common feature of perennial desert plants (Al-Tawaha et al., 2017).

3.4. Drought Adaptation and Coping Strategies Among desert plants

3.4.1. Drought escaping

In nature, plants can either be subjected to slowly developing water shortage (within days to weeks or months) or face short-term water deficits (hours to days). In the case of slowly developing water deficits, plants can either escape dehydration by shortening their life cycle or optimize their resource gain in the long term through acclimation responses. In the case of rapid dehydration, plants react by minimizing water loss or exhibiting metabolic protection (induced or constitutive) against the damaging effects of dehydration and co-developing stress (Fig.3.1).

Drought escaping plants grow only when water is available. These are usually annual plants that are ephemeral and restrict their growth to those periods, usually in the spring, when there is sufficient water for plant growth and reproduction.

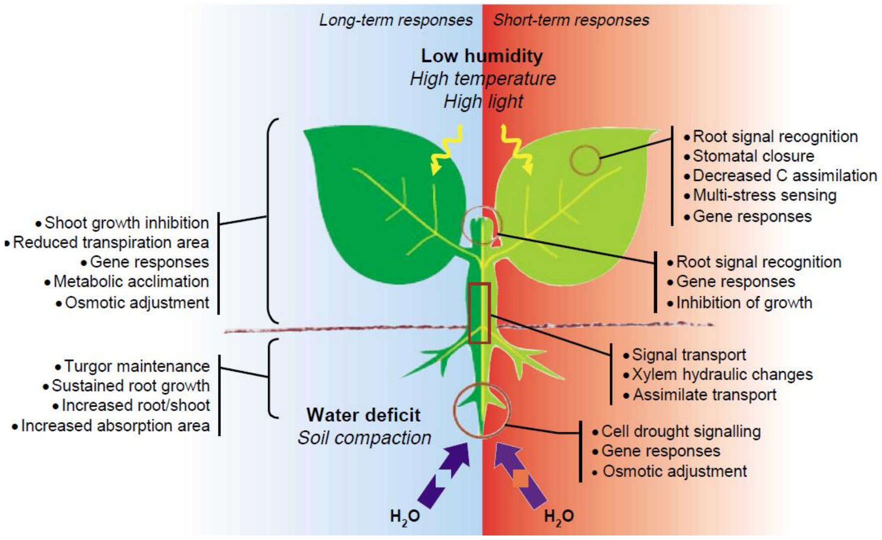

Figure 3.1 Whole-plant responses to drought stress. Left: long-term or *acclimation* responses; right: short-term responses (Chaves et al., 2003).

Fast and slow desiccation can have totally different results in terms of physiological response or adaptation (McDonald and Davies 1996), but the importance of time in shaping plant response may change dramatically according to genotype and environment.

Plants that escape drought exhibit a high degree of developmental plasticity, being able to complete their life cycle before physiological water deficits occur. Escape strategies rely on successful reproduction before the onset of severe stress. This is important in arid regions, where native annuals may combine short life cycles with high rates of growth and gas exchange, using maximum available resources while moisture in the soil lasts (Maroco *et al.* 2000*a*). Improved reproductive success also includes better partitioning of assimilates to developing fruits. This is associated with the plant's ability to store reserves in some organs (stems and roots) and to mobilize them for fruit production, a response well documented in crop plants, such as cereals (Bruce et al. 2002) and some legumes (Chaves et al., 2002). This ability to mobilize reserves is increased in droughted plants.

Avoidance simply means that growth is confined to periods whenever there is ample water supply or at least sufficient water supply to sustain the life of the plant. To cope with the prolonged annual dry period, which occurs in almost all the deserts of the Middle East, different groups of plants have evolved different survival mechanisms. Evenari et al. (1971) stated that plants are active only as long as the upper soil layer is wet, becoming inactive during the dry season. According to these authors, they can be classified into three groups, namely: winter annuals, plants with bulbs, corms or rhizomes (*Geophytes*, *cryptophytes*), and diminutive perennial herbs (*nanophanerophytes, hemicryptophytes*).

Avoidance is achieved by the disappearance of the green, transpiring organs. This can be complete disappearance, as in annuals (ephemerals), or disappearance for a definite period during the dry season, as in many geophytes (usually bulbous) and diminutive perennials. However, there are many differences among these groups. This will be explained in the following sections.

3.4.1.1. Annularity

The long-term persistence of an annual plant species in any particular area or habitat of a desert environment depends on at least four main factors: (1) the existence of long-living and sufficiently large seed banks, (2) successful development of enough plants to complete their life cycle and produce new mature seeds for the species' long-term seed bank. (3) Seeds that are buried in depressions may be re-dispersed by the turnover of soil by animals onto or near the soil surface, where they may be able to germinate. (4) A further contribution to the long-term seed bank of a plant species may be the mass introduction of seeds from nearby areas or from more distant habitats by wind or floods (Gutterman 2001a).

Annual plants live for one growing season or year and then survive until the following growing season as seeds. Desert annuals have little capacity for photosynthetic acclimation, unlike evergreen species, and are unable to handle severe drought (Smith *et al.* 1997). Some annuals are *amphiphytic*, that is, they may be annual or perennial depending on local environmental conditions. For example, several species of the grass genus *Stipagrostis* (e.g. *S. plumosa*, *S. ciliata*, and *S. hirtigluma*) are perennial under moderate conditions but are annual when conditions become more extreme (Danin 1996).

In the warm deserts, two groups of ephemeral annual plants have been recognized. One group, the winter annuals, consists of species that germinate and complete their life cycles during the winter and spring months; the other group, the summer annuals, includes species that germinate and complete their life cycles during the summer and early fall months. Normally, the seasonal occurrences of these two groups of species are highly predictable and are determined by specific temperature and moisture combinations required for germination.

Ephemeral annuals, in decided contrast to the perennial desert flora, are commonly considered to exhibit no striking adaptations to the desert climate but rather are thought to be mesophytic in nature and escape unfavorable conditions of soil water stress and high insolation by rapid completion of their life cycles during the brief periods when temperature and moisture regimes are favorable for growth (Juhren et al., 1956).

3.4.1.1. 1. Winter annuals

Winter annuals have three features that differentiate them from summer annuals:

1. *Height*—they are usually shorter than summer annuals, keeping their leaves closer to the soil surface where the ambient temperatures are warmer during the cool winter.
2. *Basal rosette*—they keep their leaves in a single layer near the soil surface.

These leaves are usually non-overlapping to maximize solar radiation in the afternoon.

3. *Leaf dissection*—leaves are highly dissected, perhaps because this decreases boundary layer effects, increasing CO2 passage into the leaf for photosynthesis (Mulroy and Rundel 1977).

3.4.1.1. 2. Summer annuals

Summer annuals have the following features:

1. *Leaf size*—leaves are displayed along the entire vertical length of the stem and are smaller in size to reduce the heat load during the day, leading to more efficient cooling by convection.
2. *Height*—they keep their leaves as high as they can above the soil surface to reduce high ambient temperatures that can lead to inhibition of photosynthesis.

3. *Solar tracking*—leaves maintain their orientation to the sun throughout the day, which provides the plant with a high rate of carbon gain when growth is more limited by light availability than by precipitation or nutrient availability. Ehleringer and Forseth (1980) found that winter annuals in the Mojave Desert show solar tracking in 28% of species but 75% of summer annual species in the Sonoran desert show solar tracking.

One means of achieving high photosynthetic performance is to load the leaves with high levels of crude protein (15-28%) and have a high leaf conductance; for this reason, desert annuals have the highest photosynthetic rates recorded in terrestrial plants (Gibson 1998). Another strategy is solar tracking, which allows plants to maintain maximum rates of photosynthesis throughout the day, while non-trackers reach a maximum for only a few hours of the day when the solar angle is high (Mulroy and Rundel 1977).

A distinction is required between winter and summer ephemerals. Despite the strict division between annuals and perennials, certain plant species have been recorded as "biennials" by some investigators or as either annuals or perennials. Species such as *Zygophyllum simplex, Arnebia hispidissima* sand *Sclerocephalus arabicus* have been observed to persist until the following growing season.

3.4.1.1. Geophytes

The term ‘geophyte’ refers to plants that use underground organs for storage. Most plants in this category belong to the monocot families Iridaceae, Liliaceae, and Amaryllidaceae. Geophytes are kind of plants having the capability to survive under arid environmental conditions; parts of their bodies are dormant fleshy underground as bulbs, corms, tubers or rhizomes (El-Amier, 2016). Geophytes are plants with underground storage organs (bulbs, corms, tubers or rhizomes) that appeared as promising raw materials for various economic uses. The leaves of these plants die annually. No evergreen plants are considered to be geophytes (Rundel, 2004).

The bulbs, corms or rhizomes of geophytes buried in the soil remain dormant during the dry season, well protected against drying out and overheating by layers of dead tissue or cork. While in this inactive state, they need very little water, if any, to remain alive and so evade the drought conditions of the environment. The dormant bulbs of *Poa sinaica,* for example, can be heated to 80°C without suffering any damage. However, shortly after the first rains and as soon as the soil in the vicinity is wet, they form roots and rootlets with incredible speed.

Examples of bulbous geophytes growing in the deserts of the Middle East include *Dipcadi erythreum,* and *Allium desertorum;* of the geophytes with corms, *Colchicum rotchii* and *Arisarum vulgare* are typical (Batanouni, 2001).

Figure 3.2 Distribution of geophytes in arid regions (Iran).

More than 200 species of geophyte plants from the major families including Liliaceae, Iridaceae and Amaryllidaceae are grown in Iran, especially in arid environments such as Khalijo-omanian ecozone. It should be noted that some species from Araceae including *Arum* spp. L. and *Biarum* spp. Schott and from Orchidaceae [*Orchis* spp., Gymnadenia spp., Dactylorhiza spp., *Steveniellas* pp., *Epipactis rechingeri* Renz, *Ophrys kurdistanica* Renz and *Ophrys turcomanica* Renz, Corydalis spp. (Fumariaceae), Leonticespp. (Polyphyllaceae) Geranium tuberosum (Geraniaceae) have not been included in Wendelbo's contribution (Farahmand and Nazari, 2015).

3.4.2. Drought evading

These plants avoid periods of limited soil moisture by using morphological features such as deep roots (e.g. in riparian trees from southern Africa such as camel thorn, *Acacia erioloba*, and shepherd’s tree, *Boscia albitrunca,* which have roots as deep as 68 m (Jennings 1974), stem succulence (e.g. cacti in the Americas and euphorbs in Africa), and/or physiological features such as stomatal control of water loss and crassulacean acid metabolism photosynthesis.

Drought avoidance is characterized by stomata that close at higher water potentials and larger leaves with less vertical orientation and less ability for the accumulation of solutes and/or maintenance of high tissue elasticity (Smith et al., 1997). Inward contraction of elastic walls can cause a loss of volume, allowing for the maintenance of turgor pressure (Smith et al., 1997). Monson and Smith (1982) showed that maintenance or seasonal adjustment of low osmotic potentials was negatively correlated with drought avoidance.

3.4.3. Drought enduring

These plants possess rapid gas exchange (with less stomatal control of water loss) and shed their leaves when droughts occur. This includes most desert shrubs, such as *Hammada scoparia* (Chenopodiaceae) in Irano-Turanian region (Jerraya et al., 2008).

3.4.4. Drought resisting

These plants have moderate rates of gas exchange when water is plentiful but are able to maintain some reduced level of gas exchange during periods of water stress. These plants are characterized by having stomata that close at low plant water potentials, small leaves with a tendency for vertical orientation, low hydraulic conductance of the xylem, and high capacity to accumulate solutes and/or maintain high tissue elasticity to ensure turgor maintenance (Smith et al., 1997). Only a few plants fall into this category, including the creosote bush *Larrea tridentata* and some plants in Middle Eastern deserts, such as *Zygophyllum dumosum* and *Anabasis articulata*. Note that *drought tolerance* is a synonym for *drought resisting*. In addition, the terms *drought stress, water stress,* and *water deficit* are often used interchangeably.

One limitation to this categorization is that it does not accommodate the mistletoes Loranthaceae and Viscaceae). These hemiparasitic plants are capable of photosynthesizing but do so at the expense of their hosts, from which they gain water and nutrients (Bowie and Ward 2004; Okubamichael et al., 2011). Through passive water uptake, mistletoes open their stomata and transpire profligate amounts of water from the xylem to access nutrients such as nitrogen. Some mistletoe (e.g. *Viscum rotundifolium,* which grows on a number of plants, especially *Ziziphus mucronata* and *Ehretia rigida*) also take up water from the phloem using active water uptake, which does not require large amounts of water (Okubamichael et al., 2011).

References

Al-Tawaha A. R., Turk M.A., Abu-Zaitoon Y.M., Hmoud S. et al., (2017) Plants adaptation to drought environment. Bulgarian Journal of Agricultural Science, 23 (3): 381–388.

Amundson R. (1994) The concepts of constraint: adaptation and the challenge from developmental biology. Philos. Sci. 61:556-578.

Basu S., Ramegowda V., Kumar A., Pereira S., (2016) Plant adaptation to drought stress. F1000 Research, 5(F1000 Faculty Rev):1554 Last updated: 30 JUN 20.

Batanouny K.H. (2001) Plants in the Deserts of the Middle East. 195 PP. Springer-Verlag Berlin Heidelberg GmbH.

Batanouny K.H., (2001) Plants in the Deserts of the Middle East. Springer-Verlag Berlin Heidelberg GmbH.

Blum A. (2002) Drought stress and its impact. Available via dialog. http://www.plantstress. com/Articles/drought_i/drought_i.htm. Accessed 12 Oct 2014.

Bruce W.B., Edmeades G.O., Barker T.C. (2002) Molecular and physiological approaches to maize improvement for drought tolerance. *Journal of Experimental Botany*, 53: 13–25.

Chaves M.M., Maroco J.P., PereiraA J.S. (2003) Understanding plant responses to drought from genes to the whole plant. *Functional Plant Biology*, 30: 239–264.

Chaves M.M., Pereira J.S., Maroco J., Rodrigues M.L., Ricardo C.P.P., Osório M.L., Carvalho I., Faria T., Pinheiro C. (2002) How plants cope with water stress in the field. Photosynthesis and growth. *Annals of Botany*, 89: 907–916.

Danin, A. (1996) Plants of desert dunes. Springer, Berlin. Desert plants. *Ecology*, 6: 113–23.

Ehleringer J.R., Forseth, I. (1980) Solar tracking by plants. Science, 210: 1094-8.

El-Amier Y.A. (2016) Vegetation structure and soil characteristics of five common geophytes in desert of Egypt. Egyptian journal of basic and applied sciences 3: 172–186.

Evenari M., Shanan L., Tadmor N.H. (1971) The Challenge of a Desert. Harvard University Press, Cambridge, Mass.

Farahmand H., Nazari F. (2015) Environmental and Anthropogenic Pressures on Geophytes of Iran and the Possible Protection Strategies: A Review. International journal of horticultural science and technology, 2(2):111-132.

Gibson A.C. (1998) Photosynthetic organs of desert Plants. BioScience, 48(11): 911-920.

Gutterman Y. (2001a) Regeneration of plants in arid ecosystems resulting from patch disturbance. Geobotany 27. Kluwer, Dordrecht.

Jarraya R., Bouaziz A., Hamdi B., Ben Salah A., Damak M. (2008) N-methylisosalsoline from *Hammada scoparia*. Acta Crystallographica Section E., 64, p. 1714.

Jennings, C.M.H. (1974) The Hydrology of Botswana. Unpublished PhD thesis, University of

Juhren M., Went F.W, Phillips E.A. (1956) Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. Ecology 37: 318-330.

Li X.R., Tan H.J., He M.Z., Wang X.P., Li X.J. (2009) Patterns of shrub species richness and abundance in relation to environmental factors on the *Alxa Plateau*: Prerequisites for conserving shrub diversity in extreme arid desert regions. Sci. China-Earth Sci. 52: 669-680.

Maroco J.P., Pereira J.S., Chaves M.M. (2000a) Growth, photosynthesis and water-use efficiency of two C_4 Sahelian grasses subjected to water deficits. Journal of Arid Environments 45: 119–137.

McDonald A.J.S, Davies W.J. (1996) keeping in touch: responses of the whole plant to deficits in water and nitrogen supply. Advances in Botanical Research 22: 229–300.

Monson, R.K., Smith, S.D. (1982) Seasonal water potential components of Sonoran

Mulroy T.W., Rundel P.W. (1977) Annual plants: adaptations to desert environments. Bioscience, 27: 109–14.

Okubamichael, D.Y., Griffiths, M.E., Ward D. (2011) Host specificity, nutrient and water dynamics of the mistletoe *Viscum rotundifolium* and its potential host species in the Kalahari of South Africa. Journal of Arid Environments, 75: 898–902.

Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol. Evol., 20:481-486.

Rundel P.W. Mediterranean-climate ecosystems: defining their extent and community dominance. In: Arianoutsou M, Panastasis VP, editors. Ecology, conservation and management of Mediterranean climate ecosystems. Rotterdam, The Netherlands: Millpress; 2004. p. 1–12.

Shao H.B., L.Y. Chu, C.A. Jaleel, P. Manivannan, R. Panneerselvam, M. A. Shao, (2009) Understanding water deficit stress-induced changes in the basic metabolism of higher plants biotechnologically and sustainably improving agriculture and the ecoenvironment in arid regions of the globe. Crit. Rev. Biotechnol., 29: 131-151.

Smith, S.D., Anderson, J.E., Monson, R.K. (1997) Physiological Ecology of North American Desert Plants. Springer, Berlin.

Steudle E. (2001) The cohesion-tension mechanism and the acquisition of water by plant roots. Annu. Rev. Plant Physiol. Plant Mol. Biol., 53: 847–875.

Chapter 4

Physiological adaptations for survival in arid conditions

Introduction

When a plant is subjected to stress, its tolerance characteristics oppose this stress. As the stress increases, the activity of tolerance traits continues to rise in opposition.

At a certain threshold, the tolerance capacity becomes insufficient to withstand the stress. At this stage, the resistance traits are initiated. The response of these traits can be short-term or long-term, according to the severity and duration of the stress. Every species has its own potential for tolerating and resisting drought. When grown under different environmental conditions, different individuals of the same species exhibit different degrees of resistance. The drier the conditions, the greater the degree of resistance manifested. This is due to the fact that desert plants are flexible as regards their response to drought. They are endowed with many adaptational traits and characteristics that help them to tolerate and resist drought.

Under desert conditions, plants are usually subjected to water stress. The term "stress" is in common use in the plant physiology literature but its meaning has at times been controversial (Kramer, 1980). The numerous physiological responses of plants to water deficit usually vary with the severity as well as the duration of the stress. Only the most sensitive processes are altered by mild stress. As the stress increases, however, the changes in the plant intensify (this is resistance) and additional processes become affected in accordance with their relative sensitivities (this is tolerance) (Levitt, 1980).

Among the terms used to describe water conditions in the plant body is "water status". It is a vague but nevertheless useful term. Water status has no units that refer to any measure of the general state of a plant in relation to water; rather, the term describes a relative state. It may refer to a plant's water potential, its relative water content, or its turgor (Passioura, 1982).

On the level of an ecosystem as such as desert ecosystem level, drought induces changes in different processes and frequently demands functional plant responses. Some ecosystems, such as savannas, steppes and scrublands, have intermittent low annual precipitation. In these water-limited ecosystems, drought can seasonally modify carbon and nitrogen cycles, resulting in poor water and mineral uptake by roots, lesser plant growth, a reduction in litter decomposition and the biogenic emission of CO2 from the soil. Severe drought can also induce a higher vegetation mortality rate due to cavitation and/or carbon starvation (reduced photosynthesis and enhanced autotrophic respiration). Thus, more frequent and intense drought periods (and the consequent death of plant species) can alter the phytosociology of entire plant communities over time (Renolds and Ortiz, 2010).

4.1. Physiological adaptations

Drought is a physiological form of water deficit where soil water available to the plant is inadequate, which adversely affects the plant’s metabolism. However, plants possess multiple morphological (reduced leaf area, reduced stem length, leaf moulding, wax content, efficient rooting system, stability in yield and number of branches), physiological (transpiration, water-use efficiency, stomatal activity and osmotic adjustment) and biochemical responses (accumulation of proline, polyamine, trehalose, increasing of nitrate reductase activity and storage of carbohydrate at cellular and organism levels) under drought stress, making it a more complex phenomenon to decipher (Conesa et al., 2016) (Fig. 4.1). Of various plant responses to water scarcity, enhanced abscisic acid (ABA) accumulation is one of the key mechanisms of adaptation to water stress (Brodribb and McAdam 2013). The plant growth regulator, ABA, plays an important role in the response and tolerance against dehydration. It seems that dehydration triggers production of ABA, which induces expression of genes PYL8 (Lim et al., 2013). There are genes that are induced by dehydration and not responsive to exogenous ABA treatments suggesting the existence of ABA independent in addition to ABA-dependent signalling pathways between initial signal of drought stress and expression of specific genes (Ding et al., 2016).

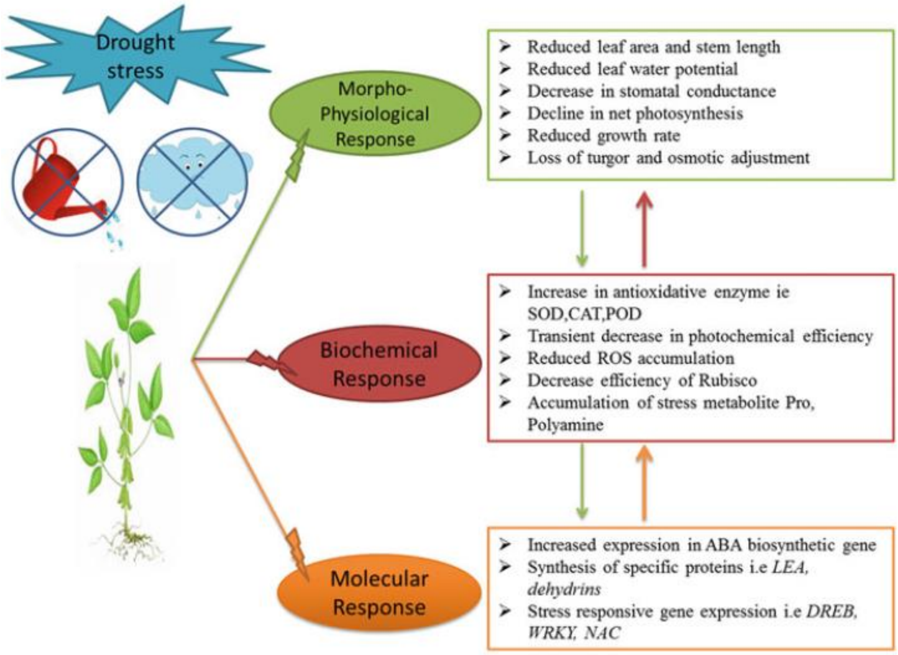

Figure 4.1 Plants' responses under drought stress (after Kumar et al., 2018)

4.1.1. Physiological drought adaptation

4.1.1.1. Stomatal conduct

Stomata are pores found in the epidermis of leaf and stem and participate in exchange of water and gaseous. Stomata (plural of stoma) are usually most abundant on the lower surface of the leaf (Figure 4.2). The word stoma is derived from the Greek *στόμα*, "mouth".

Stomata occur mostly on the lower surface of the leaf and new stomata are generated continually during leaf growth (Zhao et al., 2015). They are of an anomocytic type, lacking distinct subsidiary cells. The epidermal cells are polygonal with waxy anticlinal walls (Karthikeyan *et al*., 2012). The pores are bordered by a pair of specialized cells known as "guard cells". The guard cells are responsible for governing the opening size. The word “stomata” is also used to refer to an entire stomatal complex, both the pore itself and the guard cells (Fig. 4.2). Air containing oxygen and carbon dioxide enters the plant through stomata and is used in respiration and photosynthesis. Water vapor is released into the atmosphere through these pores in a process called transpiration (Taiz and Zeiger, 2002).

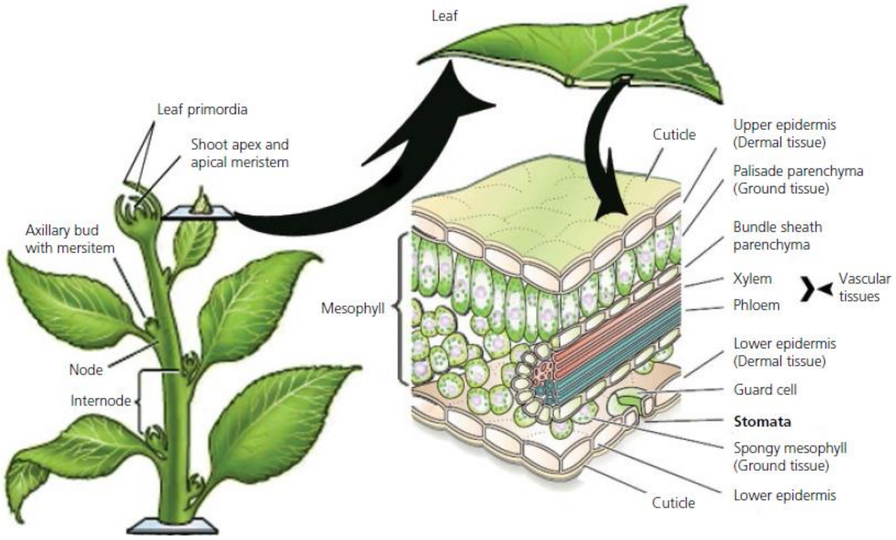

Figure 4.2 Location of stomata in plant leaf, stomata are usually most abundant on the lower surface of the leaf (Taiz and Zeiger, 2002).

Levitt (1976) stated that Stomata perform three major functions in the physiology of plants: (1) they restrict the entrance of CO2 into the green leaf to a rate sufficient to support adequate photosynthesis for normal growth and development. They have become adapted to this function by opening in response to low concentrations of CO2 inside the leaf. (2) They permit the entrance of O2 into the leaf at a rate rapid enough to support aerobic respiration sufficient to provide for metabolic needs. They have become adapted to this function by opening in response to low O2 concentrations inside the leaf. (3) If these were the only functions of the stomata they would fulfill them by remaining constantly open. Accompanying the uptake of CO2 and O2 however, there must also be an increased loss of water vapour, as long as the water potential of the external atmosphere is below that of the leaf (Levitt, 1974).

Drought is a major environmental factor impairing many physiological and metabolic processes in plants, which may lead to suppression of plant growth and development, and even lead to plant death. Across plant species, drought imposes various physiological and biochemical limitations and adverse effects (Pirasteh-Anosheh et al., 2013; Saed-Moucheshi et al., 2014; Chen et al., 2015). Cell growth is the process that is most affected by water deficit. Taiz and Zeiger (2002) reported that under more severe drought conditions inhibition of cell division, inhibition of wall and protein synthesis, accumulation of solutes, closing of stomata, and inhibition of photosynthesis were observed (Fig. 4.3). In these conditions, scientists focus on various aspects of physiology, such as stomata response to drought stress.

Water loss from plant shoot results in an increase in the vapor pressure gradient between the ambient air and leaf, and consequently increased transpiration rate. Increasing water loss from the soil also can occur due to vapor pressure gradient (Torres-Ruiz et al., 2013). Stomata closure does not always depend on the perception of drought stress signals arising from leaves.

Stomatal conductance reduces transpiration and plays essential roles in regulating plant water balance. Stomata closure also reduces cell expansion and growth rate leading to a significant reduction in biomass and yield (Rauf et al., 2015). Many scientists believe that the first reaction of virtually most of the plants to severe drought is the closure of their stomata to prevent the water loss via transpiration (Torres-Ruiz et al., 2013). Stomata closure results from direct evaporation of water from the guard cells with no metabolic action.

Stomatal closure in response to drought stress primarily results in decrease in the photosynthesis rate. The reduction in photosynthesis rate may primarily be due to stomatal limitation and secondarily be due to metabolic impairment. The stomatal limitation is the less complex phenomenon compared to metabolic impairment, though the relative importance of stomatal or metabolic inhibitions are unclear (Clauw et al., 2015).

4.1.1.2. Accumulation of compatible solutes like, prolines and aminoacids

Limited water supply is a major environmental constraint in productivity of plants (Zhu, 2002).In order to overcome the adverse effects of unfavorable drought conditions plants develop various strategies which include accumulation of compatible solutes like, prolines, aminoacids and soluble carbohydrates (Xue 2009; Ghai et al., 2014).

Although environmental stresses act in many forms, however, the most prevalent stresses have in common their effect on several physiological responses including modification of water status, mineral nutrition and reduction in growth rate along with a suite of metabolic changes (Taylor et al., 2004; Yildirim et al., 2006). The availability of water is important for its biological role as a solvent, transport and medium (Rauf et al., 2012). Because the mechanisms to prevent physical damage from mechanical stresses imposed by turgor losses are also important (Weber, 2008), therefore, water stress has been put forth causing the site-specific variation in plant, thus, should be considered in any explanation on sandy soil (Xiong and Zhu, 2002). The decrease in availability of fresh water for agricultural use is a problem common to many areas in the world, as the requirements for food and fuel production from plants increase *(*Miller et al., 2010; Akhtar et al., 2015). Desert plants generally adapt the two major strategies i.e., they tolerate the drought through phonologic and physiological adjustments referred as tolerance and avoidance (Venkateswarlu and Shanker, 2009). Aridity reduces the ability of plants to take up water and causes reduction in growth rate along with metabolic changes (Ali et al., 2011).

For a long time, proline was considered as an inert compatible osmolyte that protects subcellular structures and macromolecules under osmotic stress (Kavi Kishor, et al., 2005). However, proline accumulation can influence stress tolerance in multiple ways (Figure 3). Proline has been shown to function as a molecular chaperone able to protect protein integrity and enhance the activities of different enzymes. Examples of such roles include the prevention of protein aggregation and stabilization of M4 lactate dehydrogenase during extreme temperatures, protection of nitrate reductase during heavy metal and osmotic stress (Sharma and Dubey, 2005), and stabilization of ribonucleases and proteases upon arsenate exposure (Mishra and Dubey, 2006) .Several studies have attributed an antioxidant feature to proline, suggesting ROS scavenging activity and proline acting as a singlet oxygen quencher (Matysik et al., 2002). Proline treatment can diminish ROS levels in fungi and yeast, thus preventing programmed cell death, can protect human cells against carcinogenic oxidative stress, and can and can reduce lipid peroxidation in alga cells exposed to heavy metals [Mehta and Gaur,1999).

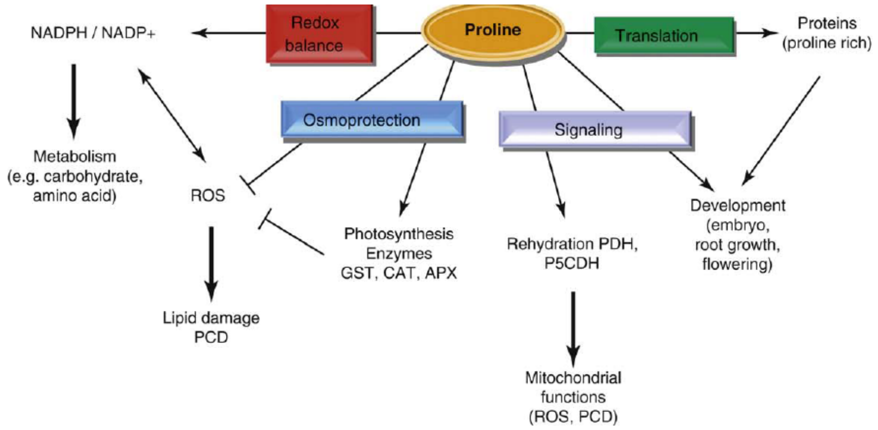

Figure 4.3 Multiple functions of proline in plants, proline is used for protein synthesis, has protective functions as an osmolyte, contributes to the maintenance of the redox balance, can regulate development and is a component of metabolic signaling networks controlling mitochondrial functions, stress relief and development. Abbreviations: APX, ascorbate peroxidase; CAT, catalase; PCD, programmed cell death (after Szabados and Savour, 2009).

As well as having protective or scavenging features, it is feasible that proline metabolism can stabilize cellular homeostasis during stress conditions in a way that is still poorly understood. Although proline is usually considered to be a metabolite with protective functions (Chen and Dickman 2005), several reports show that, under certain conditions, exogenous proline can be deleterious to plants and can inhibit growth and cell division (Maggio., et al. 2002). Proline metabolism can also influence programmed cell death in plants. In Arabidopsis, incompatible plant–pathogen interactions trigger a HR via ROS signals, which is accompanied by local activation of P5CS2 and proline accumulation (Fabro et al., 2004).

4.1.1.3. Allocation of Resources

The growth and allocation of desert plants have attracted a number of researchers owing to the often extreme environmental conditions under which plants grow (Su et al., 2013). Most studies report that the root/shoot ratio in desert plants is much greater than in plants of other ecosystems such as forests and grasslands (Barbour, 1971). The relatively higher biomass allocated to roots in comparison with above-ground parts would in theory provide plants with greater access to moisture and soil nutrients for growth and a smaller surface area for transpiration. Consequently, it should be possible to manipulate soil conditions to favour increases in above-ground biomass allocation if soil nutrient limitations (such as N) are reduced or eliminated. Indeed, in recent years, N deposition rates are increasing in desert ecosystems due to expanding metropolitan centres or large agricultural operations (Fenn et al., 2003). In desert ecosystems, biological activity is limited by water (Noy-Meir, 1973). In addition to water, this ecosystem is also limited by N, which has become the second most important factor influencing plant growth rates, community structure and soil microbial processes (Brook, 2003; Zhou et al., 2011).

In order to cope with this complexity in understanding biomass allocation in a changing environment, two general types of partitioning models have been proposed: optimal partitioning models and allometric models. The former postulates that plants respond to environmental changes by partitioning their biomass to different organs in a manner that permits the acquisition of the most limiting resource(s) such as water, carbon dioxide Nitrogen, or light (Bloom et al. 1985). For example, under light-limiting conditions, plants are predicted to allocate more biomass to the construction of stems and leaves rather than roots in order to maximize or at least increase light capture, whereas factors that limit the acquisition of below-ground resources are predicted to result in increased root growth as opposed to above-ground growth (Gebauer et al. 1996).

Several researches have confirmed desert plants have been found to allocate relatively fewer resources to their vegetative organs than to the reproductive ones (Barbour, 1971; Boaz et al. 1994; Gebauer et al. 1996; Su et al., 2013; Zhou et al., 201). This is consistent with the hypothesis of Noy-Meir (1986), that the first shift to the reproductive stage in desert conditions is triggered by water stress, and with Kozlowski and Wiegert (1986), who proposed a similar response for plants growing under conditions of short seasons and high mortality rates. The pattern is also compatible with previously proposed models (Cohen 1971; Wilson 1983) of maximization of reproduction by an early shift from the vegetative to the reproductive stage.

Drought accelerates the transition from the vegetative to the reproductive phase, and a large proportion of the biomass is then allocated to reproduction. Nonetheless, vegetative growth may continue during the reproductive phase even when a large proportion of biomass is allocated to reproduction. Cohen (1976) has argued that, if vegetative growth is an added advantage to survival or reproductive yield, a prolonged phase of both vegetative and reproductive growth can be expected to take place between the solely vegetative and solely reproductive phases.

4. 2. Photosynthetic Pathways

Photosynthesis, like other metabolic processes follows a specific metabolic pathway. Metabolic pathways can be described as the steps that a biochemical reaction follows in the process of converting molecules into readily usable materials. Photosynthetic pathways therefore refer to the steps involved in photosynthesis. For the three types of photosynthesis; C3, C4, and CAM the pathways followed are basically the same. However, the differences among these arise from the way each plant chooses to carry out photosynthesis. The choice of the type of photosynthesis that a plant would carry out is entirely dependent on the environmental conditions that surround a particular plant.

A photosynthetic pathway is the steps taken by a plant in the process of converting CO2 and water molecules into complex sugars using energy from the sun. The three basic types of photosynthesis are based on two pathways; the light stage reactions and the dark reactions.

During the light reactions, the sun’s energy is absorbed into the plant by the chlorophyll. Once this energy has been absorbed, this energy initiates and drives the transfer of electrons and hydrogen ions from the water absorbed by the plant to the $NADP^+$ which stands for nicotine-amide adenine dinucleotide phosphate (Ziegler et al., 1981). The $NADP^+$ is an acceptor that stores the energized electrons on a temporary basis. This entire reaction results in the splitting of water molecules and the release of the oxygen atom as a byproduct. Once both the hydrogen nucleus and the electrons reach the $NADP^+$, convert it to NADPH by adding the two together. The NADPH thus becomes a reducing agent to be used in the dark reactions. The light reactions also result in the formation of ATP (adenosine triphosphate) which stores the chemical energy that will be used in the next stage.

The dark reactions, also known as the Calvin cycles are the reactions that result in the actual production of the sugars or "food". The process begins by carbon fixation, which is essentially the incorporation or combination of carbon (IV) oxide from the atmosphere into the organic molecules already present in the chloroplasts of the plant cells. The CO2 is then reduced by the NADPH with the energy in the form of ATP. The final products of this reaction are the sugars and $NADP^+$ and ADP[1]. The sugars are then transported by the phloem vessels to storage while the $NADP^+$ and the ADP are recycled to be used again the light reactions. As had been mentioned earlier the three types will follow these basic pathways however, the difference will come in the details of how the processes are carried out, a difference that can be attributed to the environment of the plant.

4.2.1. C4 plants

The C4 photosynthesis differs greatly from the normal photosynthesis in that C4 takes place in the presence of the enzyme Phosphoenolpyruvate carboxylase also known carboxylase. This enzyme differs from rubisco in that it possesses a greater affinity for CO2 than oxygen therefore reducing the possibility of photorespiration. During C4 photosynthesis, CO2 obtained from carbon fixation is reacted with PEP with PEP carboxylase acting as a catalyst. The end result of this process is a 4-carbon acid known as oxaloacetate. The direct consequence of this is that the stomata can be closed for longer periods of time without harming the leaf C4 photosynthesis is therefore the most suited in hot and dry climates (Ellis et al., 1980).

Another distinguishing factor for the c4 reaction is that the reactions do not take place within the same cells. The primary reactions take place in the outer mesophyll cells that have PEP carboxylase and some chloroplasts (Fig. 4.4).

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[1] - Adenozin Dephosphate (ADP)

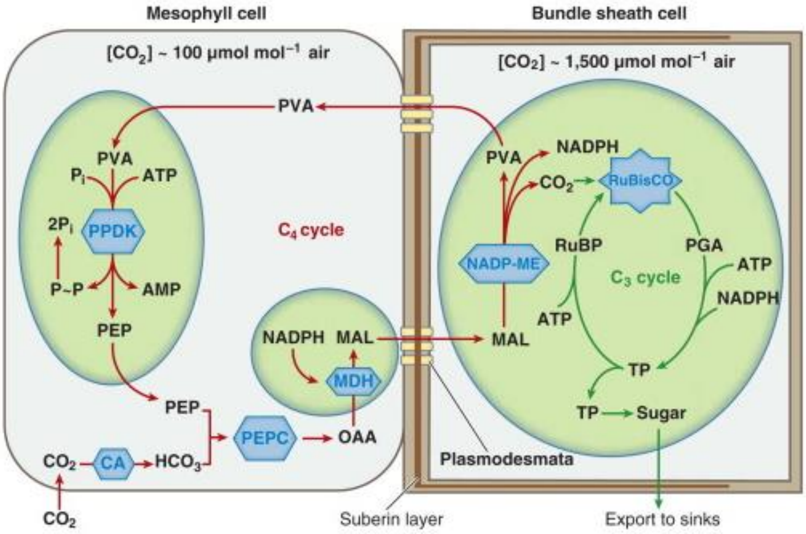

Figure 4.4 C4 photosynthetic pathway (after Kellogg K.A. 2013).

4.2.2. CAM plants

The Crassulacean Acid Metabolism commonly known as CAM bears a great deal of similarity with the c4 photosynthesis. However, the difference presents itself in the timing of the stomatal opening and closing. In this type of photosynthesis, the stomata remain open at night allowing CO2 to diffuse into the leaf and react with PEP to form the oxaloacetate acid which is then stored overnight in the central vacuoles. When day breaks, the acid is released and undergoes a process of decarboxylation to release CO2. The CO2 released is then combined with RuBP just as it does in C3 photosynthesis. A key characteristics of plants that undergo this type of photosynthesis, is that they usually possess thick and fleshy leaves that are purposed to store water or stems that perform the same function (Ellis et al., 1980). These plants are usually associated with the term succulent.

Another characteristic of these plants is that the stored carbon runs out fast and since photosynthesis only takes place for part of the day, very little sugar is produced. This means that plants that grow under these conditions tend to have very slow growth. The CAM photosynthesis is typical of desert plants, due to their slow growth in these harsh conditions, desert plants have evolved very intricate defense systems to protect against animals that would want to take away such slow gains (El-Demerdash, 1994).

4.2.3. C3 plants

Also, referred to as normal photosynthesis in some quarters, C3 pathway is by far the most common type of photosynthetic pathway. In extreme cases, C3 plants have been in the coldest arctic habitats and in the warmest deserts. Although in normal condition these types of plants tend to thrive in areas with ample supply of water. This pathway is called the C3 pathway mainly due to the initial products that are formed at carbon fixation, which are 3-carbon compounds otherwise known as phosphoglyceric acid. During C3 photosynthesis, the CO2 molecules from the carbon fixation are combined with 5-carbon sugars known as ribulose bisphosphate (RuBP) in the presence of the enzyme ribulose bisphosphate carboxylase/oxygenase or in simpler terms rubisco. Rubisco is also responsible for catalyzing the reaction of RuBP with oxygen and leads to photo respiration (Ellis et al., 1980).

Photorespiration occurs when there is too much oxygen present in the plant prompting a reaction with RuBP. Releasing 2-phosphoglycolate which can undergo further metabolism during photorespiration to releases CO2 in daylight. This process results in net reduction I photosynthesis mostly because of the competition between CO2 and oxygen molecules for the active sites of the enzyme rubisco. Once the oxygen molecules populate the active sites of the rubisco, it cannot take up CO2 hence hampering the photosynthetic process (Gowik and Westhoff, 2010).

Photorespiration is especially common in regions with higher temperatures or in hot sunny conditions because of the reduced water presence. Under normal circumstances, the oxygen molecules produced during the light reactions exit through the stomata of the leaves. However, where there is little or no water, the plants will tend to open their stomata less frequently to prevent water loss due to photorespiration. The outcome of this is the oxygen levels may build up within the leaf triggering the competition for the active sites of rubisco therefore leading to photorespiration (Ellis et al., 1980).

4.3. Osmotic pressure and osmoregulation

Drought triggers a wide variety of plant responses (Ajum, 2011). Plant growth is altered, with hanges in the architecture of individuals, which are translated into lower height, reduced leaf size, a smaller number of leaves, less fruit production and changes in the reproductive phase. Osmoregulatory processes generally occurs to protect membrane integrity and maintain the inflow of water to the cell as well as the accumulation of organic solutes as sugars, quaternary ammonium compounds (glycine betaine and alanine betaine) (Ashraf and Foolad, 2007), hydrophilic proteins (late embryogenesis abundant proteins) Chaves et al., 2009), soluble proteins and amino acids (proline) (Silva et al., 2009). Water is the most important substance in the initial phase of plant development from germination and seedling formation to establishment in the field (Jaleel et al., 2009) and a reduction in the water supply in this stage can lead to dehydration and even death.

With the exception of plants which tolerate extreme cellular dehydration (Aspinall, 1980), adaptation to water stress involves the reduction of cell dehydration by either avoidance or tolerance of stress. Some examples of avoidance of water stress are rapid completion of ontogeny, leaf shedding, leaf rolling, and low stomatal conductance to water vapor (Turner, 1979). Tolerance of water stress usually involves the development of low osmotic potentials, which characterize many plant species found in more arid environments. Higher solute levels may be the product of inherent differences in the basal osmotic potential (or osmotic potential measured at full hydration) and solute accumulation in response to water stress, or osmoregulation, which leads to the maintenance of turgor potential and hence continued plant growth.

The term osmotic adjustment is widely used to describe osmoregulation in response to water stress in higher plants where it is also used to describe changes in solute content after recovery from water stress. To maintain consistency with previous reviews in this series and with the extensive work on solute changes in lower plants, the term osmoregulation will be used generally in this review, though its use is not confined to responses to water deficits (Aspinall, 1980). Instances where turgor potential is fully or almost fully maintained are also considered evidence of osmoregulation since such effects cannot be attributed to cell wall elasticity alone. Turgor potential is partially or fully maintained by osmoregulation during water stress by a reduction in the outflow of water from the cell. However, when water is lost, the rate of change in turgor potential with change in water potential is also affected by the elasticity of the cell wall (Zimmermann, 1978).

The maintenance of turgor which results from osmoregulation also must involve maintenance of hydration, though the more specific relationship between these two factors depends on the elasticity of the cell walls (Wenkert et al., 1978). Thus, even after turgor is lost, a leaf or other organ with higher osmoregulation will have higher water content at low water potential levels.

Water stress in the plant is the result of both reductions in the soil water potential Ψs, which usually occurs progressively over a period of time, and fluctuation in evaporation rate E, which occurs with daily changes in net radiation and humidity.

The general qualitative relationship is:

$\Psi = \Psi s - Re$

Where, Re is the resistance to water flow in the plant. The increase in solutes which occurs with reduction in water potential eventually reaches a limit which varies with species and plant part. It is more obvious where full turgor maintenance occurs.

The rate at which solutes accumulate may vary, however, from being equal to or even exceeding the rate of change of water potential to being only a small fraction of that change (Morgan, 1980).

4.3.1. Factors affecting osmoregulation

4.3.1.1 Organ Type and Age

Osmoregulation invariably occurs in response to a decline in water potential in expanding organs such as roots, leaves, hypocotyls, and inflorescences, where it plays an important role in maintaining the inflow of water during expansion growth. When expansion is complete, the capacity for osmoregulation may be gradually lost. Leaves which reach full expansion later in the ontogeny of determinate species such as wheat may have a greater capacity for osmoregulation than those formed earlier (Condon, 1982).

4.3.1.2 Environmental Effects

The degree of osmoregulation is affected by both the rate of stress and stress preconditioning. It is usual to express the rate of stress as the change in water potential per day, using measurements made at one time of day. There is evidence that plants which have been previously exposed to water stress show an improved capacity to tolerate subsequent periods of water stress through increases in solute levels. Other environmental factors which are known to affect osmoregulation are light intensity and atmospheric CO2 concentration. Increases in CO2 concentration led to a marked improvement in the maintenance of leaf turgor in wheat exposed to water stress, with a decrease in osmotic potential.

4.3.1.3. Osmotic Constituents

Sugars and amino acids are major constituents of osmoregulation in expanded leaves of many species (Ackerson, 1981) and also in expanding hypocotyls (Michelena and Boyer, 1982) and inflorescences (Barlow et al., 1997). In expanding organs, osmoregulation is entirely dependent on the import of solutes which is, in turn, dependent on rates of photosynthesis.

For a supply of assimilate to be maintained, phloem transport must also be unaffected by water stress, and indeed osmoregulation also occurs in sieve tubes (Smith and Milburn, 1980). In expanded leaves, increase in sugars and amino acids presumably results from a difference between rate of fixation of carbon and rate of export (Karami et al., 1980), though the basis of differences in osmoregulation between cultivars is not clear. Changes in potassium may also contribute substantially to osmoregulation (Ford and Wilson, 1981) and may occur in concert with changes in sugars and amino acids, possibly balancing negative charges on amino acids. Other solutes which may contribute to small changes in osmoregulation are organic acids (malate, citrate), nitrate, and chloride ions (Jones et al., 1980).

4.3.1.4. Effect of water deficit on cellular processes

The normal survival mechanisms are not sufficient to secure plant life under such conditions. Thus, the protoplasmic components of the cells of perennial desert plants active in summer have specialized features that distinguish the respective plants from those of mesic regions. However, nobody can say which component of the protoplasm is most effective in this respect, and which is destroyed by the extreme conditions prevailing in the desert. Bewley and Krochko (1982) stated that "Water deficits can affect cellular processes in one or more of the following ways; (1) through a decrease in turgor pressure; (2) by a reduction of the chemical potential or activity of water in cells; (3) by changes in spatial relations in membranes and organelles resulting from decrease in volume of the protoplasm; (4) by effects of increase in solute concentrations caused by losses of water; (5) by alteration of structure of macromolecules resulting from dehydration.

The tensions occasioned by desiccation act not so much on the surface layer of protoplasm but rather within the internal protoplasm. Protoplasm consists of a latticework of threadlike proteins interspersed with water, salts, sugars, and various proteins. The initial cellular responses to water stress, which he termed "the reaction phase", result in an unequal hydration capacity of different parts of this protein framework. This leads to disorganization and loosening of the protein latticework as water is withdrawn, resulting in a reduction in the viscosity of the protoplasm and an increase in its permeability. If drying is gradual enough, the cell subsequently enters a phase of restitution or restoration during which protoplasmic bonds are strengthened, a reorganization of the protein latticework occurs, and viscosity increases. These changes result in overcompensation of the drought reaction and the plant enters a hardened condition. During rapid drying, the plant is prevented from completing the restitution phase; consequently there is an increase in drought–associated injury. In plants that are able to recover from air-drying, Stocker postulated a reactivation phase following remoistening that repairs the damage caused by desiccation.

Under osmotic stress plants produce organic osmolytes from a group of soluble sugars, such as fructose or sucrose, organic alcohols, such as *myo*-inositol, complex sugars, such as trehalose or fructans or amino acids, such as proline and modified amino acids, such as glycine betaine (Kido et al., 2013). These compounds could also function as chaperone-like molecules stabilizing membranes and maintaining the activity and stability of the enzymes crucial for a proper functioning of cell metabolism (Xoconnostle et al., 2010).

4.4. Response to Heat Stress

Over-heating is one of the main problems faced by desert plants. Unable to cool their leaves by increased evapotranspiration, they undergo a range of morphological changes that reduce heat loads as well as of physiological adaptations that permit tolerance of higher temperatures. Overheating is avoided by: (1) increasing the surface area for heat dissipation; (2) protecting the plant surface from direct sunlight; and (3) increasing the reflectance of the surface.

All these effects can be accomplished by covering the surface of the plant with a dense felt of hairs. These hairs also produce a boundary layer of still air next to the stomata that traps moisture and reduces evapotranspiration.

Hairs may also have a role in defense against herbivorous insects. Not all xerophytic plants are hairy, however, and some desert species have completely hairless, smooth surfaces. In these cases, water loss is restricted by a thick covering of wax, or by modifications of the walls of the epidermal cells (Cloudsley-Thompson 1996).

Plants interact with not only climatic factors (such as irradiation, temperature, and drought) but also soil factors (such as salinity) and biotic factors (such as herbivores and pathogens). All these factors put the plant under interrelated stresses (Levitt, 1980). Moreover, daily sudden changes in the temperature and the presence of heavy metals, toxins, and oxidants due to human activities could result in extra stresses on plants (Vierling, 1991).

Basic Stresses such as drought, salinity, temperature, and chemical pollutants are simultaneously acting on the plants causing cell injury and producing secondary stresses such as osmotic and oxidative ones (Wang et al., 2003). Plants could not change their sites to avoid such stresses, but have different ways and morphological adaptations to tolerate these stresses. Some of these are, the dominance of sporophyte that embraces the sensitive gametophyte, the presence of epidermis with stomata for gases exchange, the formation of dormant organs, and the presence of conducting tissues for long distant trans-port. Other ways of defense at the molecular level are very important for the survival and growth of plants. Plants show a series of molecular responses to these stresses. The physiological processing basis for these molecular responses will not be covered here as it has been reviewed in depth lately (Shao et al., 2007a).

Heat stress as well as other stresses can trigger some mechanisms of defense such as the obvious gene expression that was not expressed under ‘‘normal’’ conditions (Feder, 2006). In fact, this response to stresses on the molecular level is found in all living things, especially the sudden change sin genotypic expression resulting in an increase in the synthesis of protein groups. These groups are called ‘‘heat-shock proteins’’ (HSPs), ‘‘Stress-induced proteins’’ or ‘‘Stress proteins’’ (Gupta et al., 2010). Almost all kinds of stresses induce gene expres-sion and synthesis of heat-shock proteins in cells that are subjected to stress (De Maio, 1999). In Arabidopsis and some other plant species low temperature, osmotic, salinity, oxidative, desiccation, high intensity irradiations, wounding, and heavy metals stresses were found to induce the synthesis of HSPS (Swindell et al., 2007). However, stressing agents lead to an immediate block of every important metabolic process, including DNA replication, transcription, mRNA export, and translation, until the cells recover (Biamonti and Caceres, 2009). It was known a long time ago that the most damage to crop plants in fields occurs when two or more stresses are prevailing (Mittler, 2006). Hence, in order to study the plant tolerance, it is very necessary to mimic the natural conditions in a specific area. Most recent studies indicate that the plant responses to two or more factors are unique and differ from the response to one factor only. For example, subjecting the plants to drought only leads to high content of proline, but subjecting the same species to drought combined with high temperature leads to high content of sucrose and other sugars, but not pro-line. Hence, Mittler (2006) studying all prevailing abiotic factor; [s has suggested to treat this situation as a new stress condition that he called ‘‘Stress combination’’. The mechanisms of plant tolerance to a combination of diverse stress conditions, particularly those that mimic the field environment, have gained interest particularly for the biotechnologists (Munns, 2005; Shao et al., 2007b). Heat stress – high temperature – affects the metabolism and structure of plants, especially cell membranes and many basic physiological processes such as photosynthesis, respiration, and water relations (Wahid et al., 2007). On the molecular level, this effect of heat stress reflects the temperature dependence of Michaelis-Menton constant (Km) of every enzyme participating in the process (Mitra and Bhatia, 2008). Plants must cope with heat stress for survival, so they developed different mechanisms including the maintenance of cell membrane stability capturing the reactive oxygen species (ROS), synthesis of anti-oxidants, accumulation and osmoregulation of osmoticum, induction of some kinases that respond to stress, Ca-dependentkinase proteins, and enhancing the transcription and signal transfer of chaperones.The induction and synthesis of heat-shock proteins due to high temperature exposure are common phenomena in all living organisms from bacteria to human beings (Gupta et al., 2010). It seems that the synthesis of these proteins is costly energy wise that is reflected on the yield of the organism.

4.4.1. Role of heat-shock proteins

The function of any protein is determined by its formation and folding into three dimensional structures (Levitt et al., 1997). Formation of three dimensional structures requires 50% of principle amino acids sequence. That is where the role of HSPS in the folding of other proteins is important. Morimoto and Santoro (1998) indicated that HSPS protect cells from injury and facilitate recovery and survival after a return to normal growth conditions. On the other hand, Timperio et al. (2008) specified that upon heat stress, the role of HSPS as molecular chaperones is without doubt, their function in non-thermal stress could be different: unfolding of proteins is not the main effect and protection from damage could occur in an alternative way apart from ensuring the maintenance of correct protein structure. It has been suggested that HSPS general role is to act as molecular chaperones regulating the folding and accumulation of proteins as well as localization and degradation in all plants and animal species (Hu et al., 2009; Gupta et al., 2010). These proteins, as chaperones, pre-vent the irreversible aggregation of other proteins and participate in refolding proteins during heat stress conditions (Trippet al., 2009). Each group of these Hsps has a unique mechanism and the role of each is briefed.

4.4.2. Heat-shock proteins classification

Historically, the observation of the Italian Scientist R. Ritossa on gene expression of the puffing in the chromosomes of Drosophila melanogaster after exposure to heat was the start of discovering the heat-shock proteins. The result was an increase in protein synthesis that occurred also by the use of other stress factors such as azide, 2, 4-

dinitrophenol, and salicylate. After that report, these proteins were identified and named as heat-shock protein (HSP) (Tissieres et al., 1974). Researchers started studying the relationship of the synthesis of these proteins with the tolerance of stresses. On the other hand, it was reported that the induction of HSPS synthesis in Glycine max var. Wayne seedlings is accompanied by the reduction of other proteins synthesis after the exposure of such seedlings to heat shock (from 28 to 45 °C) for 10 min (longer periods killed the seedlings). Moreover, subjecting the seedlings to flashes of heat at 40 °C before exposing them to higher temperatures (45 °C) protects the seedlings (Lin et al., 1984).

Many types of Hsps have been identified in almost all organisms (Bharti and Nover, 2002). All Hsps are characterized by the presence of a carboxylic terminal called heat-shock domain. Heat-shock proteins having molecular weights ranging from 10 to 200 KD[1] are characterized as chaperones where they participate in the induction of the signal during heat stress (Schoffl et al. 1999).

In plants, general reviews (Kotak et al., 2007) suggested five principal classes of Hsps characterized by their activities as molecular chaperones according to their approximate molecular weight: (1) HSPs 100, (2) HSP 90, (3) HSP 70, (4) HSP 60, and (5) small heat-shock proteins (sHSPs). Recently, another review (Gupta et al., 2010) put the heat-shock proteins into families according to their molecular weight, amino acid sequence homologies and functions: Hsp100 family, H HSP 90 family, HSPS 70 family, HSPS 60 family, and the small HSP family (Hamilton et al., 1996). The most studied species of plants is Arabidopsis thaliana where the response to heatshock treatment occurs through the participation of a number of different HSPs:

- 13 (HSP20)
- 8 (HSP70)
- 7 (HSP90)
-8 (HSP100)
- 21 transcription factors (HSFs) (Swindell et al., 2007), but in tomato there are at least 15 HSFs (von Koskull-Döring et al., 2007).

Higher plants are characterized by the presence of at least 20 types of sHSPs, but one species could contain 40 types of these sHSPs

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[1] - kilodalton (KD)

(Vierling, 1991). Small HSPs (sHSPs), which are usually undetectable in plant cells under physiological conditions, are induced upon stress and plant tolerance to stress, including drought, salinity, oxidized species, and low temperatures (Zhang et al., 2008). It is believed that this diversification and abundance of the sHSPs in a plant reflect an adaptation of the plant to heat stress (Waters et al., 1996).

4.5. Foliar water Uptake of Water

Foliar water uptake (FWU) has been established as a common process that varies among individuals, populations, species, and ecosystems. At least 233 species spanning 77 plant families and 6 major biomes have demonstrated some capacity for FWU. The capacity for FWU also seems to be nearly universal; it has been observed in more than 85% of species studied. This process has received increasing attention in the plant sciences, with rapid growth in both the number of peer-reviewed articles and the citation of those articles. Despite the considerable interest in research on FWU and increasing recognition of the role it may play in plant, community, and ecosystem functioning, our understanding of when, where, and how FWU occurs in leaves remains limited (Goldsmith et al., 2013).

4.5.1. Physical and biological requirements of foliar water uptake

Generally, the internal structures of a leaf are assumed to be nearly or completely saturated with water (high water potential; Cernusak et al. 2018) and the atmosphere is typically unsaturated (low water potential), resulting in a net efflux of water (i.e. transpiration). For water to flow into the leaf, the driving gradient of water potentials must be reversed, *i.e.*, the leaf water potential must be more negative than the atmosphere immediately surrounding the leaf (Rundel 1982). If water crosses the leaf boundary as vapor then it is instead driven by the vapor concentration gradient instead of water potentials. Atmospheric conditions are more typically measured as vapor pressure deficit, the difference in vapor pressure between saturation and ambient conditions for pure water at a given temperature. Comparing vapor pressure deficits with atmospheric water potentials can provide insights into the conditions necessary for FWU. The water potential of the surrounding air quickly becomes more negative than typical values for leaves at very low vapor pressure deficits. For instance, at 25 °C, the water potential of the air drops below -4 MPa at

0.036 kPa vapor pressure deficit (97% relative humidity). Leaf temperature (relative to air) will also influence the leaf to air vapor pressure deficit. As leaves elevate above air temperature, the vapor pressure gradient increases which would result in greater FWU when leaves are wet. A reversal of this gradient leading to FWU can occur by increasing the vapor in the air surrounding the leaf surface or by reducing the water potential inside the leaf (Vesala et al. 2017).

The vapor pressure of the air reaches saturation due to changes in weather conditions. Foliar water uptake has been demonstrated during periods when the air is saturated and liquid water forms on leaves, such as during rain and mist (Steppe et al. 2018), fog and dew. However, there is also evidence of FWU of water vapor during periods where the air has not condensed to liquid water. Vapor uptake would be driven by vapor pressure and require the intercellular air space immediately within the leaf cuticle to have a lower vapor pressure than the vapor pressure of the air. This routinely occurs in leaf air spaces due to negative water potentials and the Kelvin effect reducing the vapor pressure (Cernusak et al., 2018). However, any movement from intercellular air space into cells would require liquid water and would need to consider the resistance of a phase change from vapor to liquid.

Leaf surface properties can affect the vapor pressure at the leaf to air interface in ways that can also alter leaf wetness and FWU. Chemical structure of cuticular waxes, stomatal structure, trichomes, leaf hairs, and endophytes have all been shown to affect water retention on leaf surfaces (Wagner et al. 2003, reviewed by Rosado and Holder 2013). Thicker wax layers decrease leaf water retention by increasing the roughness of the surface (Taylor, 2011), while trichomes and leaf hairs also appear to decrease retention in a similar manner (Pierce at al 2001). However, these relationships are not always robust, as some succulent species with hydrophilic trichomes can actually increase retention and enhance leaf wetness (Grammatikopoulos and Manetas, 1994). Fernandez et al. (2017) highlights the diversity in the chemical and structural components of leaf surfaces and their potential implications for maintaining wet leaf surfaces. Cuticular properties that differ among leaves and across species will result in variation of boundary layer conditions that may promote differential fluxes of FWU.

The most important benefit of dew under arid conditions is that it can provide a reasonable supply of water through the superficial roots. The effect of dew in decreasing transpiration is especially important during the early morning.

Water uptake from the atmosphere is generally restricted to Poikilohydric plants, since the cuticle of homeohydric plants, which is effective in restricting water loss, is also an effective barrier again water uptake. The hydration of vascular plants by dew may occur to a small extent (e.g. Kerr and Beardsell 1975). In this issue, more investigation is needed.

Dew formation is common in many regions of the world, but in arid and semiarid regions dew may represent an important water source for plants (Jacobs et. al. 1999). Dew is formed when the temperature of leaves is below dew point and relative humidity reaches values between 99 and 100% (Ben-Asher *et al*. 2010). Under these conditions, the water vapour in the air in contact with the cold surfaces of leaves condenses and forms dew (Agam and Berliner 2006).

Once deposited on leaves it can be absorbed (Andrade 2003) and benefit the plant by increasing water potential and gas exchanges. Leaves can absorb dew water by different structures, such as leaf indumentum, thickened walls rich in pectic substances, and mucilage secretion (Fahn and Cutler 1992). The water absorbed this way contribute to the maintenance of plant tissue hydration and transpiration control (Abdulrahaman and Oladele 2011) and is fundamental for the survival of plants in arid and semiarid regions as the water resources are limited and the plants should explore this window of opportunity to maintain the production of photo-assimilates (Dombroski et al. 2011).

References

Abdulrahaman A.A., Oladele FA (2011) Response of trichomes to water stress in two species of *Jatropha*. Insight Botany 1: 15–21. doi:10.5567/BOTANY-IK.2011.15.21

Ackerson R.C., 1981. Osmoregulation in cotton in response to water stress. II. Leaf carbohydrate status in relation to osmotic adjustment. Plant Physiol. 67: 489-93.

Agam N., Berliner P.R. (2006) Dew formation and water vapor adsorption in semi-arid environments a review. Journal of Arid Environments 65: 572–590.
Doi: 10.1016/j.jaridenv.2005.09.004

Ahmad P., 2016. Water Stress and Crop Plants: A Sustainable Approach, Volume 1. In: Stomatal responses to drought stress. Eds. Pirasteh-Anosheh H., Saed-Moucheshi A., Pakniyat H., Pessarakli M. John Wiley & Sons, Ltd.

Ajum S.A, Xie X.Y., Wang L.C., Saleem M.F., Man C., Lei W. (2011) Morphological, physiological and bioche.mical responses of plants to drought stress. African Journal of Agricultural, 6(9):2026-32.

Akhtar K., Khan Z.I., Ahmad K., Ashraf M.Y., et al, (2015) Effect of drought stress on change in concentration of compatible solutes in Cholistan desert grasses. Int. J. Agric. Appl. Sci., 7(2):182-188.

Ali A., M. Afzal, I. R.Noorka, E. Safdar, M.Ahmad, (2011) Sunflower (*Helianthus annuus* L.) hybrids performance Ψ at different plant spacing under agro-ecological conditions of Sargodha, Pakistan. Int. Confer. on Food Engineering and Biotechnology. IPCBEE 9: 317-322 .IACSIT Press, Singapore

Andrade J.L. (2003) Dew deposition on epiphytic bromeliad leaves: an important event in Mexican tropical dry deciduous forest. Journal of Tropical Ecology 19: 479–488. Doi:10.1017/S0266467403003535

Ashraf M., Foolad M.R. (2007) Roles to glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany, 59: 206-216.

Ashraf M., Foolad M.R. (2007) Roles to glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany, 59: 206-216.

Aspinall, D. (1980) Role of hormones in adaptation to water stress. In Adaptation of Plants to Water and High Temperature Stress, ed. N. C. Turner, P. J. Kramer, pp. 155-72. New York: iley-Inter-science.

Barbour M.G. (1971) Desert dogma reexamined: root–shoot productivity and plant spacing. American Midland Naturalist, 89: 41–57.

Barlow E.W.R., Munns R., Scott N.S., Reisner A.H. (1977) Water potential, growth and polyribosome content of the stressed wheat apex. J. Exp. Bot. 2S: 909-16.

Ben-Asher J., Alpert P., Ben-Zvi A. (2010) Dew is a major factor affecting vegetation water use efficiency rather than a source of water in the eastern Mediterranean area. *Water Resources Research* 46, W10532. Doi: 10.1029/2008WR007484

Bewley J.D., Krochko J.E. (1982) Desiccation tolerance. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds.) Physiological plant ecology II. Water relations and assimilation. Springer, Berlin

Bharti K., Nover L., (2002) Heat stress-induced signaling, In: Scheel, D., Wasternack, C. (Eds.), Plant Signal Transduction: Frontiers in Molecular Biology. Oxford University Press, Oxford, UK. , pp. 74-115.

Biamonti G., Caceres J.F., (2009) Cellular stress and RNA splicing. Trends Biochem. Sci., 34: 146–153.

Bloom A.J., Chapin F.S., Mooney H.A. (1985) Resource limitations in plants (an economic analogy). Annual Review of Ecology and Systematics, 16:363–392.

Brodribb T.J., McAdam S.A.M. (2013) Abscisic acid mediates a divergence in the drought response of two conifers. Plant Physiol. 162:1370–1377.

Brooks M.L. (2003) Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. Journal of Applied Ecology, 40:344–353.

Cernusak L.A., Ubierna N., Jenkins M.W., et al, (2018) Unsaturation of vapour pressure inside leaves of two conifer species. Scientific Reports, 8: num. 7667. Doi.org/10.1038/s41598-018-25838-2.

Chaves M.M., Maroco J.P., Pereira J.S. (2003) Understanding plant response to drought: from genes to whol plant. Functional Plant Biology, 30: 239–264

Chen Y., Yu J., Huang B. (2015) Effects of elevated CO2 concentration on water relations and photosynthetic responses to drought stress and recovery during rewatering in tall fescue. J. Amer. Soc. Horticul. Sci., 140: 19–26.

Chen, C. and Dickman, M.B. (2005) Proline suppresses apoptosis in the fungal pathogen Colletotrichum trifolii. Proc. Natl. Acad. Sci. U.S.A.102: 3459–3464

Clauw P., Coppens F., De Beuf K., Dhondt S., Van Daele T., Maleux K., Inze D. (2015) Leaf responses to mild drought stress in natural variants of Arabidopsis thaliana. Plant Physiol. DOI: 10.1104/pp.114.254284

Cloudsley-Thompson J.L. (1996) Biotic intercations in arid lands. Springer, Berlin Heidelberg

Condon, A. G. (1982) Water relations and osmotic adjustment in wheat as influenced by water stress history and plant development. MS thesis. University of Sydney, Sydney, Austra.

Cohen D. (1976) Maximizing final yield when grow is limited by time or by limiting resources. Journal of Theorical Biology, 33: 299-307.

Conesa M.R., Rosa J.M., Domingo R., Banon S., Perez-Pastor A. (2016) Changes induced by water stress on water relations, stomatal behavior and morphology of table grapes (cv. Crimson seedless) grown in pots. Sci. Hort. 202:9-16.

De Maio A., (1999) Heat shock proteins: facts, thoughts, and dreams. Shock (Augusta, Ga.) 11: 1–12.

Ding W., Fang W., Shi S., Zhao Y., Li X., Xiao K. (2016) Wheat WRKY type transcription factor gene TaWRKY1 is essential in mediating drought tolerance associated with an ABA-dependent pathway. Plant Mol. Biol. Report 34:1111–1126.

Dombroski J.L.D., Praxedes S.C., de Freitas R.M.P., Pontes F.M. (2011) Water relations of Caatinga trees in the dry season. South African Journal of Botany 77: 430–434. Doi:10.1016/j.sajb.2010.11.001

El-Demerdash M.A., Hegazy A.K., Zilay A.M. (1994) Distribution of the plant communities in the Tihamah coastal plains of Jazan region. Journal of Vegetation and Distribution, 112(2): 141-151

Ellis R., Vogel, J.C., Fuls A. (1980) Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. South African Journal of Science, 76(7): 307-314.

Fabro, G. et al. (2004) Proline accumulation and AtP5CS2 gene activation are induced by plant-pathogen incompatible interactions in Arabidopsis. Mol. Plant–Microbe Interact.17: 343–350.

Fernández V., Sancho-Knapik D., Guzmán P., Peguero-Pina J.J., Gil L., Karabourniotis G., Khayet M., Fasseas C., Heredia-Guerrero J.A., Heredia A., Gil-Pelegrín E. (2014) Wettability, polarity, and water absorption of Holm oak leaves: effect of leaf side and age. Plant Physiology 166: 168–180. Doi:10.1104/pp.114.242040

Feder M.E., (2006) Integrative biology of stress: molecular actors, the ecological theater, and the evolutionary play. International Symposium on Environmental Factors, Cellular Stress and Evolution, Varanasi, India, October 13–15, 2006, p. 21.

Fenn M.E., Baron J.S., Allen E.B., et al., (2003) Ecological effects of nitrogen deposition in the western United States. Bioscience, 53:404–420.

Fernández V., Bahamonde H.A., Peguero-Pina, J.J., et al., (2017) Physico-chemical properties of plant cuticles and their functional and ecological significance. *Journal of Experimental Botany*, 68(19): 5293–5306. Doi.org/10.1093/jxb/erx302.

Ford C.W., Wilson J.R. (1981) Changes in levels of solutes during osmotic adjustment to water stress in leaves of four tropical pasture species. Aust. J. Plant Physiol. 8:77-91.

Gebauer R.L.E., Reynolds J.F., Strain B.R. (1996) Allometric relations and growth in *Pinus taeda*: the effect of elevated CO_2 and changing N availability. New Phytologist, 134:85–93.

Functional Plant Biology, 30: 239-264 C., Sangster T.A., Lindquist S. (2002) Hsp90 as a capacitor of phenotypic variation. Nature, 417: 618-624

Ghai N., R. Kaur, K. Pahwa, J. Kaur, I. Singh, (20140) Ameliogical and biochemical attributes in mashbeans (V*igna mungo* L. Hepper) under NaCl stress. Int. J. Adv. Res. 3(2): 942-955.

Goldsmith G.R., Matzke N.J., Dawson T.E. (2013) The incidence and implications of clouds for cloud forest plant water relations. Ecology Letters, 16(3): 307-314. doi.org/10.1111/ele.12039.

Gowik U., Westhoff P. (2010) The Path from C3 to C4 Photosynthesis. Plant Physiology 155(1): 56-63.

Grammatikopoulos G., Manetas Y. (1994) Direct absorption of water by hairy leaves of *Phlomis fruticosa* and its contribution to drought avoidance. Canadian Journal of Botany, 1805-1811.

Gupta S.C., Sharma A., Mishra M., Mishra R., Chowdhuri D.K., 2010. Heat shock proteins in toxicology: how close and how far? Life Sci., 86: 377–384.

Hamilton E.W., Heckathorn S.A., Downs C.A., Schwarz T.E., Coleman J.S., Hallberg R.L., (1996) Heat shock proteins are produced by field-grown naturally occurring plants in the summer Heidelberg New York, pp 325-378.

Hu W., Hu G., Han B., (2009) Genome-wide survey and expression profiling of heat shock proteins and heat shock factors revealed overlapped and stress specific response under abiotic stresses in rice. Plant Sci. 176: 583–590.

Jacobs A.F.G., Heusinkveld B.G., Berkowicz S.M. (1999) Dew deposition and drying in a desert system: a simple simulation model. Journal of Arid Environments 42: 211–222. Doi:10.1006/jare.1999.

Jaleel C.A., Manivannan P., Wahid A., Farooq M., Al-Juburi H.J., Somasundaram R., Vam R.P. 2009. Drought stress in plants: a review on morphological characteristics and pigments composition. International Journal of Agriculture and Biology, 11(1):100-105.

Jones M.M., Osmond C.B., Turner N.C. (1980) Accumulation of solutes in leaves of sorghum and sunflower in response to water deficits. Aust. Plant Physiol. 7: 193-205

Karami E., Krieg D.R., Quisenberry J.E. (1980) Water relations and carbon-14 similation of cotton with different leaf morphology. Crop Sci., 20: 421-26

Karthikeyan R., Venkatesh P., Chandrasekhar N. (2012) Morpho anatomical studies of leaves of Abutilon indicum (linn.) sweet. Asian Pac. J. Trop. Biomed., 10: 464-469.

Kavi Kishor, P.B. et al, (2005) Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: its implications in plant growth and abiotic stress tolerance. Curr. Sci., 88: 424–438.

Kellogg K.A. (2013) C4 photosynthesis. Current biology, 23 (14): 594-599.

Kido E.A., Ferreira Neto J.R., Silva R.L., et al. (2013). Expression dynamics and genome distribution of osmoprotectants in soybean: identifying important components to face abiotic stress. BMC Bioinformatics 14(Suppl. 1): S7. Doi: 10.1186/1471-2105-14-S1-S7.

Kotak S., Larkindale J., Lee U., et al, (2007) Complexity of the heat stress response in plants. Curr. Opin. Plant Biol. 10: 310–316.

Kramer, P.J. (1980) Drought, stress, and the origin of adaptations. In: Adaptation of Plants to Water and High Temperature Stress. Eds. N.C. Turner and P.J. Kramer. John Wiley and Sons, New York, pp 7-20.

Kumar S., Sachdeva S., Bhat K.V, Vats S. (2018) Biotic and Abiotic Stress Tolerance. In: Vats S. (Ed.): In Plant Responses to Drought Stress: Physiological, Biochemical and Molecular Basis. Springer, Singapore, PP. 1-27.

Levitt J. (1980) Responses of Plant to Environmental Stress Water, Radiation, Salt and Other Stresses. Academic Press, New York, 365.

Levitt J., (1980) Responses of Plants to Environmental Stresses, vol. II. Water, Radiation, Salt and Other Stresses, second ed. Academic Press Inc., New York, London.

Levitt, J. (1974) The mechanism of stomatal movement-once more. Protoplasma 82**:** 1–17.

Lim CW, Baek W, Han SW, Lee SC (2013) Arabidopsis PYL8 plays an important role for ABA signaling and drought stress responses. J. Plant Pathol. 29(4):471–476.

Lin C.Y., Roberts J.K., Key J.L., (1984) Acquisition of thermotolerance in soybean seedlings: synthesis and accumulation of heat shock proteins and their cellular localization. Plant Physiol. 74:152–160.

Maggio, A. et al. (2002) Does proline accumulation plays an active role in stress-induced growth reduction? Plant J., 31: 699–712.

Matysik J., Alia, Bhalu B., Mohanty P. (2002) Molecular mechanisms of quenching of reactive oxygen species by proline under stress in plants. Curr. Sci., 82(5): 525–532

Mehta, S.K. and Gaur, J.P. (1999) Heavy-metal induced proline accumulation and its role in ameliorating metal toxicity in Chlorella vulgaris. New Phytol. 143: 253–259.

Michelena A., Boyer, J. S. (1982) Complete turgor maintenance at low water potentials in the elongating region of maize leaves. Plant Physiol. 69: 1 145-49

Miernyk J.A. (1999) Protein folding in the plant cell. Plant Physiol., 121: 695-703.

Mishra, S. and Dubey, R.S. (2006) Inhibition of ribonuclease and protease activities in arsenic exposed rice seedlings: role of prolineas enzyme protectant.J Plant Physiol.163: 927–936.

Mitra, R., Bhatia, C.R., (2008) Bioenergetic cost of heat tolerance in wheat crop. Curr. Sci., 94: 1049–1053.

Mittler R., 2006. Abiotic stress, the field environment and stress combination. Trends Plant Sci. 11: 15–19.

Morgan, J. M. (1980) Osmotic adjustment in the spikelets and leaves of wheat. Exp. Bot., 3(1):655-65.

Morimoto R.I., Santoro M.G. (1998) Stress-inducible responses and heat shock proteins: new pharmacologic targets for cytoprotection. Nat. Biotechnol., 16: 833–838.

Munns R. (2005) Genes and salt tolerance: bringing them together. New Phytol., 167: 645–663.

Noy-Meir I. (1973) Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics, 4:25–51.

Parsell D.A., Lindquist S. (1993). The functions of heat-shock proteins in stress tolerance: degradation and reactivation of damaged proteins. Ann. Rev. Genet. 27:437-496.

Passioura J.B. (1982) Water in the soil Plant atmosphere continuum. In Physiological Plant Ecology II. Water Relations and Carbon Assimilation. Encyclopedia of Plant Physiology, New Series, Vol. 12B. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, Berlin, Heidelberg, pp. 5-33.

Pierce S., Maxwell K., Griffiths H., Winter K. (2001) Hydrophobic trichome layers and epicuticular wax powders in Bromeliaceae. American Journal of Botany, 88(8): 1371–1389. Doi.org/10.2307/3558444.

Pirasteh-Anosheh H., Emam Y., Pessarakli M. (2013) Changes in endogenous hormonal status in corn (*Zea mays*) hybrids under drought stress. J. Plant Nut., 36: 1695–1707.

Queitsch C., Sangster T.A., Lindquist S. (2002) HSP90 as a capacitor of phenotypic variation.
Nature, 417: 618-624

Rauf S., Al-Khayri J.M., Zaharieva M., Monneveux P., Khalil F. (2015) Breeding strategies to enhance drought tolerance in crops. In: Advances in Plant Breeding Strategies; Agronomic, Abiotic and Biotic Stress Traits, Al-Khayri J.M., et al. (Eds), Springer, Berlin, pp. 1–70.

Rauf S., M. Shahzad, J.A.T. Silva, I.R. Noorka (2012) Biomass Partitioning and Genetic Analyses of Salinity Tolerance in Sunflower (*Helianthus annuus* L.) J. Crop Sci. Biotech. 15 (3): 53-57.

Reynolds M.P., Ortiz R. Adapting crops to climate changes: a summary. In: Reynolds M.P. (ed.) Climate Change and Crop Production. CABI series in climate change V.1. Chippenam: CPI; 2010. P 1-8.

Rosado B.H.P., Holder C.D. (2013) The significance of leaf water repellency in ecohydrological research: A review. Ecohydrology, *6*(1): 150–161. Doi.org/10.1002/eco.1340

Rundel P.W. (1982) Water uptake by organs other than roots. In Encyclopedia of plant physiology Vol. 12B (pp. 111–134). Berlin: Springer-Verlag.

Saed-Moucheshi A., Pakniyat H., Pirasteh-Anosheh H., Azooz M.M. (2014) Role of ROS as signaling molecules in plants. In: Oxidative Damage to Plants Antioxidant Networks and Signaling, Ahmad P. (Ed.), Elsevier, Oxford.

Schoffl F., Prandl R., Reindl A., (1999) Regulation of the heat shock response. Plant Physiol. 117: 1135–1141.

Shao H.B., Guo Q.J., Chu L.Y., et al, (2007a) Understanding molecular mechanism of higher plant plasticity under abiotic stress. Colloids Surf. Biointerfaces 54: 37–45.

Shao H.B., Jiang S.Y., Li F.M., Chu L.Y., Zhao C.X., Shao M.A., Zhao X.N., Li F., (2007b) Some advances in plant stress physiology and their implications in the systems biology era. Colloids Surf B: Biointerfaces 54: 33–36.

Sharma P., Dubey R.S. (2005) Modulation of nitrate reductase activity in rice seedlings under aluminium toxicity and water stress: role of osmolytes as enzyme protectant. J. Plant Physiol.162: 854–864.

Silva E.C., Nogueira R.J.M.C., Vale F.H.A., Melo N.F., Araujo F.P. (2009) Water relations and organic solutes production in four umbu tree (Spondias tuberosa) genotypes under intermittent drought. Brazilian Journal of Plant Physiology, 21(1): 43-53.

Smith, I.A.C., Milburn, I.A. (1980) Phloem turgor and the regulation of sucrose loading in Ricinus communis L. Planta, 148:42-48.

Steppe K., Vandegehuchte M.W., Van de Wal B.A.E., Hoste P., Guyot A., Lovelock C.E., Lockington D.A. (2018) Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove Avicennia marina. Tree Physiology, (April), 1–13. DOI. 10.1093/treephys/tpy024.

Su J.Q., Li X.R., Li X.J., Feng L. (2013) Effects of additional N on herbaceous species of desertified steppe in arid regions of China: a four-year field study. Ecological Research, 28: 21–28.

Swindell W.R., Huebner M., Weber A.P., (2007) Transcriptional profiling of Arabidopsis heat shock proteins and transcription factors reveals extensive overlap between heat and non-heat stress response pathways. BMC Genomics 8: 125.

Szabados L.S., Savoure A. (2009) Proline: a multifunctional amino acid. Trends in Plant Science, 15(2): 89-97.

Taiz L., Zeiger E. (2002) Plant Physiology, 3rd Edn. Sinauer Associates, Inc. Sunderland, USA. 647 pp

Taylor N.L., D.A. Day, A.H. Millar, (2004) Targets of stress-induced oxidative damage in plant mitochondria and their impact on cell carbon/nitrogen metabolism. J. Exp. Bot., 55: 1-10.

Taylor P. (2011) The wetting of leaf surfaces. Current Opinion in Colloid and Interface Science, 16(4), 326–334. Doi: 10.1016/j.cocis.2010.12.003.

Timperio A.M., Egidi M.G., Zolla L., (2008) Proteomics applied on plant abiotic stresses: role of heat shock proteins (HSP). J. Proteomics 71: 391–411.

Tissieres, A., Mitchell, H.K., Tracy, U.M., (1974) Protein synthesis in salivary glands of D. Melanogaster. Relation to chromosome puffs. J. Mol. Biol. 84, 389–398.

Torres-Ruiz J.M., Diaz-Espejo A., Morales Sillero A., Martin Palomo M.J., Mayr S., Beikircher B., Fernandez J.E. (2013). Shoot hydraulic characteristics, plant water status and stomatal response in olive trees under different soil water conditions. Plant Soil 373: 77–87.

Tripp J., Mishra S.K., Scharf K.D., (2009) Functional dissection of the cytosolic chaperone network in tomato mesophyll protoplasts. Plant Cell Environ. 32, 123–133.

Turner, N. C. (1979) Drought resistance and adaptation to water deficits in crop plants. In Stress Physiology in Crop Plants, ed. H. Mussell, R. C. Staples, pp. 1 8 1-94. New York: Wiley-Inter-science.

Venkateswarlu B., A.K. Shanker, (2009) Climate Change and agriculture: adaptation and mitigation strategies. Indian J. Agron., 54: 226-230.

Vesala T., Sevanto S., Grönholm T., Salmon Y., Nikinmaa E., Hari P., Hölttä T. (2017) Effect of leaf water potential on internal humidity and CO2 dissolution: reverse transpiration and improved water use efficiency under negative pressure. Frontiers in Plant Science, 8(February), 1-10. Doi.org/10.3389/fpls.2017.00054.

Vierling E., 1991. The role of heat shock proteins in plants. Ann. Rev. Plant Physiology 42: 579–620.

von Koskull-Döring, P., Scharf, K.D., Nover, L., (2007) The diversity of plant heat stress transcription factors. Trends Plant Sci. 12, 452-457.

Wagner P., Fürstner R., Barthlott W., Neinhuis C. (2003) Quantitative assessment to the structural basis of water repellency in natural and technical surfaces. Journal of Experimental Botany, 54(385): 1295-1303. Doi: 10.1093/jxb/erg127.

Wahid A., Gelani S., Ashraf M., Foolad M.R. (2007) Heat tolerance in plants: an overview. Environ. Exp. Bot. 61: 199–223.

Wang W., Vinocur B., Altman A., (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218, 1–14.

Waters E.R., Lee, G.J., Vierling, E., (1996) Evolution, structure and function of the small heat shock proteins in plants. J. Exp. Bot., 47: 325–338.

Wenkert W., Lemon, E.R., Sinclair, T.R. (1978) Water content-potential relationship in soyabean: Changes in component potentials for mature and immature leaves under field conditions. Ann. Bot. 42: 295-307.

Xiong L., Zhu J.K., (2002) Molecular and genetic aspects of plant responses to osmotic stress. Plant, Cell and Environ. 25: 131-139.

Xoconostle-Cazares B., Ramirez-Ortega F.A., et al., (2010) Drought Tolerance in Crop Plants. Am. J. Plant Physiol. 5: 241–256. DOI: 10.3923/ajpp.2010.241.256.

Xue X. (2009) Proline accumulation and transcriptional regulation of proline biosyntheses and degradation in *Brassica napus*. BMB Rep., 42: 28-34.

Yildirim E., A.G. Taylor, T.D. Spittler, (2006) Ameliorative effects of biological treatments on growth of squash plants under salt stress. Scientia Horitcult. 111: 1-6.

Young J.C., Moarefi I., Hartl F.U. (2001) Hsp90: a specialized but essential protein-folding tool. J. Cell Biol. 154:267-273.

Zhang J.H., Wang L.J., Pan Q.H., Wang Y.Z., Zhan J.C., Huang W.D. (2008) Accumulation and subcellular localization of heat shock proteins in young grape leaves during cross-adaptation to temperature stresses. Scientia Horticulturae 117: 231–240.

Zhao W., Sun Y., Kjelgren R., Liu X. (2015) Response of stomatal density and bound gas exchange in leaves of maize to soil water deficit. Acta Physiol. Plant 37: 1-9.

Zhou X., Zhang Y., Niklas K.J. (2014) Sensitivity of growth and biomass allocation patterns to increasing nitrogen: a comparison between ephemerals and annuals in the Gurbantunggut Desert, north-western China, Ann. Bot. 113(3): 501–511.

Zhou X.B., Zhang Y.M., Ji X.H., Downing A., Serpe M. (2011) Combined effects of nitrogen deposition and water stress on growth and physiological responses of two annual desert plants in northwestern China. Environmental and Experimental Botany, 74:1–8.

Zhu J.K. (2002) Salt and drought stress signal transduction in plants. Ann. Rev. Plant Biol. 53: 247-273.

Ziegler H., Batanouny K. H., Sankhla N., Vyas O.P., Stichler W. (1981) The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt and Iraq. Oecologia, 48(1): 93-99.

Zimmermann U. (1978) Physics of turgor and osmoregulation, Annu Rev Plant Physiol. 29:121-148.

Chapter 5

Functional morphology of leaves

Introduction

Plants growing under desert conditions usually develop structural characteristics that are adaptations to arid habitats. It has been shown that the surface area of the leaves is reduced in desert plants, a feature correlated with the reduction of water loss. One of the most obvious features of the leaves of desert plants is the small surface-to-volume ratio. Fahn (1989) stated that reduction of the surface is accompanied by certain changes in the internal structures of leaves, e. g. reduction in cell size, increase in the thickness of the cell walls, greater density both of the vascular system and of the stomata and increased development of palisade tissue at the expense of spongy tissue.

Leaves of desert plants are often covered with trichomes. One cannot, however, claim that these play a role in reducing water loss. The trichomes themselves lose water through transpiration. Perhaps the dead trichomes serve as a protective layer that helps in reducing water loss and that protects the photo synthesising plant organs from insolation. At least dead trichomes reduce the temperature of exposed organs. Hairs or scales, as well as epicuticular wax and resin, may play a role in reducing insolation and in reflecting light (Hartmann 1979; Heide Jorgensen 1978; Fahn 1989).

The well-known adaptations of roots to desert conditions include the succulence of the root system (e. g. in *Citrullus colocynthis* and *Hyoscyamus muticus),* the development of thick bark, sclerification of the cortical cells, and isolation of the vascular cylinder by formation of periderm or by necrosis of the cortical parenchyma.

Two interesting features have been observed in the primary roots of desert plants. According to Fahn (1989), these are: (1) a reduced number of cortical layers, thereby shortening the distance between the soil and the stele, and (2) wide casparian strips, which imply greater efficiency of the endodermis.

5.1. External leaf characters affect energy fluxes

Aboveground green organs harvest sunlight and house all metabolic steps of photosynthesis, and they resist stresses with mechanisms to manage the energy budget and water relations of the entire plant. For many species of desert plants, where water is a major limiting factor, heat resistance is generally achieved by avoidance mechanism, which is largely morphological-anatomical in nature.

Unfavorable thermal regimes may result in death due to either high or low extremes, lowered photosynthetic capacity, or unprofitable respiratory costs.

In particular, epidermal features play an important role in controlling water content of photosynthetic organs, set limits for carbon uptake and water loss, and ultimately determine longevity of aboveground organs and whole-plant survival. Thus, an integrated, multifactorial analysis of energy balance, shoot water relations, and primary productivity is required to determine the adaptational significance of each shoot design. Such analyses are somewhat different for non-succulent plants, which have very little water or solar energy storage, and succulents, which may have large organ capacitance for water and heat storage (Levitt, 1980).

In general, it can be stated that external leaf characters affect energy fluxes, consequently leaf physiology, whereas internal structural modifications directly influence conductance in the gas diffusion pathway and the related photosynthetic capacity of the chlorenchyma. Biochemical mechanisms are primarily responsible for protoplasmic tolerance of water and temperature stresses (Levitt, 1980).

5.2. Leaf energy equivalence

The temperature of any plant organ (trunk, leaf or root) depends on the balance between incoming energy and energy loss. When the rate of energy absorption exactly balances the rate of energy loss, the temperature of the absorbing tissue stays constant and is said to be in a ‘steady state’. However, when the rate at which energy is absorbed is greater than the rate of loss, the tissue in question will heat up, at a rate that depends on the difference between the incoming and outgoing fluxes and on its heat capacity. Therefore, large and massive tissues such as cactus tend to heat up more slowly than do thin tissues such as leaves, which track the changes in air temperature more closely.

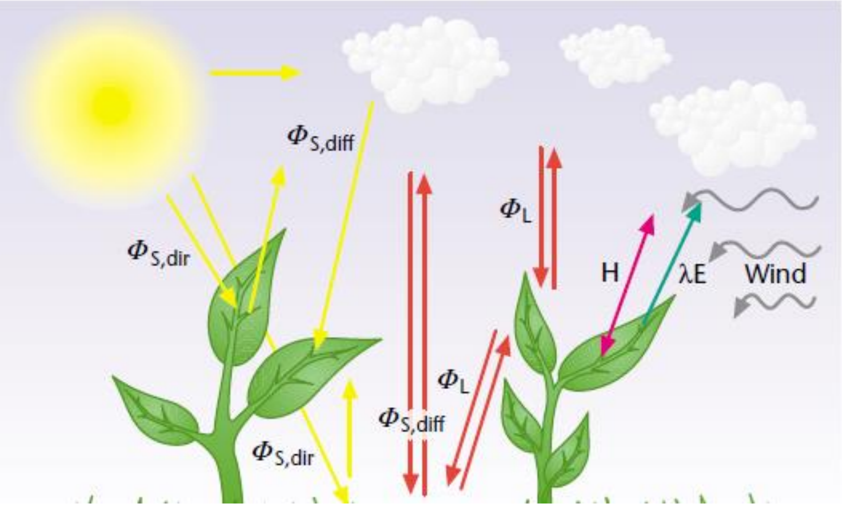

Fig. 5.1 A simplified illustration of the various components of the energy balance of plant leaves in a canopy. The various short-wave radiation fluxes (illustrated in yellow), include both the direct solar beams (ΦS, dir) incident on the vegetation, and the diffuse solar radiation (ΦS,diff) scattered by the atmosphere or by canopy elements. The long-wave radiation (ΦL) fluxes (illustrated in red) refer to thermal radiation exchanges between the atmosphere and the vegetation. The sensible heat (illustrated in magenta) and the latent heat flux from the vegetation (in green) are also shown. These latter mass fluxes depend largely on convection driven by the wind (after Hamlyn and Rotenberg, 2001).

The different processes involved in energy exchange between plants and their environment will be discussed in some detail in subsequent sections of this article, with particular emphasis on radiative exchanges. The first law of thermodynamics (the principle of conservation of energy) states that energy cannot be created or destroyed, so we can write an equation showing the fact that the difference between all the energy fluxes into and out of the leaf equals the rate of energy storage (equation1).

$$\Phi_n - H - \lambda E + M + S \qquad (1)$$

Where Φ_n is the rate of net heat gain from radiation, H is the rate of net heat loss by what is called 'sensible' heat exchange by conduction and convection processes, λE is the rate of 'latent' heat loss resulting from evaporation, M is the net rate of heat storage in metabolic reactions (e.g. photosynthesis or respiration) and S is the net rate of physical heat storage (used to raise the temperature of the body). The main components of the energy exchange of any organ such as a leaf are illustrated in Fig. 5.1.

5.2.1. Absorptance and Reflectance

Photosynthetic capacity and leaf temperature are strongly affected by the quality and quantity of absorbed solar irradiation, determined by (1) angle and location within the canopy of the photosynthetic organ relative to the direction of the sun's rays, and (2) reflectance of intercepted light energy. Values of leaf area index for most desert plants, which have small leaves and light-penetrating canopy designs, are low relative to those of other ecosystems (Cannell, 1982). This allows many leaves to receive full-sun irradiance during a portion of the day.

Whenever the sky is dry, cloudless, and relatively dust-free, instantaneous absorbed direct solar irradiation will be maximal for a leaf oriented perpendicular to the sun's rays and minimal when it is oriented parallel to the sun's rays (Fig. 5.1). A species may have fixed leaf angles or sun tracking leaves. Sun-tracking is a reversible leaf movement, achieved by turgor changes in leaf base or petiole, which allow a leaf or leaflet to remain perpendicular to the sun's rays throughout the daytime (diaheliotropic) or parallel to them (Koller 1990).

Diaheliotropism results in maximizing PPFD, total diurnal exposure to direct solar irradiance, and net daily photosynthesis, but can also cause increased leaf temperatures. A leaf not perpendicular to the sun's rays may have lower heat load, but will concomitantly have a lower photosynthetic rate because of reduced absorption of PPFD.

Leaves with fixed vertical or very steep angles (erectophilic) and with azimuth east-west orientation have been observed in deserts and semi-deserts (Werk and Ehleringer 1984). These leaves predictably receive most incident light in early morning and late afternoon and very little at midday (Fig. 5.1). Formerly, this condition had been simply interpreted as a strategy to reduce midday heating to levels tolerated by leaf metabolism; however, it may also represent an adaptation to maximize PPFD interception during periods, especially early morning, when leaf water potential generally is highest and air vapor pressure deficit is lowest. Bimodal diurnal illumination can be a more efficient daily use of PPFD, wherein a higher WUE is achieved by increasing photosynthesis with lower transpirational losses (Werk and Ehleringer, 1986).

Whereas possible physiological effects of erectophily can be modeled and tested for single full-sun leaves, as well as for vertical cladodes (Nobel, 1988), consequences of vertical leaf orientation have been extremely difficult to estimate for an entire canopy, such as an evergreen shrub with relatively high leaf area index. Self-shading may be associated with a variety of strategies to maximize certain daily or seasonal physiological parameters of uppermost canopy leaves only or total canopy productivity as the azimuth of the sun varies over the course of the year (Nobel et al., 1993).

A great deal of speculation has always ensued concerning the spectral properties of desert plants and their adaptation to intense heat and light. Figurs 5.2 (d) and (a) show the spectral absorbance and reflectance of some desert plants which are succulents. Most of these plants consist of enlarged fleshy stems and do not exhibit leaves in the usual popular conception of a leaf. The fleshy stems are green and do contain chlorophyll within chloroplasts. The transmittance of the fleshy stems is zero and hence these plants have only one mechanism for controlling their degree of coupling to the radiation environment, that is, by means of reflectance. It is clear from Figs. 5.2(d) and (a) that these desert plants reflect substantially more radiation at all wavelengths than do the more mesophytic types considered earlier. Reference to Extending out a considerable distance from the surface and casting a shadow on the surface, as do the large thorns of Cereus giganteus, reduce slightly the heat load without obstructing the flow of air.

Reflectance measurements were made of the cuticle stripped from the Agave americana plant. The reflectance was nearly neutral with wavelength values of about 30% throughout the visible and falling to 22% at 2.1 μ. At wavelengths less than 500 mu the cuticle reflectance drops off steeply. The water bands were extremely weak in the cuticle reflectance and transmittance curves (David et al., 1965).

5.2.2. Effects of Leaf Size and shape

Among the explanations for the adaptive significance of leaf morphological variation, perhaps the most prominent is the role of a leaf's size and shape in its thermal regulation. In particular, the two-dimensional proportions of a leaf are said to govern its temperature via the thickness of its air boundary layer, in which heat transfer is slow relative to the more turbulent air beyond it (Monteith and Unsworth, 1990; Schuepp, 1993). All other things being equal, the thickness of a leaf boundary layer increases with distance from the windward edge and therefore with leaf size, such that heat convection per unit area is greater between leaf and air for small leaves than large leaves. This leads to equilibrium temperatures closer to the air for small than large leaves and is the most widely accepted explanation for the presence of smaller leaves in regions such as deserts (e.g., Gibson, 1998).

In a similar way to size, the shape of leaves potentially can affect heat transfer: a leaf lamina with dissected margin or lobes functioning like many small leaves, making it a more suitable shape for hot, exposed environments than a less-dissected or entire leaf of equivalent area (Gurevitch and Schuepp, 1990; Winn, 1999).

Energy conducted from the leaf or stem occurs across an unstirred air layer, the boundary layer, adjacent to the structure, through molecular or electronic collisions. Heat transferred from a leaf or stem is convected away outside the boundary layer. Conduction and convection may be strongly affected by boundary layer thickness, which is related to size and shape of the organ as well as to wind speeds. Transpiration, i.e., evaporation of water vapor from the plant surface, can produce a significant cooling effect from energy input requirements of vaporization, but the degree of cooling depends greatly on the size of the structure to be cooled and rate of water vapor loss from the surface.

Accordingly, the narrow leaf design is adaptive for hot desert climates by enabling a leaf to avoid lethal high temperatures without expending leaf water, merely by reducing boundary layer thickness and increasing the convective coefficient for heat loss. For surviving summer drought, the cooler narrow leaf can be expected to have reduced transpirational loss. If internal leaf temperature is reduced by some degrees, then the temperature-dependent water vapor concentration within the leaf also decreases substantially, producing a smaller gradient to the dry atmosphere and hence a smaller driving force for evaporation from the leaf (Nobel, 1991a).

Another adaptive advantage of a cooler narrow leaf is that, during hot days, a narrower leaf will operate closer to the thermal optimum for photosynthesis and at a reduced cost of respiration, maximizing carbon gain if photosynthesis occurs, and minimizing loss if it does not.

5.3. Leaf size

Deserts tend to lack shade, and because there is so little humidity in the air, much more solar radiation is found in deserts than in other climates. This is too much sunlight for most plants to handle. Desert plants have found a variety of ways to cope with these extreme conditions, and survive where other plants cannot.

One of the chief adaptions of plant life to desert climates has been to reduce leaf and stem size. This allows the plant to concentrate its water instead of spreading it out over a wider surface area. Desert trees and shrubs tend to be short, with fewer leaves and branches.

5.3.1. Microphilly

It is universally recognized that typical nonsucculent desert leaves or leaf segments are small and narrow, i.e., microphyllous. Moreover, each desert species characteristically displays narrower leaves than those of the sister taxon or population appearing outside the desert ecosystem (e.g., Mooney 1980a), evidence that strong selection has occurred for small and narrow leaves in arid habitats. Seedling leaves, formed when rapid growth is required for establishment and when soil moisture is high, generally are broader and have greater area than leaves formed on older, established plants, which must survive during the driest months; such plants are frequently aphyllous or have caducous, microphyllous leaves.

Microphyllous: Small leaves with reduced surface area. Because of their small size, microphyllous leaves typically have reduced water loss through transpiration. Microphyllous leaves are characteristic of xerophytic plants of desert biomes, including redberry (Rhamnus), smoke tree (Psorothamnus) and Acacia (Fig. 5.3).

Figure 5.3 *Acacia tortilis* in a desert area of Jebel Al-Nakhsh (Khashm and Nakhsh). South-western Qatar, 2016

An analysis of some chamaephytes and low phanerophytes from the warm desert zones reveals that more than 89% of the nonphreatophytic, nonsucculent woody species have simple leaves, pinnatifid segments, leaflets, flattened rachises, or phyllodes less than 10 mm wide, and in most cases leaf segments are characteristically less than 5 mm wide. Most of these woody perennials are either drought-deciduous or essentially aphyllous, with green photosynthetic stems.

In view of energy budget parameters, the most plausible explanation for microphylly in deserts is that leaf temperature can be maintained very close to ambient temperature without substantial transpirational cooling costs. This (1) prevents heat stress via avoidance and (2) reduces leaf temperature, which, in turn, results in lower transpiration rates.

5.3.2. Broad Leaves

Broad leaves may have remarkable over-temperatures when transpiration rates are low, but also may have under-temperatures when transpiration rates are extremely high. A remarkabledsefrt leaf cooling for *Citrullus colocynth is,* a broad-leaved desert vine in the

Sahara, which, at midday in late summer and with a well-watered soil, had a temperature depression of 13 DC. Midday under-temperatures were confirmed for *Datura wrightii,* and *Sphaeralcea ambigua,* broad-leaved perennials of the Sonoran Desert, ranging from 8.4 to 18.1 DC, resulting from high transpiration rates between 6.2 and 14.3 mmol Hp m^{-2} S^{-1}, which are values expected for well-watered mesophytes (Smith 1978).

Examples of desert plants having broader leaves occur in most growth forms. Most are cases where actively growing shoots need abundant water to meet high transpiration losses, especially to reduce leaf temperature by evaporative cooling during a hot season. Evergreen shrubs, which often have leaves greater than 10 mm wide tend to have comparatively low transpiration rates but in addition, they have evolved biochemical tolerance to high leaf temperature (Mooney et al., 1980b).

Remarkable for desert floras is *Rumex hymenosepalus* of western North America, an arido-passive herbaceous perennial that may have leaves greater than 100 mm wide, and *Rheum palaestinum* (desert rhubarb) is a similar broadleaved ephemeral. Desert *Datura* is broad-leaved, arido-active forms. Some geophytes, such as *Jatropha macrorhiza,* appear during the summer rainy season of Mexican deserts. Other species of *Jatropha,* especially *J. cinerea* of Baja California and *J. cardiophylla* of the northern Sonoran Desert, have semisucculent stems with relatively broad leaves. Pachycauls and caudiciforms with relatively wide leave include *Pachypodium* and *Adenium* of African deserts.

5.3.3. Heteroblasty

According to Goebel (reviewed by Zotz, 2011), that heteroblasty is indeed adaptive and functional under current ecological conditions, a view implicitly or explicitly shared by most subsequent researchers. Heteroblasty can be seen as one possible "*strategy*" used by plants to cope with heterogeneous environmental conditions similar to, e.g., phenotypic plasticity (which includes heterophylly) or polymorphism (Lloyd, 1984).

It is a basic assumption that heteroblasty should only evolve when there is a highly predictable difference in the abiotic or biotic conditions of "juveniles" and larger conspecifics. Heteroblastic species include both relatively short-lived and long-lived taxa, and ecological context is likewise diverse. Not surprisingly then, we can hardly expect a single cause behind this phenomenon, which justifies the diverse and partly contradictory hypotheses put forward in the literature regarding its possible function. Moreover, since heteroblasty can be manifest in a number of different ways (e.g. habit heteroblasty, morphological changes, topic response) in phylogenetically distant plant lineages, we should expect at least some cases of heteroblasty to be functionally "neutral". Such a non-adaptive explanation is the more likely the shorter the duration of the "juvenile" phase, e.g. when many Acacia species retain the ancestral compound habit in the first few plastochrons.

Water Relations Heteroblasty is quite common among tillandsioids in the family Bromeliaceae (Benzing, 2000). In these plants, there is a conspicuous and abrupt shift from "juveniles" with the morphological characteristics of atmospherics (i.e. plants possessing non-impounding rosettes of small, linear leaves, which are densely covered with foliar trichomes) to larger conspecifics with tanks (i.e. featuring broad leaves, which overlap basally forming water-filled chambers). All these characteristics are related to plant water relations, which are known to be of most critical importance in the epiphytic habitat (Zotz et al., 2004). Noteworthy, there are species with the atmospheric habit throughout their lifetime, which are typically found in more arid (microenvironments), e.g. in drier forests or in the outer canopy of moister forests such as Tillandsia recurvata or T. flexuosa, which from early on led researchers to believe that the early atmospheric stage is primarily an adaptation to drought (reviewed by Zotz, 2011). This interpretation agreed with the results of experimental work with heteroblastic Tillandsia deppeana (Adams and Martin, 1986a, b), and those of a quantitative assessment of tank water relations in two other, homoblastic species: the efficiency of tanks to bridge rainless periods decreases in smaller plants, suggesting that the observed morphological change represents a strategy shift from drought-tolerant "juvenile" to drought-avoiding tank form.

However, the already mentioned study with another heteroblastic species (Werauhia sanguinolenta) suggested that a simple comparison of small atmospheric and large tanks confounds the effects of heteroblasty with those of ontogenetic drift (Zotz et al., 2004).

Water stress has also been invoked as selective factor in heteroblasty of ground rooted heteroblastic species in New Zealand (Mc Glone and Clarkson, 1993). A direct test, however, did not support this hypothesis: using pressure-volume curves, Darrow et al. (2002) found no consistent differences in plant water relations parameters between early and late stage of heteroblastic species. Noteworthy, this study was one of the few in which a homoblastic species was included to control for ontogenetic drift.

5.3.4. Seasonal heteroblasty

Numerous species of drought-deciduous woody perennials have heteromorphic leaves, relatively broad ones that develop during a season with high soil moisture, and narrow ones that are formed as soil moisture is depleted (Zotz, 2011). Perennials with distinctively heteromorphic leaves, e.g., *Encelia farinosa* and *Ambrosia dumosa* in the Sonoran Desert, *Artemisia herba-alba, Gymnocarpos fruticosus, Farsetia aegptiaca,* and *Phlomis brachyodon* in the Middle East and Sahara, form broad "green" leaves in cool weather and densely pubescent, narrower "white" leaves in hot weather.

Heteromorphic leaves on adult plants have been described in California for the halophyte *Atriplex hymenelytra* and phreatophytic species of *Prosopis* (Gibson, 1996). Sun and shade leaves also occur in some desert perennials, as demonstrated by anatomical and biochemical measurements in *Hyptis emoryi*. Winter annuals commonly produce leaves in a basal rosette, which may be a strategy to improve heating during cool weather.

Basal leaves tend to be broader and have greater laminal area than cauline leaves, and they typically wither first with the onset of soil water stress and increasingly hot soil surface temperatures, whereas the narrower or highly dissected cauline leaves persist as fruit set continues. In *Cymopterus longipes,* a herbaceous perennial, elevation of basal leaves at the onset of hot weather was thought to be a mechanism for avoiding heat stress (Gibson, 1996). Reduced self-shading in winter annuals with basal rosettes may also contribute to rapid growth. Many annuals facultatively form broader leaves when soil moisture levels are relatively high and in narrower leaves in dry years and at dry sites.

Especially winter annuals having widely spaced Microphyllous cauline leaves and wider leaves in a basal rosette, have canopy designs that produce little self-shading, and therefore probably contribute to rapid growth.

5.3.4.1. Heteroblasty of the caryopses in Aegilops geniculate (an example)

Aegilops geniculata is a Mediterranean annual that covers the Sina Desert. The lignified spike is a synaptospermic dispersal unit. It is composed of two to four spikelets that contain three to seven caryopses. Each of these caryopses differs in shape, size and hairiness. They also differ in color: cinnamon, burnt amber, snuff brown, brown-pink, as well as in germinability, according to position in the dispersal unit (Datta et al., 1970).The caryopses located in these lignified dispersal units form a well-protected long-term seed bank.

The lowest and largest caryopses (a.) of the two in the spikelet is located in the lowest spikelet of the spike (A).The second caryopsis to germinate (b.) is located in the second spikelet (B) and is the lowest one of the two caryopses located in this spikelet. The last one to germinate, and possibly the caryopsis of the longest-term seed bank, is either one of the five caryopses (c) in the third spikelet (C), or the caryopsis located in the fourth spikelet (D). During a year with less rain, most of the single spikes are composed of only two spikelets. The relative number of spikes with two, three, or four spikelets is also regulated by the origin of the caryopsis from which the mother plant developed and from the different day lengths and the temperatures under which it did so.

A water-soluble germination inhibitor is found in the hulls of *A. geniculata.* The highest germination inhibitory effect on *Lactuca sativa* achenes, which are sensitive to germination inhibitors, was found to be caused by leachate from hulls of spikelets (c) of a spike with three spikelets), and the lowest germination inhibitory effect from hulls. The lower the concentration of the leachate, from 100 to 50 to 25 %, with water as a control, the lower was the inhibitory effect on germination of *L. sativa* achenes.

Inhibitors may act as 'rain gauges' or 'rain clocks'. They delay germination until the water content of the soil is suitable for seedling development, usually after the dry soil has absorbed water from the first rainfall following the summer. The main inhibitor is mono-epoxylignanolide which, in high concentrations, may inhibit germination of lettuce achenes in incandescent white light, to a greater extent than in darkness (Gutterman, 1993).

5.3.4.2. Leaf surface reflectance

Interaction of radiation with plant leaves is extremely complex. General features this interaction have been studied further by Allen and Richardson (1986), Olinger (2010) and by Li et al., (2014). In crops spectral data may be correlated to leaf area index, leaf dry biomass and chlorophyll content (Ajai et al., 1983). The relationship varied among parameters like composition, leaf orientation and soil background (Roy et al, 1986). A study of vegetation reflectance involves the study of (i) reflection from plant parts, (ii) reflection from plant canopies, (iii) nature and state of plant canopies, and (v) structure and texture of plant canopies.

A synthesis of these data will be required to fully understand the remote sensing data collected by space-based and aerial platforms. It has been attempted for crop canopies through the development of models but has not yet been fully achieved. This review will initially discuss the electromagnetic spectrum and its interaction with vegetation canopies.

Factors affecting the spectral reflectance of plant canopies with its possible. Epidermal structures of leaves can be highly diverse in arid ecosystems. In these habitats, the epidermis controls the interaction between the living plant and a harsh environment with extreme values of heat, radiation and very low air humidity (Von Willert, 1992).

Reflectance from a plant surface can be modified by the presence of trichomes, cellular contours of the epidermis, or copious wax. Trichomes occur on many desert leaves, and, in general, desert species often appear to have denser and thicker indumentum than sister taxa from semiarid habitats, although many opposite examples can be found. Trichomes occurred on 42% of xerophytes (Fahn and Cutler 1992); however, no study has determined whether occurrence of trichomes in deserts is statistically different than for species in semiarid plant communities. Indeed, numerous common perennials have glabrous to glabrescent leaves, suggesting that presence of trichomes is not a prerequisite for survival in warm desert ecosystems. Some trichomes shrivel or dehisce with age. Trichome types are genetically determined and often show phylogenetic affinities, e.g., T-shaped or two-armed (many Brassicaceae) and L-shaped (Fabaceae), vesicular (Chenopodiaceae and Aizoaceae), stellate (Malvaceae and Euphorbiaceae), and dendritic (Lamiaceae). Dead nonglandular trichomes may significantly reduce absorbed IR and thereby leaf temperature. North American desert species with highest reflectance have relatively dense multicellular trichomes having several cellular designs.

5.3.4.3. Leaf solar tracking

Solar tracking (Diaphotonastic) movements of leaves have been reported for several different species. Most of these studies have been concerned with the mechanism of action of diaphotonastic movements (Shell and Lang, 1975). Recently attention has been focused on possible adaptive benefits that might be conferred by solar tracking movements. Two species have been described as possessing both diaphotonastic and parahelionastic (leaf cupping) movements. Both species occur in arid regions and it has been hypothesized that their cupping movements are beneficial during periods of water stress (Vogelmann, 1984). Additionally other studies have shown that carbon-gain benefits might be realized by species whose leaves track the sun (Mooney and Ehleringer, 1978). *Lupinus arizonicus* is a widespread winter annual in the deserts of southwestern North America. Its solartracking and leaf-cupping movements have been described (Vogelmann, 1984). It has hypothesized that parahelionastic movements allow plants to better withstand periods of drought.

5.3.4.4. Leaf rolling

The anatomy and mechanism of leaf rolling in grasses have been studied for over a century. Loss of turgor in the bulliformc ells on the adaxial (upper) surface generally is considered to induce rolling. Shrinkage of the adaxial subepidermal sclerenchyma and mesophyll, due to water loss, also contributes to involution; rolling can occur in leaves that lack bulliformc ells. Some grasses have permanently rolled or folded leaves. Leaves of native grasses from semi-arid grassland roll in response to increased plant water deficit (Redman, 1985).

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Leaves of native grasses from semiarid grassland roll in response to increased plant water stress during dry periods. More mesic grasses such as cereal crops also exhibit leaf rolling when exposed to water stress (O'Toole et al., 1979). Leaves of Sorghum bicolor roll and unroll in response to diurnal changes in plant water status, provided stress is not too severe (Begg, 1980).

Figure 5.4 Leaf rolling is a mechanism plants use to limit water loss as seen here in sorghum (A) and Marram grass (B).

Poaceae are structurally predisposed for in rolling by having a leaf design characterized by parallel vascular bundles, reinforced by strands or girders of abaxial and adaxial fibers and often demarcated by intercostal furrows, and separated by flexible "hinges" of colorless cells extending between epidermal layers (Scott and DeLucia, 1991). Abaxial epidermis has stiff, thickened cell walls, so that when thin-walled cells of the adaxial epidermis, as well as other living and nonliving cells, shrink during water stress, laminal margins cup upward and inward, becoming U-shaped, convolute, or involute, thus placing the abaxial surface on the outside. Leaf rolling is especially pronounced where large, vacuolate bulliform cells are positioned in the adaxial epidermis outside the hinges, and these cells buckle from passive compression.

Rolling of desert grass leaves can further reduce leaf width, already narrow (< 10 mm), reducing leaf available to absorb radiation, and thereby affecting its energy budget. Leaf temperature would be expected to drop closer to air temperature, and intercepted PPFD in the internal mesophyll would also be reduced.

Leaf rolling has frequently been considered important for reducing transpiration, because inrolled leaves may experience a 46-83% reduction in transpiration (Begg, 1980). However, a recent analysis of fiat versus rolled leaves of *Spartina pectinata,* a mesic C4 grass with hyperstomatic leaves, suggested that decrease in transpiration was from a direct effect of stomatal closure, not changes in boundary layer conductance of the diffusion pathway or major temperature reduction; fiat versus folded leaves of amphistomatic leaves from a different C4 prairie grass showed similar results (Heckathorn and DeLucia, 1991).

In poikilohydric "resurrection" vascular cryptogams, rolling of fern founds or entire photosynthetic shoots occurs during dehydration. When physiologically active, shoots of *Selaginella lepidophylla* form a flattened rosette, but during desiccation, the entire shoot curls tightly into a sphere. Curling reduces exposure of dehydrated photosynthetic tissues to high light and leaf temperature, and serves to limit damage by reducing photoinhibition and breakdown of the chloroplast photo system apparatus. When curled, S. *lepidophylla* experiences a 99.7% light attenuation.

Woody dicotyledons having leaves with revolute margins are rarely encountered in warm deserts, in contrast to their common occurrence in sclerophyllous scrub communities of Mediterranean type climates or cool and high elevation xerophytic plant communities (Lebkuecher and Eickmeier, 1990).

References

Ajai A., Kamat D.S., Chaturvedi G.S., Singh A.K., Sinha S.K. (1983) Spectral assessment of leaf area index, chlorophyll content and biomass of Chickpea. Photogrammetric Engineering, Remote Sensing, 9(49): 1721-1727.

Allen W.A., Richardson A.J. (1968) Interaction of Iight with a plant canopy, *Proc. 5th lnt. Symp.* Remote sensing of Env. Ann Arbor, USA 219-232

Arthur C. Gibson, (1996) Structure-Function Relations of Warm Desert Plants, A.C. Gibson. Springer-Verlag Berlin Heidelberg. Doi: 10.1007/978-3-642-60979-4

Begg J.E. (1980) Morphological adaptationso f leaves to water stress.P p. 33-42 in N. C. Turner and P.J. Kramer (editors), Adaptation of Plants to Water and High Temperature Stresses. John Wiley and Sons, Toronto.

Benzing D.H., Burt K.M. (1970) Foliar permeability among twenty species of the Bromeliaceae. Bulletin of the Torrey Botanical Club 97: 269–279.

Cannell M.G.R. (1982) World forest biomes and primary production data. Academic Press, London.

Cloudsley-Thompson J.L. (1996) Biotic intercations in arid lands, Springer, Berlin Heidelberg. ISBN 978-3-642-60977-0

Darrow H.E., Bannister P., Burritt D.J., Jameson P.E. (2001) The frost resistance of juvenile and adult forms of some heteroblastic New Zealand plants. New Zealand Journal of Botany 39: 355–363.

Datta SC, Gutterman Y, Evenari M (1972a) The influence of the origin of the mother plant on yield and germination of their caryopses in *Aegilops ovata*. Planta, 105(2): 155-164.

David M.G., Harry J.K., John C.S., Victor R.W. (1965) Spectral Properties of Plants. Applied Optics, 4(1): 11-22

Fahn A., (1989) Plant anatomy, 3rd edn. Pergamon Press, Oxford, 544 pp.

Fahn A., Cutler D.F. (1992) Xerophytes. Handbuch der Pflanzenanatomie, Bd 13(3). Borntraeger, Berlin.

Gibson A.C. (1998) Photosynthetic organs of desert plants. Bioscience, 48: 911-920.

Gurevitch J., Schuepp P.H. (1990) Boundary layer properties of highly dissected leaves - an investigation using an electrochemical fluid tunnel. Plant Cell and Environment, 13: 783-792.

Gutterman Y (1993). Seed germination in desert plants: Adaptations of desert organisms.

Hamlyn G.J., Rotenberg E. (2001) Energy, Radiation and Temperature Regulation in Plants. DOI: 10.1038/npg.els.0003199.

Hartmann H., (1979) Surface structures of leaves: their ecological and taxonomical significance in members of the subfamily Ruschioideae Schw. (Mesembryanthmaceae Fenzl.). In: Cutler D.F., Hartmann H (eds) Scanning electron microscope studies of the leaf epidermis in some succulent. Tropische and subtropische Pflanzenwelt, vol. 28. Mainz Akad Wiss Lit, pp 31-55.

Heckathorn S.A., DeLucia E. (1991) Effect ofleaf rolling on gas exchange and leaf temperature of *Andropogon gerardii* and *Spartina pectinata*. Bot. Gaz., 152: 263-268.

Heide-Jorgensen H.S. (1978) The xeromorphic leaves of *Hakea suaveolens* R.B.: structure of epidermal cells, cuticle development and ectodesmata. Bot. Tidsskr 72: 227-244.

Koller D. (1990) Light-driven leaf movements. Plant Cell Environ, 13: 615-632.

Lebkuecher J.G., Eickmeier W.G. (1990) Desiccation-induced plant curling and high-irradiance damage in the desert resurrection plant *Selaginella lepidophylla.* Bull Ecol. Soc. Am. 71: 227

Levitt J., (1980) Responses of plants to environmental stresses, 2nd edn. Academic Press, New York.

Li L., Zhang Q., Huang D. (2014) A Review of Imaging Techniques for Plant Phenotyping. Sensors, 14: 20078-2011; DOI: 10.3390/s141120078.

Lloyd, D.G. (1984) Variation strategies of plants in heterogeneous environments. Biological Journal of the Linnean Society 21: 357–385.

McGlone M.S., Clarkson B. D. 1993. Ghost stories: Moa, plant defences and evolution in New Zealand. Tuatara 32: 1–21

Monteith J.L., Unsworth M.H. (1990) Principles of Environmental Physics, (Second Ed.). Edward Arnold, London.

Mooney H.A., Gulmon S.L., Rundel P.W., Ehleringer J. (1980b) Further observations on the water relations of *Prosopis tamarugo* of the northern Atacama Desert. Oecologia 44: 177-180

Nilsen ET, Sharifi MR, Rundel PW, Virginia RA (1986) Infiuences of micro climatic conditions and water relations on seasonal leaf dimorphism of *Prosopis glandulosa* var *torreyana* in the Sonoran Desert, California. Oecologia 69: 95-100

Nobel P.S. (1988) Environmental biology of agaves and cacti, Cambridge University Press, New York

Nobel P.S. (1991a) Physicochemical and environmental plant physiology, Academic Press, San Diego

Nobel P.S., Forseth I.N., Long S.P. (1993) Canopy structure and light interception, In: Hall DO, Scurlock J.M.O., Bolhar-Nordenkampt H.R., Leegood R.C., Long S.P. (eds) Photosynthesis and production in a changing environment: a field and laboratory manual. Chapman and Hall, London, pp 79-90. 1993.

Olinger S.V., (2010) Sources of variability in canopy reflectance and the convergent properties of plants. New Phytologist, 189: 375–394

O'Toole J.C., R.T. Cruz. (1980) Responses of leaf water potential, stomatal resistance and leaf rolling to water stress. Plant Physiol. (Lancaster) 65: 428-432.

Redmann R.E., (1985) Adaptation of grasses to water stress-leaf rolling and stomate distribution. Annals of the Missouri Botanical Garden, 72(4): 833-842.

Roy P.S., Saxena K.G., Kamat D.S. (1986) Biomass estimation through Remote Sensing; Technical Report II R.S., Dehradun, pp 1-78.

Schuepp P.H. (1993) Tansley Review No. 59, Leaf boundary layers. New Phytologist, 125: 477-507.

Scott A.H., DeLucia E.H. (1991) Effect of Leaf Rolling on Gas Exchange and Leaf Temperature of Andropogon gerardii and Spartina pectinata, Botanical Gazette, 125(3): 263-268.

Shell G.S.G., Lang A.R.G. (1975) Description of leaf orientation and heliotropic response of sunflower using directional statistics. Agricultural Meteorology 15: 33–48.

Smith W.K. (1978) Temperatures of desert plants: another perspective on the adaptability of leaf size. Science 201: 614-616

Vogelmann T.H. (1984) Site of light perception and motor cells in a sun-tracking lupine (*Lupinus succulentus*). Physiologia Plantarum, 62(3): 335-340.

Von Willert, D.J. Life Strategies of Succulents in Deserts: With Special Reference to the Namib Desert; CUP Archive: New York, NY, USA, 1992; p. 372.

Werk K.S., Ehleringer J. (1984) Non-random leaf orientation in *Lactuca serriola.* Plant Cell Environ, 7:81-87

Werk K.S., Ehleringer J. (1986) Field water relations of a compass plant, *Lactuca serriola* L. doi.org/ 10.1111/*j*.1365-3040.1986.tb01627.x.

Winn A.A. (1999) The functional significance and fitness consequences of heterophylly. International Journal of Plant Sciences, 160: S113-S121.

Zotz G., Enslin A., Hartung W., Ziegler H. (2004) Physiological and anatomical changes during the early ontogeny of the heteroblastic bromeliad, Vriesea sanguinolenta, do not concur with the morphological change from atmospheric to tank form. Plant, Cell and Environment 27: 1341–1350.

Zotz G., Kerstin Wilhelm K., Becker A., (2011) Heteroblasty- A Review. Bot. Rev. DOI 10.1007/s12229-010-9062-8

Chapter 6

Plants responses to saline conditions in arid regions

Introduction

Salt affected soils represent a typical feature of arid landscapes. However, not all the arid territories are equally subjected to salinization. They differ in the percent of salt affected soils in the soil cover, in the degree and chemistry of salinization, and in the distribution of salts in the soil profiles. According to Lobova and Khabarov (1997), arid territories comprise up to 35% of terrestrial surface. According to the FAO[1] estimates, the area of salt affected soils on the Earth reaches 950 million hectares. The portion of salt affected soils in arid regions of different continents varies from 3 to 60% and averages about 22%. The minimum portions of salt affected soils in arid regions are in North America and Africa, and the largest portion is in Australia. According to Szabolcs (1989), who analyzed data on the distribution of salt affected soils throughout the world, the estimates given by the FAO should be considered as tentative values, because there are no reliable data on the distribution of salt affected soils in many parts of the world. It should be noted that different criteria of soil salinization are applied by researchers, which also complicates calculations of their total area (Pankova and Moscow, 2006). However, it is evident from the available data that arid regions of the world differ from one another in the portions of salt affected soils and in the character of salinization. What are the reasons for these differences? Are they related to the modern climatic conditions

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1- Food and Agiculture Organization (FAO) in general and to the aridity and continentality of the climate, in particular? What changes in the distribution of salt affected soils can be expected upon climate changes?

Saline regions are widespread throughout the deserts of the world. For instance, in deserts of the Middle East distribution of saline areas mainly related to the geographical location of the region. This region is bordered on several sides by large bodies of saline water, including the Mediterranean Sea, the Red Sea, the Indian Ocean, the Arabian Sea, Persian Gulf and the Gulf of Oman. The presence of saline water bodies along the shores of the countries in the region creates vast areas of coastal salt marshes. In addition, there are extensive areas occupied by inland saline tracts. The area of salt-affected land is increasing in the region as a result of anthropogenic factors.

6.1. Salinity and Aridity

It is appropriate to point out some basic facts on water and salt balance in ecosystems and landscapes. Under an arid climate regime, most of the water brought in by rain, snow, dew, irrigation is lost by evaporation and transpiration (Fig. 6.1). A more or less small percentage only, depending on surface properties, may reach the scarce lower groundwater in soil. Thus, the predominant flow of capillary water is upwards. As a consequence the carried soluble salts are deposited after evaporation in the upper soil horizons or on top as a salt crust. On a larger scale the scarce run-off feeds inland lakes which in drylands are often endorrheic salt lakes with no outlet to the ocean. These are the regions where primary salinity in salt deserts developed (Reimold and Breckele 1993; Breckle 2002a, b). The input of water by precipitation in humid areas is higher than the loss by evaporation.

As a consequence water-budget is positive and a river system develops with wells, creeks, streams, rivers which discharge to the ocean.

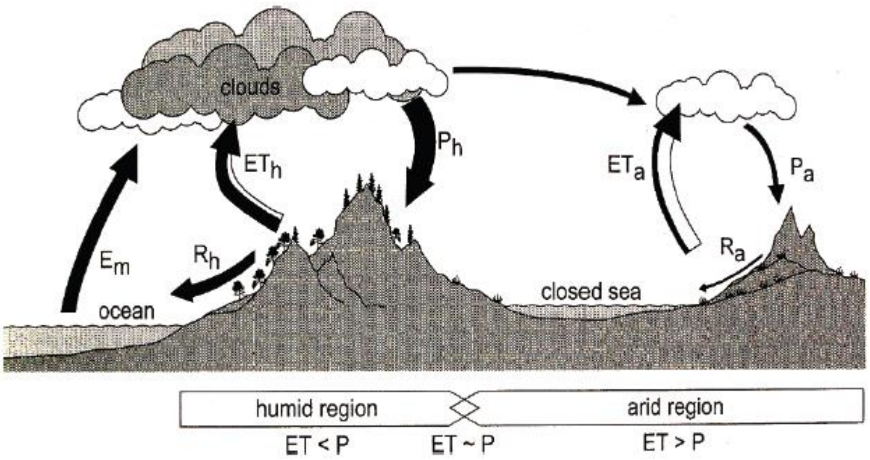

Figure 6.1 Scheme of the hydrological cycle of the earth in humid and arid regions
A = arid, E = evaporation, ET = evapotranspiration, h = humid, m = marine, P = precipitation, R = surface and subsurface runoff. The hydrological cycle is coupled with the salt cycle! The closed areas (“inland sea”) as well as the ocean contain considerable amounts of salt

6.2. Saline soils

Soils that form in desert climates are predominantly mineral soils with low organic matter content. However, the repeated accumulation of water in certain soils causes salts to precipitate out. When the water table rises to within about 2 m of the ground level, water may begin to rise to the surface by capillary action. When a rising water table intersects with salts that were previously held below the root zone, the salt will dissolve, and be carried up to the surface, concentrating in the upper layers of the soil as water is evaporated. Most playa lakes will consequently be highly saline.

Seawater is typically 50–55 $dS.m^{-1}$. When soil salinity exceeds about 2 $dS.m^{-1}$, agricultural crops will generally fail. Salinity disrupts the ion exchange mechanism between soil moisture and plant cells. As a result, plant cells dry out, plants wilt and, therefore, salinity steadily rises. Harmful quantities of nutrients or trace minerals (such as boron, copper, manganese and zinc) can also damage or kill a plant. Salinity changes the electrochemical balance of soil particles. It also destroys physical soil properties, reduces its draining capacity, and increases evaporation and soil erosion.

One form of saline soil is created by gypsum. Eckardt et al. (2001) considered that gypsum primarily precipitates at isolated points, such as inland playas. Deflation of evaporitic-rich gypsum dust from these playas contributes to the formation of gypsum duricrusts on the coastal gravel plains of the Namib Desert surrounding these playas. Duricrusts are formed when dew creates hardened soil layers, usually consisting of calcium carbonate and aluminium-rich or silica-rich compounds, which act as protective caps on ridges. Eckardt and Schemenauer (1998) tested whether Namib desert fog water carries exceptionally high concentrations of sulphate, which may be responsible for the formation of gypsum deposits in the desert [the chemical formula of gypsum is $CaSO4 .2(H_2O)$]. It appears that fog is not an efficient sulphur source for the formation of gypsum deposits, unless rare deposition events with high concentrations of marine Sulphur compounds occur. They proposed that, following primary marine aerosol deposition, both inland playas and coastal *sabkhas* (salty plains where sand is cemented together by minerals left behind from seasonal wetlands) generate gypsum which goes through the process of playa deflation and gravel plain re-deposition, thereby contributing to the extensive soil crusts found in the Namib Desert region. There is some variability among deserts in terms of soil salinity (Pankova and Dokuchaev 2006). For example, the Mongolian part of the Gobi desert is a stony desert in the canter of Asia with a dry climate that is largely affected by its great distance from the ocean. The mean annual precipitation is about 35 mm, and in some years the desert remains absolutely dry. Strong winds, particularly in the spring, and deep soil freezing in the winter (permafrost) are typical of the Mongolian Gobi. Although flat interfluvial areas account for 90% of the total area in the Gobi desert, about 3–5% of soils (derived from the clayey red-coloured deposits of the Cretaceous–Palaeogene age) are saline. The salt transfer by wind into the adjacent regions leads to soil salinization, even if the soils are developed from non-saline deposits. In the Trans-Altai Gobi, extremely arid soils are widespread. They are saline at the surface and are underlain by rocks without salts. Saline takyrs (flat or sloping deep clayey soils that act as natural catchments) and solonchaks (highly soluble salt accumulation within 30 cm of the soil surface), oft en in combination with saline sandy soils, are formed in these depressions. In wet years, during rainfall in the mountains, the mudflows reaching the depressions form temporary lakes. This is the zone of surface run-off accumulation. When the lakes dry out, the surface transforms into solonchaks. In the Ekhiin-Gol natural oasis, the solonchaks may contain up to 40–70% of salts in the surface horizons; the salt content decreases in the deeper layers (50–200 cm). Thus, while the main area of the Mongolian Gobi is occupied by non-saline soils, soil salinization is restricted to the areas of surface run-off accumulation in closed depressions and to natural oases where there is discharge of deep saline groundwater.

6.3. Halophytes

Over a long period of time, the plants that have adapted to the dry saline conditions of desert regions have been halophytes. Halophytes use many different strategies to survive under these conditions (Khan and Weber 2006). Halophytes are plants that adapt in various ways to high salt regimes. The accumulation of saline and alkali salts in desert environments is due to high evaporation rates which exceed precipitation to the point that moisture in the soil is carried up to the soil surface, rather than leaching downwards (Day and Ludeke 1993).

6.4. Seed Germination Strategies

6.4.1. Seed germinate in the presence of high salinity and a range of temperatures

In Glycophytes, seed germination is inhibited by an increase in salinity whereas; halophytes seeds can germinate in very high salinity. For instance seeds of *Kochia scoparia* can germinate in high salinity levels and are an example of adaptation of halophytes to high saline soils (Al-Ahmadi and Kafi 2007).

They found that seeds of *Kochia scoparia* could germinate over a wide range of temperatures (8–40°C). *Salicornia rubra* is one of the most salt tolerant species in the western half of the United States. The seeds of *S. rubra* can germinate at very high salinity levels (Khan et al. 2000). Because glycophytes seeds are inhibited by high salinity whereas halophytes can germinate in the present of high salinity, the halophytes are the plants that become established in the high saline areas.

6.4.2 Seeds Dormancy Due to the High Salinity of the Soil

When the rains come and addition of the moisture reduces the salinity on the seeds, the additional moisture also provides soil moisture for the development of the seedling after seed germination. Seeds of *Chenopodium glaucum* were inhibited from germinating as salinity increased but the seeds germinated readily when the salinity was removed (Duan et al. 2004). Seeds of *Desmostachya bipinnata*, a perennial grass of near–coastal and inland deserts could germinate in low salinity soils but at high salinity the seeds were inhibited. When the seeds were transferred to low salinity, they germinated rapidly (Gulzar et al., 2007). Song et al. (2005) found that seeds of *Suaeda physophora* and *Haloxylon ammodendron* had a higher concentration of Na^+ in the seed coats as compared to a xerophyte. The higher Na^+ concentration inhibited seed germination.

There are many different interactions of plant growth regulators in halophytes. There is evidence that growth regulators are a factor in the saline dormancy of halophyte seeds. The addition of growth regulators broke the saline dormancy of *Allenrolfea occidentalis* seeds (Gul et al. 2000). Even though halophytes take up considerable amount of Na^+ to their plant body, their seeds do not have a high salt content (Weber et al. 2007).

6.4.3. Some halophytes have two types of seeds, one seed that germinates quickly and another that germinates after a longer period of time

The halophyte, *Suaeda salsa*, produces dimorphic seeds. The soft brown seeds absorb water more quickly and have a higher germination rate than the hard black seeds. The brown seeds can germinate earlier than the black seeds (Li et al., 2005). Dimorphic seeds were also found in *Atriplex rosea*. The brown seeds germinate in the early part of the growing season, whereas the black seeds are capable of surviving harsher conditions and then germinate at later time periods. Characteristics of the dimorphic seeds increase chances for survival in the harsh saline desert environment (Khan et al., 2004).

6.5. Strategies for growth and development of halophytes in desert regions

6.5.1. Adaptations and mechanisms

Saline regions are characterized mainly by a high content of NaCl and a high osmotic potential. High concentrations of sulphates, carbonates, and bicarbonates, and high soil pH, as well as poor soil structure and disturbed aeration may also occur in many saline places. In the Middle East, aridity aggravates the problems created by salinity, and both have an adverse effect on the nutrition, growth, and reproduction of most plants. Halophytes in arid regions, though sharing some characteristics with those in humid places, have acquired various adaptive mechanisms during the course of their evolution. The ability of a plant to survive, grow and reproduce, or even survive without net growth means that it is endowed with particular adaptations that enable it to resist and/or tolerate salinity. Adaptations appear and are incorporated into the genotype, along with those resulting from pressures imposed by other environmental conditions. The harmony between the various mechanisms and adaptations is precarious. Exclusion of particular ions and reduction of their absolute or relative concentrations in cells and tissues are undertaken by a variety of mechanisms. Osmotic adjustment and the accumulation of salts is yet another adaptive mechanism. Under arid conditions, plants need to be endowed with mechanisms that enable them to maintain their water balance positive, at least for certain periods of the year.The delicate equilibrium between these various mechanisms can be observed in the life of the plants.

Breckle (1986) and Batanouny (1994) have classified the mechanisms and adaptations of halophytes under desert conditions. The main categories are shown in Table 6.1.

Halophytes growing in a wide range of habitats exhibit adaptations and degrees of acclimation that may differ in nature and/or efficacy. There is kind of plasticity in the responses of these plants, which varies according to the severity of any particular condition. Each species has its own array of adaptive mechanisms. Although halophytes have attracted the attention of scientists for many years, our knowledge of their adaptations is still limited. Table 6.1 shows the adaptive mechanisms of plants to survive salinity stress.

Table 6.1 Adaptive mechanisms of plants to cope with salinity stress (After Batanouny 1992b).

Type of mechanism	**Plant reaction**
Avoidance	Growth only during seasons of favourable low salinity; such plants have short life cycles
	Growth only on favourable sites with low salinity
	Limitation of root growth and absorption to distinct soil horizons
Evasion	Selectivity against Na$^+$ and Cl$^-$ separation of salts from the assimilating tissue
	Compartmentalization of salt within plant organs, tissues and cells
	Re-translocation of salts to roots and its excretion by the roots
	Leaching of salt out of the shoot
	Shedding of salt-loaded tissues and organs
	Secretion of salts by salt glands or bladders
	Production of adventitious roots and mound building
Tolerance	Increasing the salt resistance of tissues, cell and organelles
	Production of protectants
Osmotic adjustment	Ion-specific adaptation of the cytoplasm
	Increase of halo-succulence; leaf and stem succulence

6.5.2. Root Development by Salinity and Salt Exclusion

Large root development is important in survival of plants in desert regions. The root mass may represent 75% of the plant mass in desert regions. The root morphology and development was promoted for *Suaeda physophoira*, *Suaeda nitratria* and *Haloxylon ammendendron* at certain salt concentrations (Yi et al., 2007). Large root development is inhibited in glycophytes by high salinity. In monocot halophytes, salt exclusion can be a factor in tolerating saline soils but osmotic compounds need to be produced to pull water into the plant (Weber, 1995).Tester and Davenport (2003) found a number of halophytes that selectively excluded toxic ions from the roots.

6.6 Halophytes in desert regions accumulate NaCl to increase their ability to absorb water into the plant

The absorption of water from saline soils is critical for plants to survive in desert environments. Halophytes from an inland saline lake were found to accumulate Na^+ and glycinebetaine as their major response to increased salinity (Tipirdamaz et al. 2006). Most halophytes take up more Na+ from the soil and hence the Na^+/K^+ ratio in the rhizosphere tends to decrease (Xi et al., 2004). A true halophyte needs saline water to develop whereas pure water can often inhibit growth. Song et al., (2006) found that in succulent halophytes the accumulation of nitrate as well as cation and anions in the vacuole lowered their osmotic potential to a degree that uptake of water from saline soils was accomplished.

Aster tripolium and *Sesuvium portulacastrum* used different strategies to survive saline habitats (Balasuban et al., 2006). In *A. tripolium* more K^+ was accumulated in comparison to Na^+ as the salinity of the soil increased. In contrast in *S. portulacastrum* more Na^+ was accumulated in comparison to K^+. The non-photochemical quenching (NPQ) increased in both plants as the concentration of NaCl increased, but the NPQ for *S. portulacastrum* was almost half the NPQ value for *A. tripolium*. In the halophyte, *Cynara cardunculus*, high concentrations of KCl were more deleterious than high concentrations of NaCl (Benlloch-Gonzalez et al., 2005).

Plants vary in the degree of their salt tolerance and in the means by which they regulate salt content of their tissues. Mechanisms such as salt exclusion, salt accumulation, and salt secretion and export by means of salt glands are reported for different plants in coping with saline media (Scholander et al., 1966).

Atriplex species are among the few salt-tolerant plants that have any agricultural value in extremely arid and saline areas because of their unusually high protein content and exceptional salt tolerance. These plants do not have salt glands but are characterized by the presence of several layers of balloon-like, vesiculated hairs (trichomes) on the leaf surface. Different functions have been assigned to these hairs, such as absorption of water from the atmosphere water storage, and salt secretion. Upon bursting, these cells deposit salt on the surface of the leaves. However, the salt content of these hairs has never been measured to see how effectively they function in salt removal. Nor has direct absorption of water by the hairs ever been studied.

6.6.1 Synthesize Compatible Solutions

The production of osmotically compatible solutions results in the ability of the halophyte to absorb water from the saline soil. In two halophytes, *Carex paleacea* and *Scirpus americanus*, the concentration of glycine betaine increased three fold and in *Puccinellia phryganodes* the proline concentration was increased five times (Ewing et al., 1989).

Monosaccharides and disaccharides play an important role in osmotic adjustment in plants subjected to salinity stress (Gorham et al., 1981). Ashraf et al. (2006) observed mono and disaccharides played a role in water absorption in forage grasses in the Cholistan Desert.

6.7. Secreting Salt from Leaves

In certain cases, halophytic plants excrete the salts through salt glands or by concentrating the salts in certain cells of the plant. *Limonium* and *Distichlis* are two examples of halophytes that have salt secreting glands (Weber 1995). In *Aeluroopus littoralis*, a salt secreting halophyte, the main ions secreted from the salt glands were Na^+ and Cl^- (Barhoumi et al. 2006). In *Reaumuria hirtella*, six ions were excreted with Na^+ and Cl^- being the predominate ions and represented 86% of the excreted ions. Of the ions absorbed from the soil, 67% were excreted from the plant (Ramadan, 1998).

6.7.1 Salt glands and salt bladders

Salt bladders are composed of one bladder cell, without or with one or more stalk cells while salt glands consist of either two- or multi-cellular structures (the details are discussed in the section, The Reported Recretohalophytes and the Structural Characteristics of Salt Glands). Single epidermal cells can function as a salt bladder, as seen in *Mesembryanthemum crystallinum* and bladders are often modified richomes. Salt bladders once differentiated, expand rapidly and after exposure of the plant to salt may break up releasing ions to the environment. Salt glands form stable structures that directly secrete salt out of the plant to the external environment.

In recent decades, remarkable progress has been made in explaining salt exclusion and secretion mechanisms and the development of salt bladders and salt glands, with most studies concentrating on two plants, *Chenopodium quinoa* and *Limonium bicolor*. *Chenopodium quinoa* is a typical recretohalophyte that possesses salt bladders, and its salt secretion mechanism and salt transport pathway were illustrated in detail in a recent review (Shbala et al., 2014). Comparison of metabolic changes in salt-treated relative to control samples without NaCl treatment showed that 352 different metabolites were identified in bladder cells of *M. crystallinum* under salt treatment (Barkla and vera-Estrela, 2015.). Recent studies of Oh et al (2015) presented a transcriptomic analysis of bladder cells of *M. crystallinum* demonstrating cell-type-specific responses during adaptation to salt. The latest study of *Atriplex canescens* showed that the increasing of Na^+ accumulation in salt bladders can enhance the salt tolerance (Pan et al., 2016). *L. bicolor* has multicellular salt glands and the mechanisms of development and salt secretion, in particular the candidate genes, have been studied (Feng et al., 2014; Yuan et al., 2015): more detail is provided below.

The salt glands in different species possess various structural characteristics. The number of component cells has been used to separate multi-cellular salt gland and bi-cellular salt gland.

Figure 6.2 Salt glands on the leaves of *Tamarix smyrnensis* (after Manousaki et al., 2008)

In general, the salt glands in dicotyledonous recretohalophytes are multi-cellular and sunken into the epidermis. For instance, eight cells were identified in *Tamarix aphylla* with six secreting cells and two collecting cells in a symmetrical structure (Thomson and Patt-Aloia, 1985)(Fig. 6.2).

Similarly, in *L. bicolor*, the salt glands consist of 16 cells, with four groups each of outer cup cells, inner cup cells, accessory cells and secretory cells (Ding et al., 2010a; Feng et al., 2015; Yuan et al., 2015). Species of mangroves (of the Verbenaceae) grow in intertidal zone and possess salt glands with different numbers of secretory cells, e.g., 6-8 secretory cells in *A. officinalis* (Tan et al., 2010), 8-12 reported in *A. marina* (Drennan et al., 1987), and eight found in *Avicennia germinans* (Balsamo and Thomson, 1993). In contrast to the multi-cellular glands, bi-cellular salt glands are found in the monocotyledonous recretohalophytes of the Poaceae, in species of *Aeluropus*, *Sporobolus*, *Spartina*, and *Zoysia* (see Ramadan and Flowers, 2004; Chen et al., 2009; Semenova et al., 2010; Ceccoli et al., 2015). In all of the above examples, the innermost cells of the salt glands were positioned adjacent to the mesophyll cells, e.g., the collection cells in *Tamarix* and the outer cup cells in *Limonium*.

6.7.2. Structure of salt glands

A significant proportion of halophytes have evolved specialized epidermal structures called salt glands to store and exclude salt (Flowers and Colmer, 2015; Santos et al., 2016). The epidermis is the surface through which a plant interacts with its environment, and thus the epidermis has a wide variety of functional specializations at the cellular level. Some of these, including stomata for gas exchange and cuticlecovered pavement cells that prevent dehydration and pathogen attack, are shared by most land plants and all angiosperms.

In addition, plants have developed a myriad of epidermal structural adaptations to defend themselves from or to exploit their environments, such as trichomes, nectaries, prickles, and hydathodes, which range in complexity from specialized single cells to multicellular structures consisting of several cell types (Esau, 1965). Although all salt glands function to increase salt tolerance, they differ in structural complexity and mechanism of salt exclusion, suggesting that salt glands have multiple evolutionary origins (Flowers et al., 2010).

Salt glands are found mostly on leaves of plants that grow on dry saline soils, on salt marsh grasses, and in a variety of mangroves, which are woody plants that inhabit tropical and subtropical intertidal zones (Flowers et al., 1986; Tomlinson, 1986). Therefore, most of the salt gland baring plants are also considered as halophytes, but a few exceptions are found throughout land plants (Chen and Chen, 2005; Maricle et al., 2009; Peng et al., 2016).

6.7.3. Diversity of salt glands

The term “salt gland” is quite broad, and has been applied to a wide variety of structures with different anatomical features and functional mechanisms. Halophytes with salt glands are collectively termed salt secretors or recretohalophytes (Breckle, 1990). From a structural perspective, all salt glands appear to be largely epidermal in origin and thus are in essence specialized trichomes. From a functional perspective, there are two types of salt glands, those that directly secrete salts to the surface of the leaf (exo-recretohalophytes), and those that collect salt in the vacuole of a specialized bladder cell (endo-recretohalophytes) (Ding et al., 2010b). Although few species of plants have salt glands, they are distributed among four major divisions of flowering plants: Caryophyllales, asterids, rosids, and Poaceae (Santos et al., 2016).

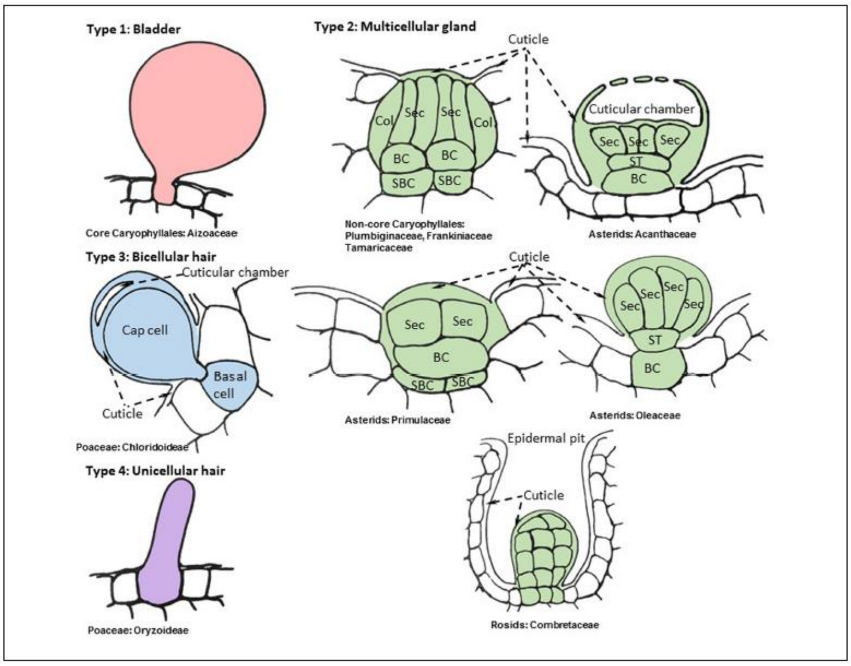

Figure 6.3 Representative cellular organizations of distinct salt gland structures found in angiosperms. Drawings are based on consensus representations of species specific salt gland structures. References used to create consensus figures for each type are given in Table 1. The cells that constitute the salt gland are colored while the adjacent cells are kept blank. The continuous cuticle around the salt gland is also colored and changed to blank when the cuticle overlays the surrounding epidermis. The dynamic intracellular structures such as vacuoles, vesicles, and laminated membranes are not depicted in the representative figures. Collecting cell (Col), secretory cell (Sec), basal cell (BC), sub-basal cell (SBC), stalk cell (ST) (courtesy of Dassanayake and Larkin, 2017).

This broad phylogenetic distribution suggests that salt glands have originated independently multiple times as previously proposed for halophyte origins (Flowers et al., 2010). Yet the salt glands of widely divergent species have many phenotypic similarities, providing some striking examples of convergent evolution that give insight into the mechanisms through which salt glands protect plants. The similarities among salt glands enable categorization into four broad structural groups: (1) salt bladders consisting of a large vacuolated cell with or without 1 to 2 stalk cells, found only in Aizoaceae and Amaranthaceae (Fig. 6.3, Type 1), (2) multicellular salt glands varying from 4 to 40 cells, with cells typically differentiated into collecting and secretory cells in a cuticle lined structure, widely distributed phylogenetically (Fig. 6.3, Type 2), (3) bicellular secretory hairlike structures with a basal cell and a cap cell, found in chloridoid grasses (Fig. 6.3, Type 3), and (4) unicellular highly vacuolated secretory hairs (found in Porteresia) (Fig. 6.1, Type 4). The first two structural types are found in eudicots while the third and fourth types are found in monocots.

In Mesembryanthemum crystallinum (Aizoaceae) salt is simply deposited in the large vacuole of specialized swollen epidermal cells called salt bladders (Agarie et al., 2007). Eventually the bladder cells may rupture, depositing salt on the epidermal surface. Several species in the Amaranthaceae, exemplified by *Atriplex lentiformis*, *Bienertia sinuspersici*, and *Chenopodium quinoa* (Adolf et al., 2013; Shabala et al., 2014), have a slightly more elaborate structure for salt bladders compared to that of *M. crystallinum*, in which the bladder cell is located on top of a short stalk consisting of one or few cells (Fig. 6.4). The mechanism used by these plants for sequestering salt in the bladder cell vacuole resembles the storage of salt in enlarged vacuoles of the mesophyll cells within succulent leaves in many halophytes (Park et al., 2009).

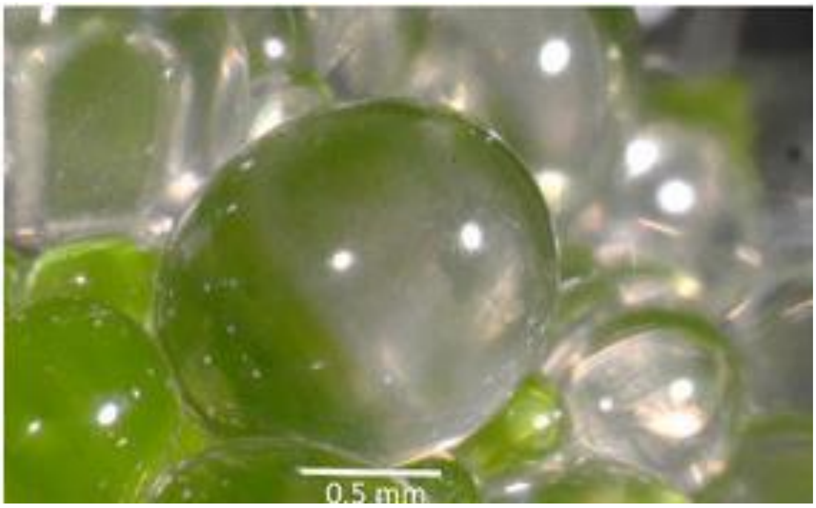

Figure 6.4 Epidermal bladder cells (EBCs) from *Mesembryanthemum crystallinum* (after Oh et al., 2015)

The level of convergence is quite remarkable in the second type of salt glands spanning the diverse clades of Caryophyllales, asterids, and rosids (Shi et al., 2005) (Figure 4). These multicellular glands typically have cell types differentiated into basal collecting cells and distal secretory cells (Thomson et al., 1988). The collecting cells are presumed to create a salt efflux gradient to collect salt from neighboring mesophyll cells and transport it to secretory cells. The secretory cells are completely surrounded by a cuticle, with the exception of where they contact the subtending basal collecting cells, a feature which appears to channel the flow of salt through the secretory cells and prevent leakage back into the neighboring tissue via the apoplast (Tan et al., 2013).

6.7.4. Ecological Factors Affecting Salt Secretion

The rate of salt excretion is affected by numerous environmental factors. These include: the salt concentration of the growth medium, the ions that are present, light, temperature, oxygen pressure, the presence of metabolic inhibitors and ratios between essential and toxic ions all of which can become limiting.

Changes in the Na^+/K^+ ratio may determine the activity of several key metabolic processes. Selective secretion of Na^+ and Cl^- against nutritive ions prevents the domination of Na^+ and Cl^- over these ions and has been demonstrated in most species of salt-secreting plants (Rains and Epstein 1967; Ramadan, 1998).

6.7.5. Importance of Bladder Hairs for Salt Tolerance in some genera of *Chenopodiaccae*

Some *Atriplex* species, especially those widely distributed, are preferentially common in communities near the sea. Species from the *A. prostrata* group are very typical along the coasts of almost all continents (Osmond et al. 1980). With regard to mineral nutrition, the most important attributes of salt marsh soils are the low concentration of $NO3^-$ and the high concentration of Na^+ and Cl^-. Other important characteristics of this soil are large fluctuations of the water potential and consequently of ion concentrations and of nutrient availability in the soil solution (Osmond et al. 1980). Tolerance to Na^+ and Cl^- of salt marsh inhabitants must result from an interaction of processes as ion uptake, transport, and removal in order to ensure effective osmotic balance by salt accumulation (Flowers and Yeo 1988). Nitrate availability seems to limit growth of some species in coastal salt marshes (Jefferies and Perkins 1977). However, many halophytes from the salt marsh are known to accumulate high concentrations of nitrate in leaf and stem tissue. Those species show high levels of extractable nitrate reductase and exhibit high *in vivo* rates of nitrate reduction, suggesting high capacity for nitrate assimilation (Lee and Stewart 1978).

In some genera of *Chenopodiaccae,* especially in all *Atriplex* species, salt bladders do occur (Reimann and Breckle 1988). By a specialized mechanism of salt removal from leaves, they prevent dangerous accumulation of toxic salt levels. Leaves of most *Atriplex* species, particularly from field plants, are replete with bladders. In mature leaves, the bladders collapse and produce a thick layer all over the leaf surface. Due to its density, it is usually difficult to see the leaf epidermis (Osmond et al, 1980).

Salt secretion by micro-hairs has been detected only in certain Chloridoideae, all having ‘chloridoid type’ micro-hairs with basal cell partitioning membranes. It has not been detected in many species with micro-hairs lacking basal cell partitioning membranes. For example, the ‘chloridoid type’ micro-hairs of *Sporobolus elongates* and *Eleusine indica* do not secrete salt, despite their possession of partitioning membranes (Amarasinghe and Watson 1988).

At leaf level, there are certain appendages which help the plant to secrete excess salts from the main body. Most important among these are salt secretory trichomes (e.g., *Atriplex* spp.), second type is multicellular salt glands which occur in many desert and coastal habitat flowering plants, and are confined to the members of families including Poaceae, Aveceniaceae, Acanthaceae, Frankeniaceae, Plumbaginaceae and Tamaricaceae (Mauseth 1988; Marcum and Murdoch 1994). In contrast, the stem of halophyte *Salicornia fruiticosa* has a simple cortex and single layered epidermis which is thin–walled and the photosynthetic tissue has palisade and parenchymatous cells for storage of water (Hameed et al., 2010).

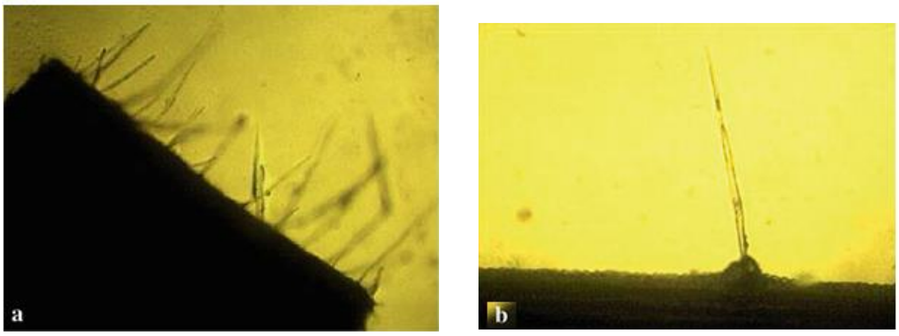

Figure 6.5 Structural and Functional Adaptations in Plants for Salinity Tolerance Glandular hairs on leaf surface in (a) *Aeluropus lagopoides* and (b) *Lasiurus scindicus* (after Hameed et al., 2010).

6.8. Salt accumulation in Certain Plants Regions.

In *Salicornia pacifica var. utahensis*, salt ions move up into the shoot and accumulate in the cortex region, after a period of time the salt concentration becomes too high and the lower segments of the shoot die but the vascular tissue in the center of the shoot continues to function. The water continues to move up to the upper living segments of the shoot. The dead segments act as a region of deposit for the excess salts. *Diplachne fusca* has the ability to sequester high levels of Na^+ and Cl^- in the sheath away from the leaf blades as well as maintaining a high selectivity for K^+ over Na^+ (Warwick and Halloran 1992).

Salt accumulation in the cell or vacuole sap appears to be the primary means of osmotic adjustment in the family Chenopodiaeeae. Species of Atriplex (Flowers and Yeo, 1988) exhibit growth stimulation by NaCl which is attributed to the relationship between salt uptake and turgor pressure leading to extension growth. On the other hand, high Na^+ levels in the plant may also be toxic. The nearly universal increase in water content observed when halophytes are grown on NaCl has been regarded as an adaptive mechanism to dilute potentially toxic levels of Na^+ in the cell sap. However, Storey and Jones (1979) presented evidence that the succulence phenomenon in *Atriplex spongiosa* and *Suaeda monica* resulted simply from the higher turgor pressure of plants grown on low levels of NaCl compared to those grown on fresh water.

Briens and Larher (1982) found a strong correlation between the water and mineral content of 15 salt marsh halophytes collected from the wild. They interpreted the data as suggestive of a close relationship between the water relations of halophytes and their capacity for uptake and storage of mineral ions (Glenn and O'Leary, 1984).

When the salt concentrations of outside medium is more as compared to the inside of the cell, more amount of salt move inside the plant body and if this condition persists it may lead to high amount of salt depositions inside the shoot therefore halophytes must have the ability to keep the salt concentrations within their body low (Borsani et al., 2003). Plant cells respond to high salt concentrations of the soil by increasing sodium efflux at the plasma membrane and by the accumulation of sodium in the vacuole (Zhu, 2000) (Fig. 6.6).

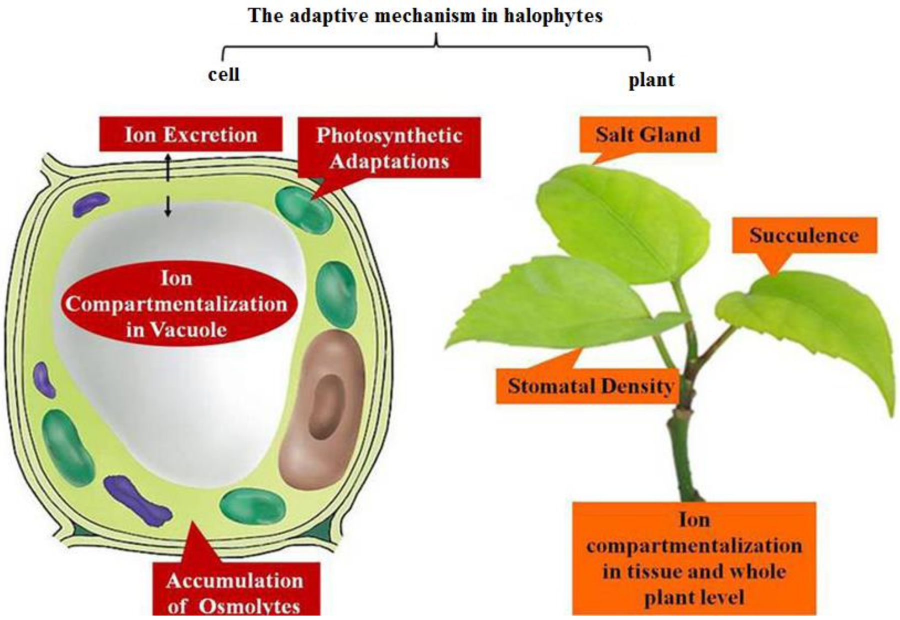

Figure 6.6 The mechanism in halophytes from cells to whole level (courtesy Xu et al., 2016)

6.8.1 Ions Compartmentalization

However, the compartmentalization of sodium and chloride in the vacuole can be attained only if sodium and the chloride ions are transported actively in the vacuole and if the tonoplast permeability to these ions is relatively low so that an ion concentration gradient can be sustained at an energy cost that can then be prolonged for months (Maathius et al., 1992).

Halophyte tonoplast channels must therefore be modified either to be increasingly discriminating against sodium and chloride, or the channels remain closed for the greater part of time, or to have a decreased number of channels per cell. Halophytes generally utilize the control accumulation and sequestration of inorganic ions for the adjustment of osmotic potential of their internal tissues to the external salinity (Flowers and Yeo, 1986; Cheeseman, 1988).

However, the extent to which halophytes accumulate ions and the degree of salt tolerance is widely different among halophytes (Glenn and O'Leary, 1984; Glenn et al., 1996). Cells are able to increase salt levels in the vacuoles by intracellular compartmentalization of ions hence preventing the high levels of salts in the cytoplasm (Gorham, 1995).

Molecular mechanisms involved in providing resistance against salinity in plants: According to Xiong and Zhu (2002), one of the important strategies against high salt concentrations is to regulate the expression of certain genes. Genes that may be regulated by salt stress may belong to different groups based on their function. These genes encode:

1. LEA protein (late embryogenesis abundant proteins),
2. Enzymes (involved in biosynthesis of osmolytes, hormones, detoxification, and general metabolism),
3. Transporters (ions transporters, that are, ATPbinding cassette (ABC) transporters, and aquaporins),
4. Regulatory molecules such as protein kinases and phosphotases.

The most common and the most important stress regulated genes are LEA-like genes or LEAs. LEA genes encode LEA proteins or late embryogenesis abundant proteins (Baker et al., 1988). Although, these genes have a wide occurrence but the function of this group of genes are still not well defined except in some cases where the over expression of individual LEA genes resulted in some degree of stress protection (Xu et al., 1996).

The expression of transcription factor that regulate the expression of LEA-like genes has been enhanced under stress in transgenic plants, it indicates that these proteins do have protective affect against abiotic stress (Liu et al., 1998; Aslam et al., 2011). However, the fact that these genes are not expressed under normal growth but they are only expressed during stress (salt drought or low temperature stress) suggest that their products have some role in protecting the cellular structure during stress. One major hypothesis is that these genes product may act as chaperon hence protecting the denaturation of some key proteins of the cell (Xiong and Zhu, 2002).

A large number of enzymes are believed to be involved in providing tolerance against high salt concentrations in the halophytes. Such enzymes are found to be sensitive against sodium chloride. It has been observed in *Suaeda maritima*, when the concentration of sodium chloride is increased, the activity of various enzymes is inhibited. It also includes those enzymes that are involved in protein synthesis. It happens at 200 to 400 mM NaCl concentrations (Munns and Tester, 2008). There is particularly very little evidence that an inherent difference exists between the enzymes isolated from halophytes and non-halophytes.

Reactive oxygen species (ROS) species is produced under salt stress conditions in plants. These ROSs have the ability to interact with the cell membrane and other cellular components of the cell leading to the damage to these cellular components. Plants contain variety of antioxidants and antioxidant enzymes which are responsible for maintaining the level of ROSs relatively low (Gao et al., 2008). In plants enzymes like superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) may be responsible in protecting the cell from oxidative damage (Mittler, 2002). In various reports the role of CAT, POD, SOD have been reported in providing resistance during salt stress by preventing oxidative damages to the cell (Rahnama and Ebrahimzadeh, 2005). On the basis of these findings it can be suggested that the presence of antioxidant enzymes can be the most important strategy of plants grown under high salinity levels. The role of some of the antioxidant enzymes is given below:

1. SOD can easily repair the damage that is caused by ROS. SOD is one of the important enzymes responsible for the maintenance of normal physiological conditions of the plants and hence coping with the stress (Mittler, 2002). A large number of studies have been carried out which highlight the positive correlation between the salt stress and level of SOD (Shalata and Tal, 2002; Al Scher et al., 2002; Badawi et al., 2004).

2. POD has wide distributions among the families of higher plants. POD plays various roles in the plants like lignifications, oxidative metabolism, salt tolerance and heavy metal stress (Passardi et al., 2005). The increased POD activity is believed to be responsible in providing an antioxidant mechanism during the conditions of salt stress (Gao et al., 2008).

3. CAT is the most active enzyme in providing resistance against oxidative damage in the plant. This enzyme basically brings out the degradation of hydrogen peroxide into water and oxygen (Mittler, 2002). The CAT activity may depend upon the species as well as the developmental and metabolic state of the plant as well as duration and stress intensity and hence varies (Chaparzadeh et al., 2004; Aslam et al., 2011).

6.8.2 Ion selectivity

A major feature of the solute transport by plants in saline conditions is the degree of selectivity, particularly between potassium and sodium (Ashraf et al. 2005). One of the most important physiological mechanisms of salt tolerance is the selective absorption of K^+ by plants from the saline media (Ashraf et al. 2006). Halophytic or salt tolerant species differ from salt–sensitive ones in having restricted uptake or transport of Na^+ and Cl^- to the leaves despite an effective compartmentalization of these ions. This is critical in preventing the build–up of toxic ions in cytoplasm (Ashraf, 2004). Ion imbalance, particularly that caused by Ca^{2+} and K^+ is the most important and widely studied phenomenon affected by salt stress, which is directly influenced by the uptake of Na^+ and Cl^- ions (Munns et al., 2006). Maintaining better concentrations of K^+ and Ca^{2+} and limiting the Na^+ uptake are vital for the salt stress tolerance in plants (Karmoker et al. 2008). Higher K^+/Na^+ or Ca^{2+}/Na^+ ratios are characteristic to the tissue salt tolerance, and are often used as a screening criteria for the salt tolerance (Munns and James 2003, Ashraf, 2004; Song et al., 2006).

6.9. Avoiding High Salinity in Relation to Photosynthesis

The cells that photosynthesize are protected from the entry of salts by ion pumps. Analysis of the ion content in cells of *Salicornia* *pacifica* var. *utahensis* indicated that ion pumps prevented the accumulation of salinity in the palisade cells. An increase in salinity in *Atriplex portulacoides* did not have an adverse effect on photosystem II (Redondo-Gomez et al., 2007). The decrease in growth response appears to depend on the changes in its photosynthetic gas exchange mainly through stomatal conductance. One way to decrease water loss is through the closing of the stomata in the leaves of halophytes. Perera et al., (1994) found that when the NaCl concentration increased in the leaf cells of *Aster tripolium*, there was a suppression of the stomatal opening. He suggested that the accumulation in the cell vacuoles caused the Na^+ ions to accumulate in the apoplast around the guard cells which caused a partial closure of the stomata opening.

6.10. Leaf *succulency*

Succulence is another strategy of halophytic plants to maintain moisture under drought conditions. *Haloxylon ammodendron* and *Zygophyllum xanthoxylum* are succulent xerophytes that absorb large quantities of Na^+ for osmotic adjustment. The Na^+ was absorbed by the roots and then transported to the succulent leaves, which resulted in salt dilution (Wang et al., 2004).

During the summer, the desert is hot and the protection of water loss is related to the surface wax of the halophyte.

In *Allenrolfea occidentalis*, a glabrous succulent bush, Hess and Weber (1995) found the surface wax had hydrocarbons from C22 to C38. These large hydrocarbons were stable in the summer heat. The hydrocarbons chain length was longer than the chain length of the surface hydrocarbons of glycophytes. *Suaeda aegyptiaca* were analyzed by proteomics in relation to increased salt concentration (Askari et al., 2006). Out of 700 protein spots 102 spots increased in response to increased salinity. Some of the proteins were determined to be glycinebetaine synthesis, cytoskeleton remodeling, photosynthesis ATP production, protein degradation, cyanide detoxify cation and chaperone activities. Kant et al. (2006) suggested that salt sensitive glycophytes and salt-tolerant halophytes employ common mechanism to cope with salinity, and that the differences in salt tolerance arise because of changes in the regulation of a basic set of salt tolerant genes. The regulation of proline accumulation and catabolism and the tight control of Na^+ uptake in *T. halophila* appeared to be the key factors.

Increased succulence in halophytes in response to increasing salinity is presumed to be of adaptive nature. Succulence is very much greater in halophytic dicotyledonous species than in monocotyledonous ones (Flowers et al. 1986). There is also evidence of a rapid increase in vacuolar volume and in the concentration of Na^+ (Mimura et al., 2003) in the cells of mangrove *Bruguiera sexangula*, which is a potential mechanism to cope with a rapid increase in external salt concentration.

6.11. Shedding of old leaves

In most species investigated by Albert (1975), chloride concentration rises distinctly with increasing leaf age, too, whereas concentration shifts of alkaline earth ions and of sulfate are of comparably less importance. Saturation water increases markedly in succulent species *(Suaeda maritima, Chenopodium glaucum, Spergularia media, Lepidium erassi/olium)* and to a less degree in xerophytic monocotyledons (*Puccinellia distans, Crypsis aeuleata, Bolboschoenus maritimus*). However, this surplus of water in older leaves is not sufficient to dilute the salt to such an extent that a rise in concentration can be prevented (except chloride in *Suaeda maritima* and *Chenopodium glaucum).*

Rosette plants (*Triglochin maritimum, Plantago maritima, Seorzonera parvi/lora, Aster tripolium*) with the ability to renew their leaves continuously throughout the growth period are characterized by only insignificant changes of saturation water content with increasing leaf age. In these plants shedding of old salt-saturated leaves is thought to be the main strategy for salt regulation.

6.12. Photosynthetic pathways in halophyte pants

Both C3 and C4 photosynthetic pathways occur in halophytes. While many succulent chenopods are C4 plants, e. g. *Suaeda* spp., and *Seidlitzea rosmarinus*, there are other succulent C3 chenopods, e. g. *Arthrocnemum* sp., *Halocnemum* sp. and *Halopeplis* sp. that do not use the C4 pathway.

Halophytic grasses belonging to the subfamilies Panicoideae and the Chloroideae are salt-resistant C4 plants (Batanouny et al., 1998). The salt tolerance of some of these species is achieved by salt excretion. The presence of both photosynthetic pathways in halophytic plants may be evidence that the type of photosynthetic pathway is not correlated with tolerance of or resistance to salinity. However, Laetsch (1974) stated that the primary adaptation of C4 plants was probably to saline environments and that the structural and functional adaptations are a prerequisite for efficient assimilation and growth. The photosynthetic spectrum studied by Frey et al. (1985) showed a characteristic zonation of C3 and C4 species along transect in littoral salt marshes in different places in southwest Asia where moisture and salinity are the determining factors. The formations in which the C4 pathway dominates are subject to stress with regard to both soil moisture and salinity. These are mainly xerohalophytes. By contrast, the halophytes in which the C3 pathway is prevalent only have to withstand salt stress. These are the hygrohalophytes and mesohalophytes represented in the study of Frey et al. (1985) on the vegetation of the *Avicennia* and *Halopeplis* zone. Such plants achieve their salt tolerance by means of different adaptations. Both types of stress (salt stress and water stress) must apparently occur together if there is to be a selection advantage for the C4 pathway (Xu et al., 2016). Although it is recognized that some halophytes require Na^+ as a micronutrient, it has nevertheless been shown that this requirement is restricted to C4 plants (Bose et al., 2017). In most respects the effects of salinity on photosynthesis are mediated via the water relationships and associated processes of the leaves. It is therefore not surprising that induction to crassulacean acid metabolism (CAM) in succulent annuals such as *Mesembryanthemum crystallinum* in response to NaCl can also be brought about by any treatment that reduces water uptake, such as growth in nutrient solutions at low temperature or low osmotic partial pressure (Winter 1982). Although succulent annuals are most commonly found in saline habitats that are seasonally arid, the change in CO2 fixation is a response to water stress, not to salinity per se (Batanouny, 2001).

References

Adolf V.I., Jacobsen S.E., Shabala S. (2013) Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). Environ. Exp. Bot. 92, 43–54.
Doi: 10.1016/j.envexpbot.2012.07.004

Agarie S., Shimoda T., Shimizu Y., Baumann K., Sunagawa H., Kondo A., et al., (2007) Salt tolerance, salt accumulation, and ionic homeostasis in an epidermal bladder-cell-less mutant of the common ice plant *Mesembryanthemum crystallinum*. J. Exp. Bot. 58, 1957–1967. Doi: 10.1093/jxb/erm057

Al scher R.G., Erturk N., Heath L. (2002) Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. J. Exp. Bot., 53: 1331-1341.

Al-Ahmadi M.J., Kafi M. (2007) Salinity effects and cardinal temperatures on germination properties of *Kochi scoparia* L. J. Arid Environ 68: 308–314

Albert R. (1975) Salt Regulation in Halophytes Salt Regulation. Oecologia (Berl.) 21: 57- 71

Amarasinghe V., Watson L. (1988) Comparative ultrastructure of micro hairs in grasses. Bot. J. Linnean Soc., 98: 303–319.

Ashraf M., Hameed M., Arshad M., Ashraf M.Y., Akhtar K. (2006) Salt tolerance of some potential forage grasses from Cholistan desert of Pakistan. In: Khan M.A., Weber D.J. (Eds) Ecophysiology of high salinity tolerant plants. Springer, Netherlands, pp 31–54

Ashraf M., Hameed M., Arshad M., Ashraf Y., Akhtar K. (2006) Salt tolerance of some potential forage grasses from Cholistan desert of Pakistan. In: Khan M.A. Weber D.J. (Eds) Ecophysiology of high salinity tolerant plants. Springer, Dordrecht. The Netherlands, pp. 31–54.

Ashraf M., Harris P.J.C (2004) Potential biochemical indicators of salinity tolerance in plants. Plant Sci. 166:3–16

Ashraf M.Y., Ashraf M., Sarwar G. (2005) Physiological approaches to improving plant salt tolerance. In: Ramdane D. (Eds) Crops: growth, quality and biotechnology, WFL Publisher, Helsinki, pp 1206–1227

Askari H., Edqvist J., Hajheidari M., Kafi M., Salekdeh G.H. (2006) Effects of salinity levels on proteome of *Suaeda aegyptiaca* leaves. Proteomics 6: 2542–2554.

Aslam R., Bostan N., Amen N-e, Maleeha Maria M., Waseem S. (2011) A critical review on halophytes: Salt tolerant plants. Journal of Medicinal Plants Research, 5(33):7108-7118.

Badawi G.H., Yamauchi Y., Shimada E., Sasaki R., Kawano N., Tanaka K. (2004) Enhanced tolerance to salt stress and water deficit by over expressing superoxide dismutase in tobacco (*Nicotianatabacum*) chloroplasts. J. Plant Sci., 166: 919-928.

Balasuban R., Reeck T., Debez A., Stelzer R., Huchzermeyer B., Papenbrock J. (2006) *Aster tripolium* L. and *Sesuvium protulacastrum* L.: two halophytes, two strategies to survive in saline habitats. Plant Physiol. Biochem. (Paris) 44: 395–408.

Barhoumi Z., Djebali W., Smaoui A., Chaibi W., Abdelly C. (2006) Contribution of NaCl excretion to salt resistance of *Aeluropus littorallis* (Willd) Parl. J Plant Physiol 164: 842–850.

Barkla B.J., Vera-Estrella R. (2015) Single cell-type comparative metabolomics of epidermal bladder cells from the halophyte *Mesembryanthemum crystallinum*. *Front. Plant Sci.* 6:435. Doi: 10.3389/fpls. 2015.00435

Batanouny K.H. (1992b) Adaptation of plants to saline conditions in arid regions. In: Lieth H,
Masoom Al (Eds) towards the rational use of high salinity tolerant plants, vol 1. Kluwer Academic, Amsterdam, pp 387-401.

Batanouny K.H., (1994) Halophytes and halophytic plant communities in the Arab region. In: Squires V.R., Ayoub AT (Eds) Halophytes as a resource for livestock and for rehabilitation of degraded lands, vol 1. Kluwer-Academic, Amsterdam, pp 139-163

Batanouny K.H., (2001) Adaptations of desert organisms. In: Cloudsley-Thompson J.L. (ed) Plants in the deserts of the Middle East.

Batanouny K.H., Stichler W., Ziegler H. (1998) Photosynthetic pathways, distribution and ecological characteristics of grass species in Egypt. Oecologia, 75(4): 539-548.

Benlloch-Gonzalez M., Fournier J.M., Ramos J., Benlloch M. (2005) Strategies underlying salt tolerance in halophytes are present in *Cynara cardunculus*. Plant Sci. (Oxford) 168: 653–659.

Bennert H.W., Schmidt B. (1983): Untersuchungen zur Salzabscheidung bei *Atriplex hymenelytra* (TORR.) WATS. (*Chenopodiacceae*). Flora 174: 341-355.

Borsani O., Diaz P., Botella J. (2003) Developing salt tolerant plants in a new century: a molecular biology approach. Plant Cell Tiss Organ Culture, 73: 101-115.

Bose J., Munns R., Shabala S., Gilliham M., Pogson B., Tyerman D.T. (2017) Chloroplast function and ion regulation in plants growing on saline soils: lessons from halophytes. J. Exp. Bot., 68(12): 3129–3143

Breckle S.W. (1986) Studies on halophytes from Iran and Afghanistan. II. Ecology of halophytes along salt gradients. Proc. R. Soc. Edinb. 89B:203-215

Breckle S.W. (1990) “Salinity tolerance of different halophyte types,” in Genetic Aspects of Plant Mineral Nutrition, Eds. N. El Bassam, M. Dambroth, and B. C. Loughman (Berlin: Springer), 167–175. Doi: 10.1007/978-94-009-2053-8_26

Breckle S.W. (2002b) Salt deserts in Iran and Afghanistan. In: Böer B., Barth H.J. (eds) Sabkha ecosystems. Kluwer, Dordrecht, the Netherlands, pp 109–122

Briens M., Larher F. (1982) Osmoregulation in halophytic higher plants a comparative study of soluble carbohydrates, polyols, betaines and free proline. Plant, Cell and Environment, 5:287–292.
Céccoli G., Ramos J., Pilatti V., Dellaferrera I., Tivano J.C., Taleisnik E., et al., (2015) Salt glands in the Poaceae family and their relationship to salinity tolerance. Bot. Rev., 81: 162–178. Doi: 10.1007/s12229-015-9153-7

Chaparzadeh N., Amico M.L., Nejad R.K., Izzo R., Izzo F.N. (2004) Antioxidative responses of *Calendula officinalis*under salinity conditions. Plant Physiol. Biochem., 42: 695-701.

Cheeseman J.M., (1988) Mechanisms of salinity tolerance in plants. Plant Physiol., (87): 547-50.

Chen C.C., Chen Y.R. (2005) Study on laminar hydathodes of Ficus formosana (Moraceae) I. Morphology and ultrastructure. Bot. Bull. 46: 205–215.

Chen J., Yan J., Qian Y., Jiang Y., Zhang T., Guo H., et al., (2009) Growth responses and ion regulation of four warm season turfgrasses to long-term salinity stress. Sci.Hortic. (*Amsterdam*) 122, 620–625.doi: 10.1016/j.scienta.2009.07.004

Dassanayake M., John C. Larkin J.C. (2017) Making Plants Break a Sweat: The Structure, Function, and Evolution of Plant Salt Glands. Frontiers in plant sciences, 8(406): 1-20.
Doi: 10.3389/fpls.2017.00406

Day A.D., Ludeke K.L. (1993) Plant nutrients in desert environments. Springer, Berlin.

Ding F., Chen M., Sui N., Wang B.S. (2010a) Ca2C significantly enhanced development and salt secretion rate of salt glands of

Limonium bicolor under NaCl treatment. S. Afr. J. Bot. 76: 95 101. doi:10.1016/j.sajb.2009.09.001

Ding F., Yang J.-C., Yuan F., Wang B.S. (2010b) Progress in mechanism of salt excretion in recretohalopytes. Front. Biol. 5:164–170. Doi: 10.1007/s11515-010-0032-7

Drennan P.M., Berjak P., Lawton J.R., Pammenter N. (1987) Ultrastructure of the salt glands of the mangrove, *Avicennia marina* (Forssk.) Vierh, as indicated by the use of selective membrane staining. *Planta* 172, 176–183.doi: 10.1007/BF00394585

Duan D.Y., Liu X.J., Khan M.A., Gul B. (2004) Effects of salt and water stress on the germination of *Chenopodium glaucum'* seeds. Pak. J. Bot., 36: 793–800.

Eckardt F.D., Drake N.A., Goudie A.S., White K., Viles H. (2001) Th e role of playas in the formation of pedogenic gypsum crusts of the Central Namib Desert. Earth Surface Processes and Landforms, 26: 1177–93.

Eckardt F.D., Schemenauer R.S. (1998) Fog water chemistry in the Namib Desert, Namibia. Atmospheric Environment, 32: 2595–9.

Esau K. (1965) Plant Anatomy. New York, NY: John Wiley & Sons, Inc.

Ewing K., Earle J.C., Piccinin B., Kershaw K.A. (1989) Vegetation patterns in James Bay costal marshes II Physiological adaptation to salt-induced water stress in three halophytic graminoids. Can J. Bot. 67: 521–528.

Feng Z., Deng Y., Zhang S., Liang X., Yuan F., Hao J., et al. (2015) KC accumulation in the cytoplasm and nucleus of the salt gland cells of *Limonium bicolor* accompanies increased rates of salt secretion under NaCl treatment using NanoSIMS. *Plant Sci.* 238, 286–296. DOI:10.1016/j.plantsci.2015.06.021

Feng Z., Sun Q., Deng Y., Sun S., Zhang J., Wang B. (2014). Study on pathway and characteristics of ion secretion of salt glands of *Limonium bicolor*. Acta Physiol. Plant, 36: 2729–2741. Doi:10.1007/s11738-014-1644-3

Flowers T.J., Colmer T.D. (2015) Plant salt tolerance; adaptations in halophytes. Ann. Bot. 115, 327–331. Doi: 10.1093/aob/mcu267

Flowers T.J., Galal H.K., Bromham L. (2010) Evolution of halophytes; multiple origins of salt tolerance in land plants. Funct. Plant Biol. 37: 604–612. DOI: 10.1071/FP09269.

Flowers T.J., Yeo A.R. (1986) Ion relations of plants under drought and salinity. Austr. J. Plant Physiol., 13: 75-91.

Flowers T.J., Yeo A.R. (1988) Ion relations of salt tolerance, In: Baker, D.A., and Hall J.L. (eds.): Solute Transport in Plant Cells and Tissues. Longman Sci. and TechnicaL: Essex, UK., 392-416.

Freitasi H, Siegmar W. B., (1995) Importance of Bladder Hairs for Salt Tolerance of Field-Grown *Atriplex* Species from a Portuguese Salt Marsh. Flora 187: 283 – 297

Frey W., Kiirschner H., Stichler W. (1985) Photosynthetic pathways and ecological distribution of halophytes from four littoral salt marshes, (Egypt Sinai, Saudi Arabia, Oman and Iran). Flora, 177:107-130

Gao S., Ouyang C., Wang S., Xu Y., Tang L., Chen F. (2008) Effects of salt stress on growth, antioxidant enzyme and phenylalanine ammonia-lyaseactivitie in *Jatrophacurcas* L. seedling. Plant Soil Environ. 54: 374-381.

Glenn E., James O'Leary J.M., (1984) Relationship between salt accumulation and water content of dicotyledonous halophytes Plant Cell and Environment, 7: 253-261

Glenn E.P., Poster R., Brown J.J., Thompson T.L., O'Leary J.W. (1996) Na and K accumulation and salt tolerance of Atriplexcanescens (Chenopodiaceae) genotypes. Am. J. Bot., 83: 997-1005.

Gorham J. (1995) Betaines in higher plants biosynthesis and its role in stress metabolism. In Amino Acids and Their Derivatives in Higher Plants (ed. R.M. Wallsgrove), pp. 171–203. Cambridge University Press, Cambridge.

Gorham J., Hughes I., Wyn-Jones R.G. (1981) Low molecular weight carbohydrates in some salt stressed plants. Physiol. Plant 31: 149–190

Gul B., Weber D.J. (1998) Role of dormancy relieving compounds and salinity on the seed germination of *Allenrolfea occidentalis*. Ann Bot 82: 555–562.

Gulzar S., Khan M.A., Liu X. (2007) Seed germination strategies of *Desmostachya bipinnata*: a fodder crop for saline soils. Range Ecol. Manage. 60: 401–407.

Hameed M., Ashraf M., Ahmad M.S.A., Nargis N. (2010) Structural and Functional Adaptations in Plants for Salinity Tolerance. DOI: 10.1007/978-90-481-9370-7-8.

Hess W.M., Weber D.J. (1995) Morphology of epicuticular wax and comparison of lipids of *Allenrolfea occidentalis*. In: Khan MA, Ungar I.A. (eds) Biology of Salt Tolerant Plants. Dec. 12–16, 1994. pp. 107–117. Book Crafters, Department of Botany, University of Karachi, Karachi, Pakistan.

Jefferies R.L., Perkins N. (1977) The effects on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk. J. Ecol., 6S: 867-882

Kant S., Kant P., Raveh E., Barak S. (2006) Evidence that differential gene expression between the halophyte, *Thellungiella halophila* and *Arabidopsis thaliana* is responsible for higher levels of the compatible osmolyte proline and tight control of Na+ uptake in *T. halophila*. Plant Cell Environ 29:1200–1234.

Karmoker J.L., Farhana S., Rashid P. (2008) Effects of salinity on ion accumulation in maize (*Zea mays* L. cv. Bari–7). Bangladesh J. Bot. 37:203–205

Khan M.A., Gul B., Weber D.J. (2004) Temperature and high salinity effects in germinating dimorphic seeds of *Atriplex rosea*. Western North American Naturalist 64: 193–201.

Khan M.A., Weber D.J. (2006) Ecophysiology of High Saline Tolerant Plants. Tasks for Vegetation Science, vol 40. 399 pp. Springer, Dordrecht, The Netherlands.

Laetsch W.L.M. (1974) The C4 syndrome: a structural analysis. Annul Rev. Plant Physiol. 25:27-52

Lee J.A., Stewart G.R. (1978) Ecological aspects of nitrogen assimilation. Adv. Bot. Res. 6: 1-41.

Liu Q., Kasuga M., Sakuma Y., Abe H., Miura S., Yamaguchi-Shinozaki K., Shinozaki K. (1998) Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low temperature-responsive gene expression, respectively, in *Arabidopsis*. Plant Cell, 10: 1391-1406.

Lobova E.V., Khabarov, A.V. “Soil resources in arid and semiarid zones of the world,” in Arid Soils, Their Genesis, Geography, and Use (Nauka, Moscow, 1977), pp. 7–15 [in Russian]

Maathius F.J.M., Flowers T.J., Yeo A.R. (1992) Sodium chloride compartmentation in leaf vacuoles of the halophytes *Suaedamaritima* (L.) and its relation to tonoplast permeability. J. Exp. Bot., 43: 1219-1223.

Manousaki E., Ksdukova J., Papadantonakis N., Kaoerakis N. (2008) Phytoextraction and phytoexcretion of Cd by the leaves of Tamarix smyrnensis growing on contaminated non-saline and saline soils. Environ. Res. 106(3): 326-32.

Marcum K.B., Murdoch C.L. (1994) Salinity tolerance mechanisms of six C4 turfgrasses. J. Am. Soc.

Maricle B.R., Koteyeva N.K., Voznesenskaya E.V., et al., (2009) Diversity in leaf anatomy, and stomatal distribution and conductance, between salt marsh and freshwater species in the C4 genus Spartina (Poaceae). New Phytol. 184: 216–233. Doi: 10.1111/j.1469-8137.2009. 02903.x

Masoom A.l., Lieth H. (Eds) Towards the rational use of high salinity tolerant plants, vol 1. KluwerAcademic, Amsterdam, pp 387-401, (1994)

Mauseth J.D. (1988) Plant anatomy; The Benjamin/Cummings Publishing Company, California
Mimura T., Kura–Hotta M., Tsujimura T., Ohnishi M., Miura M., Okazaki Y., Mimura M., Maeshima M., Washitani–Nemoto S. (2003) Rapid increase of vascular volume in response to salt stress. Planta 216:397–402

Mittler R. (2002). Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci., 7: 405-410.
Munns R., James R.A. (2003) Screening methods for salinity tolerance: a case study with tetraploid wheat. Plant Soil 253: 201–218

Munns R., James R.A., Läuchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J. Exp. Bot. 57:1025–1043

Munns R., Tester M. (2008) Mechanisms of salinity tolerance. Ann. Rev. Plant Biol., 59: 651-681.

Oh D., Barkla B., Vera-Estrella R., Pantoja O., Lee S., Bohnert H., et al. (2015) Cell type-specific responses to salinity-the epidermal bladder cell transcriptome of *Mesembryanthemum crystallinum*. New Phytol. 207: 627–644. Doi: 10.1111/nph.13414

Oh D-Ha, Bronwyn J.B., Vera-Estrella R., Pantoja O., Lee S., Bohnert S.J., Dassanayake M. (2015) Cell type-specific responses to salinity-The epidermal bladder cell transcriptome of Mesembryanthemum crystallinum. New Phytologist 207(3): 1-18. DOI: 10.1111/nph.13414.

Osmond C., Bjorkman D., Anderson D.J. (1980) Physiological Processes in Plant Ecology. Towards a synthesis with Atriplex. Berlin. Eco1. Studies 36

Osmond C.B., Winter K., Ziegler H. (1982) Functional significance of different pathways of CO2 fixation in photosynthesis. In: Lange O.L., Nobel P.S., Osmond C.B., Ziegler H (eds) Encyclopedia of plant physiology, new series, vol 12B. Physiological plant ecology. Springer, Berlin Heidelberg New York

Pan Y., Guo H., Wang S., Zhao B., Zhang J., Ma Q., et al. (2016) The photosynthesis, NaC/KC homeostasis and osmotic adjustment of *Atriplex canescens* in response to salinity. *Front. Plant Sci.* 7:848. Doi: 10.3389/fpls.2016.00848

Pankova E.I., Vorob’eva L.A. (2006) “Diagnostics and criteria of soil salinization,” in Salt Affected Soils of Russia (IKTs Akademkniga, Moscow, 2006), pp. 6–50 [in Russian]

Pankova Y.I., Dokuchaev V.V. (2006) Soil salinity in the Gobi (Mongolia). 18th World Congress of Soil Science, Philadelphia, P.A.

Park J., Okita T.W., Edwards G.E. (2009) Salt tolerant mechanisms in single-cell C4 species *Bienertia sinuspersici* and *Suaeda aralocaspica* (Chenopodiaceae). Plant Sci. 176: 616–626. Doi: 10.1016/j.plantsci.2009.01.014

Passardi F., Cosio C., Penel C., Dunand C. (2005) Peroxidases have more functions than a Swiss army knife. Plant Cell Rep., 24: 255-265.

Peng Z., He S., Sun J., Pan Z., Gong W., Lu Y., et al. (2016) NaCl compartmentalization related to salinity stress tolerance in upland cotton (Gossypium hirsutum) seedlings. Sci. Rep. 6:34548. Doi: 10.1038/srep34548

Perera L.K., Mansfield T.A., Malloch J.C. (1994) Stomatal responses to sodium ions in *Aster tripolium*: a new hypothesis to explain regulation in above ground tissues. Plant Cell Environ 17: 335–340.

Rahnama H., Ebrahimzadeh H. (2005) The effect of NaCl on antioxidant enzyme activities in potato seedlings. J. Plant Biol., 49: 93-97.

Rains D.W., Epstein E. (1967) Preferential absorption of potassium by leaf tissue of the mangrove *Aticennia marina:* an aspect of halophytic competence in coping with salt. Aust J Bioi Sci 20:847-857

Ramadan B.T. (1998) Ecophysiology of salt excretion in the ero-halophyte, *Reaumuria hirtella*. New Phytol 139:273–281.

Ramadan T., Flowers T.J. (2004) Effects of salinity and benzyladenine on development and function of microhairs of *Zeamays* L. *Planta* 219, 639–648. doi: 10.1007/s00425-004-1269-7

Redondo-Gomez S., Mateos-Naranjo E., Davy A.J., Fernandes-Munozn F, Castellance EM, Luque T., Figueroa M.E. (2007) Growth and photosynthetic responses to salinity of the saltmarsh shrub *Atriplex portulacoides*. Ann. Bot. 100: 555–563.

Reimann C., Breckle S.W. (1993) Sodium relations in Chenopodiaceae, a comparative approach. Plant Cell Environ. 16: 323–328.

Reimann C., Breckle, S.W. (1988) Salt secretion in some *Chenopodium* species. - Flora 180: 289-296.

Santos J., Al-Azzawi M., Aronson J., Flowers T.J. (2016) eHALOPH a database of salt-tolerant plants: helping put halophytes to work. Plant Cell Physiol. 57:e10. Doi: 10.1093/pcp/pcv155.

Scholander P. F., Bradstreet E.D., Hamml H.T., Hemminsen A.T.A. (1966) Sap concentrations in halophytes and some other plants. Plant Physiol., 41: 529-532.

Semenova G.A., Fomina I.R., Biel K.Y. (2010) Structural features of the salt glands of the leaf of *Distichlisspicata* ‘Yensen4a’ (Poaceae). *Protoplasma* 240, 75-82. Doi: 10.1007/s00709-009-0092-1

Shabala S., Bose J., Hedrich R. (2014) Salt bladders: do they matter? Trends Plant Sci. 19, 687–691.Doi:10.1016/j.tplants.2014.09.001

Shalata A., Tal M. (2002) The effect of salt stress on lipid peroxidation and antioxidants in the leaf of the cultivated tomato and its wild salttolerant relative *Lycopersicon pennelli.* Physiol. Plant., 104: 169-174.

Shi S., Huang Y., Zeng K., Tan F., He H., Huang J. (2005) Molecular phylogenetic analysis of mangroves: independent evolutionary origins of vivipary and salt secretion. Mol. Phylogenet. Evol. 34, 159–166. Doi: 10.1016/j.ympev.2004.09.002

Song J., Ding X.D., Feng G., Zhang F. (2006) Nutritional and osmotic roles of nitrate in a euhalophyte and xerophyte in saline conditions. New Phytol. 171: 357–366.

Song J., Feng G., Tian C., Zhang F. (2005) Strategies for adaptation of *Suaeda physophora, Haloxylon ammodendron* and *Haloxylon persicum* to a saline environment during seed germination. Ann. Bot. (London) 96: 399–405.

Song J., Feng G., Zhang F. (2006) Salinity and temperature effect on three salt resistant euhalophytes, *Halostachys capsica, Kalidium foliatum* and *Halocnemum strobilaceum*. Plant Sci., 279: 201–207

Storey R., Wyn Jones R.G. (1979) Response of Atriplex spongiosa and *Suaeda monica* to salinity. Plant Physiol. 63:156–162

Szabolcs I., Salt Affected Soils (CRC Press, Boca Raton, 1989.

Tan W.K., Lim T.M., Loh C.S. (2010) A simple, rapid method to isolate salt glands for three-dimensional visualization, fluorescence imaging and cytological studies. *Plant Methods* 6:24. Doi: 10.1186/1746-4811-6-24

Tan W.K., Lin Q., Lim T.M., Kumar P., Loh, C.S. (2013) Dynamic secretion changes in the salt glands of the mangrove tree species Avicennia officinalis in response to a changing saline environment. Plant Cell Environ. 36, 1410–1422. Doi: 10.1111/pce.12068

Tester M., Davenport R. (2003) Na+ tolerance and Na^+ transport in higher plants. Ann. Bot. 91: 503–527.

Thomson W., Faraday C.D., Oross J.W. (1988) "Salt glands," in In Solute Transport in Plant Cells and Tissues, Eds D. A. Baker and J. L. Hall (Harlow: Longman Scientific & Technical), 498–537.

Thomson W., Platt-Aloia K. (1985) The ultrastructure of the plasmodesmata of the saltglands of *Tamarix* as revealed by transmission and freeze-fracture electronmicroscopy. Protoplasma 125: 13–23. Doi: 10.1007/BF01297346

Tipirdamaz R., Gagneul D., Duhaze C., Ainouche A., Monnier C., Ozkum D., Larher F. (2006) Clustering of halophytes from an inland salt marsh in Turkey according to their ability to accumulate sodium and nitrogenous osmolytes. Environ. Exp. Bot. 57: 139–153.

Wang S.M., Wan C.G., Wang Y.R., Chen H., Zhou Z.Y., Fu H., Sosebee R.E. (2004) The characteristics of Na+, K+, and free proline distribution in several drought-resistant plants of the Alxan Desert, China. J. Arid Environ. 56: 525–539.

Warwick N.W.M., Halloran G.M. (1992) Accumulations and excretion of sodium, potassium and chloride from leaves of two accessions of *Diplachne fusca* (L) Beauv. New Phytol. 121: 53–61

.

Weber D.J. (1995) Mechanisms and reactions of halophytes to water and salt stress; In: Khan M.A., Ungar I.A. (Eds) Biology of Salt Tolerant Plants. pp. 170–180. Book Chapter, Department of Botany, University of Karachi, Karachi, Pakistan.

Weber D.J., Ansari R., Gul B., Khan M.A. (2007) Potential of halophytes as source of edible oil. J. Arid Environ. 68:315–321.

Weber D.J., Hess W.M., Kim C.K. (1980) Distribution of ATPase in cells of *Salicornia pacifica* var. *utahensis* as determined by lead phosphate precipitation and x-ray microanalysis. New Phytol. 84: 285–291.

Winter K., Ziegler H. (1982) Functional significance of different pathways of CO2, fixation in photosynthesis. In: Lange O.L., Nobel P.S., Osmond C.B., Ziegler H. (Eds) Encyclopedia of plantphysiology. New series, vol 12B. Physiological plant ecology II. Springer, Berlin Heidelberg, New York

Xi J., Zhang F., Chen Y., Mao D., Yin C., Tian C. (2004) A preliminary study on salt contents of soil in root-canopy area of halophytes. Yingyong Shengtai Xuebao 15: 53–58.

Xiong L., Zhu J.K. (2002). Molecular and genetic aspects of plant responses to osmotic stress. Plant Cell Environ, 25: 131-139.

Xu C., Tang X., Shao H., Wang H. (2016) Salinity Tolerance Mechanism of Economic Halophytes From Physiological to Molecular Hierarchy for Improving Food Quality Current Genomics, 17:207-214.

Xu D.P., Duan X.L., Wang B.Y., Hong B.M., Ho T.H.D., Wu R. (1996) Expression of a late embryogenesis abundant protein gene, HVA1, from barley confers tolerance to water deficit and salt stress in transgenic rice. Plant Physiol., 110: 249-257.

Yi L., Ma J., Li Y. (2007) The comparisons of root systems and root hair morphological characteristics among three desert halophytes. Bull Bot Res 27: 204–211.

Yuan F., Lyv M.J.,Leng B.Y., Zheng G.Y., Feng Z.T., Li P.H., et al. (2015) Comparative transcriptome analysis of developmental stages of the *Limonium bicolor* leaf generates insights into salt gland differentiation. Plant Cell Environ. 38: 1637–1657. Doi:10.1111/pce.12514

Zhu J.K. (2000) Genetic analysis of plant salt tolerance using Arabidopsis. Plant Physiol., 124: 941-948.

Chapter 7

Desiccation tolerance

Introduction

Desiccation stress causes considerable loss of cellular water and thus significant cellular disorganization. Early studies on desiccation tolerance in resurrection plants focused on ultra-structural studies on folded cell walls. Studies of cell wall folding in the endosperm of dry seeds suggested the importance of cell wall folding as a mechanism to maintain structural organization as well as cell viability in the desiccated state.

The vegetative tissues of resurrection plants are able to survive protoplastic dehydration of less than 2% relative water content. The majority of flowering plants and also gymnosperms have desiccation-tolerant seeds or pollen. This trait is strictly developmentally regulated; it is acquired during embryogenesis (Bartels et al., 1988) or pollen development, but lost during germination.

Among plants, desiccation tolerance is common in primitive plants such as lichens and bryophytes. This form of anhydrobiosis seems to comprise constitutively expressed cell protection mechanisms associated with inducible repair systems that are activated after rehydration (Oliver and Bewley, 1997). Also among algae, it is possible to find species able to tolerate desiccation, either in terrestrial or in marine intertidal algae (Trainor and Gladych 1995; Abe et al., 2001).

The taxonomic representation of desiccation tolerance in plants is now fairly well established. Although desiccation tolerance in plants is very uncommon, it occurs in many different taxa except gymnosperms (Alpert, 2000). Desiccation tolerant species are found on all continents and among species of all growth forms except trees, but it remains a mystery why desiccation tolerance is not more widespread.

7.1. Evolution of Desiccation Tolerance

Many primitive autotrophs, such as cyanobacteria, are desiccation tolerant. This indicates that desiccation tolerance is a very early trait in evolution. According to Oliver et al. (2000), phylogenetic evidence exists that among land plants tolerance to vegetative desiccation was present in the basal clade of bryophytes. This adaptive trait was likely to be critical for colonization by primitive terrestrial forms of the relatively dry land environment (Kappen and Valladares, 1999). With the evolution of more complex vascular plants, desiccation tolerance was lost in vegetative tissues but was retained in reproductive tissues (Oliver et al., 2000). The acquisition of desiccation tolerance is part of a maturation programme during seed development in higher plants (Angelovici et al., 2010). The majority of terrestrial plants are capable of producing desiccation-tolerant structures such as seeds and pollen, which can remain viable in the desiccated state for long periods as demonstrated in the case of the ancient Nelumbo nucifera (sacred lotus) seed from China (Shen-Miller et al., 1995). It is hypothesized that desiccation tolerance was crucial for ancestral freshwater autotrophs to live on land. Independent evolution or re-evolution of desiccation tolerance has happened in the Selaginellales, leptosporangiate ferns, and in at least ten families of angiosperms. Evolutionary progress may be evident from the fact that pteridophytes, like bryophytes, are able to synthesize rehydrin proteins but can also synthesize dehydrin proteins, which are typical for angiosperms (Oliver et al., 2000).

The genes involved in desiccation tolerance were not lost, but were instead recruited for activation of drying responses in reproductive structures through inductive mechanisms during developmental programs of the plant. It seems that resurrection plants have re-directed gene expression of seed-specific genes to be expressed in vegetative tissues (Illing et al., 2005).

The presence of this information in the genomes of vascular plants permitted many species to spread over regions with seasonal rain fall and to re-evolve desiccation tolerance in vegetative tissues based on inducible responses triggered by environmental cues (Rascio and La Rocca, 2005).

7.2. Resurrection plants

Desiccation tolerance is a feature of plants capable of experiencing protoplasmic dehydration without permanent injury. Except for the seed stage, this latter mechanism is poorly developed in the majority of higher plants. Losses greater than 40-90 % of normal water content or equilibration with relative humidity lowers than 91-98 % (Levitt et al., 1972) are lethal for higher plants. By contrast, many lower plants (and some angiosperms) are remarkable in the ability of their vegetative tissues to withstand extreme drought and desiccation. Known also as poikilohydrous plants (Walter, 1955b), poikiloxerophytes (Henckel and Pronina, 1968), or resurrection plants, these desiccation-tolerant plants are loosely defined by their unique ability to revive from an air-dry condition (the air having a low relative humidity). Plants that succumb to desiccation are called desiccation- sensitive, desiccation-intolerant or homoiohydrous plants (Walter, 1955b).

7.2.1. Geographic Distribution

Resurrection plants are found in places where rainfall is seasonal and sporadic. They often grow on rocky outcrops at low to moderate elevations in tropical and subtropical climates (Porembski and Barthlott, 2000). Under these conditions, they are subjected to frequent cycles of drying and rehydration throughout the year and thus tolerate being dry in a broad range of temperatures (Mundree et al., 2002; Moore et al., 2007). Most resurrection plants have been reported from the southern hemisphere of Africa, India, Australia, and South America.

Resurrection plants have been identified within the angiosperms among both monocotyledonous and dicotyledonous plants. The dicotyledonous plants are represented mainly in the Linderniaceae, Scrophulariaceae, and Myrothamnaceae families, whereas the monocotyledonous are more scattered among different families. A first phylogenetic analysis among the Scrophulariaceae suggests a clustering of desiccation-tolerant plants represented by the genera Craterostigma and Lindernia (Rahmanzadeh et al., 2005).

It has been suggested that desiccation tolerance is connected with a size limitation, since all examples of desiccation-tolerant flowering plants do not exceed a certain height (Bewley and Krochko, 1982), the largest known resurrection plant is the small woody shrub

Myrothamnus flabellifolius, which can be between 0.5 m and 1.5 m tall (Moore et al. 2007). Most resurrection plants are herbaceous plants. Most of the desiccation-tolerant angiosperms such as *Myrothamnus flabellifolia*, Xerophyta spp., or Craterostigma spp. are native to Southern Africa (especially South Africa, Namibia, and Zimbabwe).

7.2.2. Morphological aspects

Leaf folding is one of the most obvious morphological changes in desiccation tolerant vascular plants (Vander Willigen et al. 2003; Farrant et al., 2007). Leaves of *Craterostigma wilmsii* or *C. plantagineum*, which are fully expanded when watered, progressively curl inward during drying and become tightly folded so that only the abaxial surfaces of the older leaves in the outer whorl are exposed to the sun. Leaf folding is thought to limit oxidative stress damage from UV radiation and is thus an important morphological adaptation for surviving desiccation. Indeed, *C. wilmsii* plants do not survive desiccation in sunlight, if the leaves are mechanically prevented from folding (Farrant et al., 2003).

The leaf blades of *Aloe X. humilis* fold in half along the midrib upon dehydration, leaving only the abaxial surface exposed to the light. In *Sporobulus stapfianus*, the leaf adaxial side, which is most exposed to sun radiation, is very rich in epicuticular waxes, whose function is, besides decreasing transpiration, to reflect light and to limit irradiation and temperature increase (Dalla Vecchia et al., 1998). Leaf movements occurring during dehydration have been suggested to reduce the effective transpiring surface during early stage dehydration and/or to prevent excessive irradiation of air-dry younger tissue (Farrant, 2000).

Resurrection plants developed different mechanisms to avoid the potential mechanical stress during dehydration. A loss of water from cells leads to shrinkage of the central vacuole and to a drawing inward of the cell contents. This causes tension between the plasmalemma and the cell wall, which generally exhibits limited elasticity.

In some resurrection plants, mainly dicotyledons, the protoplast shrinkage occurring upon dehydration is accompanied by an extensive folding of cell walls, which results in a contraction of the entire cell and avoids the tearing of the plasmalemma from the cell wall (Vicre´ et al., 2004). This phenomenon prevents the development of negative turgor pressure and reduces the potential for irreversible mechanical damage (Vander Willigen et al., 2003). Also, high degree of cell wall flexibility induces the tensile strength of the cell wall, allowing it to contract and to fold without collapsing in the dried tissue.

An increase in expansin activity during desiccation is associated with a rise in cell wall flexibility and folding. This increase in cell wall flexibility is correlated with an increase in expansin transcript levels and activity (Jones and McQueen-Mason 2004; Moore et al. 2008). Expansins are cell wall loosening factors and are thought to act by disrupting the hydrogen bonds between cellulose and hemicellulose polymers in the cell wall (McQueen-Mason and Cosgrove, 1995). Thus, the ability of cell walls to fold by changing their chemistry and texture is an adaptive strategy of resurrection plants, but the molecular basis of this alteration is hardly known. Recently, a glycine-rich protein has been correlated with cell wall flexibility in Boea hygrometrica (Wang et al., 2009). These exceptional features are remarkable when compared to the rigidification of the cell wall in response to drought in non-resurrection plants (Munns et al. 2000).

7.3. Poikilohydric plants

Poikilohydric plants can occupy habitats that are unavailable to intolerant plants because, relative to potential carbon gain, they can benefit from: (1) extreme desiccation (and sometimes temperature) tolerance; (2) utilization of dew or water vapour for hydration (some species only); and (3) rapid emergence from the quiescent state, including photosynthetic recovery with the availability of water.

Nonetheless, these benefits must be considered against the potential carbon costs associated with: (1) stored energy and/or time costs for physiological reactivation upon rehydration; (2) physiological deterioration with increasing time in the dry state, (3) low photosynthetic rates, and (4) decline in membrane integrity permitting carbohydrate and nutrient losses during rehydration with liquid water.

Different species have developed different ecological, morphological, and (presumably) physiological adaptations to ultimately accomplish a net gain in their photosynthetic productivity.

Apart from bacteria, lichens are the most successful pioneers in extreme environments: members of this group can tolerate very hot, very cold, and very dry conditions and some species are even found on permanently inundated habitats. There do not appear to be any common morphological features that distinguish poikilohydrous plants from intolerant species. Tolerance of desiccation can be attributed largely to properties of the protoplasm. Tolerant plants do not undergo severe water deficit without perturbation to their metabolic and cellular integrity, but critical features of desiccation-tolerance may be the ability to limit damage caused by desiccation to a repairable level and to repair damage quickly upon subsequent rehydration. The integrity of the majority of metabolic systems (or at least of their components) is probably retained in the dry state, and these systems are quickly reactivated upon rehydration. This is probably also an important feature, since hydration of many poikilohydrous plants is a transient phenomenon. Obviously, any plant in any environment can only survive if it is able to achieve a net gain in its carbon status, and the adaptations of poikilohydrous plants should be viewed in relation to this fact.

When poikilohydrous plants are dry, they become dormant and their metabolic processes are reduced to a minimum. In this state their reactivity to the environment is much reduced. According to Batanouny (2001), they are physiologically and ecologically quasi-isolated from their surroundings and therefore more resistant to drought and high temperature. Because of their activation and inactivation cycles, desert thallophytes have limited periods during which the production of dry matter takes place. Therefore their rate of growth is extremely slow.

7.3.1. Desiccation tolerance in lichens

Lichens are symbiotic organisms, comprising a fungus (the mycobiont) and either an alga or a cyanobacterium (the photobiont). They range in size from tiny crusts less than 1 mm^2 to pendulous forms that hang more than 2 m from tree branches. Lichenization is one of the most successful ways that fungi use to fulfill their need for carbohydrates, and about 20% of all fungi are lichenized (Hawksworth, 1988). There are 13,500 species of lichens in the world, corresponding to 15% of all fungi. However, these obligatory symbiotic species are not randomly distributed within the fungal kingdom. Lichenization is almost restricted to the Ascomycota (ascolichens), which claims more than 98% of all lichenforming species (Hawksworth, 1988); 42% of the Ascomycota are lichenized.

Lichens represent a minor component of most terrestrial ecosystems; they form the dominant plant life on 8% of the world's land surface, mainly indesert, arctic and antarctic regions (Neg, 2000). These habitats are characterized by severe abiotic stresses such as desiccation, temperature extremes, and high light intensities. For this reason, lichens have been called "extremophiles," organisms that can thrive in conditions that would kill other, less-specialized organisms. Scientists have found that lichens can survive a trip into space—during a recent experiment by the European Space Agency, lichens were placed onboard a rocket and launched into space, where they were exposed to vacuum, extreme temperatures, and ultraviolet radiation.

The life of most lichens is characterized by rapidly changing water contents and correspondingly rapidly changing physiological activity such as respiration and photosynthesis (Kappen and Valadares, 1999). Variations in precipitation and dewfall largely account for the varying hydric conditions of the lichens and their corresponding CO2 exchange activity. To survive, it is clear that most lichens must be desiccation tolerant. Desiccation occurs reasonably slowly, most lichens can withstand drying to water contents of 5% or less, and most can remain viable for months, providing they are stored at low relative humidities. Even aquatic species such as *Dermatocarpon fluviatile* can survive desiccated for 4 weeks.

7.3.2. Morphology of lichens

Lichen is a composite, symbiotic organism comprising two or more constituents, the most frequent being an alga and a fungus. In cross section (Fig. 1.1), typical lichen is composed mainly of fungal tissue, but embedded in the upper cortical layers are eukaryotic algal cells. Some lichens are also associated with cyanobacteria (blue-green algae) found in special structures called cephalodia, and lichens may also associate with other microorganisms. Hence, lichen can be considered as an 'ecosystem' in which several constituent organisms collaborate (Farrar, 1976).

There are three major types of lichen growth form, viz. the crustose type composed of a thin crust that is tightly attached to the substratum, the foliose type that comprises a series of radially arranged leaflike lobes, and the fruticose type in which the lichen thallus is attached to the substratum at a single point and forms a complexnbranched structure. Various morphological adaptations in lichens result in an increase in this ratio by changing growth form, branching pattern, or thallus thickness (Larson, 1984).

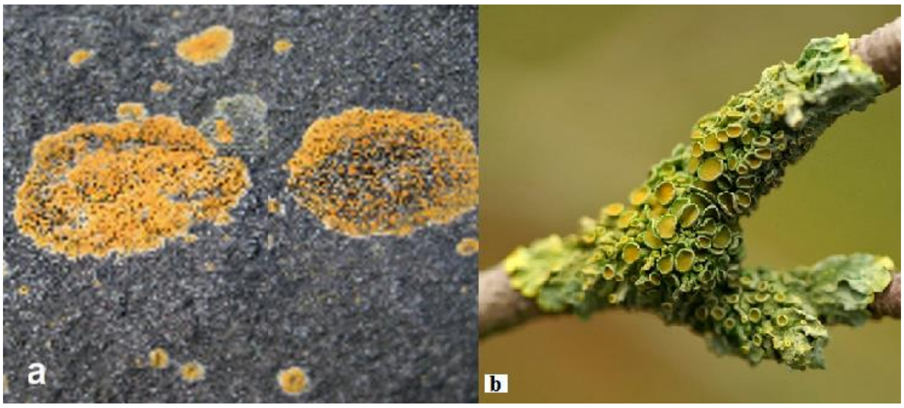

Figure 7.1 The two main growth forms of lichens: (a) the crustose lichen *Caloplaca marina* (Wedd.) Zahlbr. Ex Du Riez, (b) the foliose lichen *Parmelia sulcata* T. Tayl (coutesy of Armstrong, 2017).

Lichens in deserts exhibit many of the characteristics of Grime's stress-tolerant organisms, i.e. slow growth rates, significant longevity, and low demand for nutrients, and adaptations to stressful conditions.

Nevertheless, lichen species also occur in considerable frequency in the tropics where competition is intense. Hence, despite being stress-tolerant organisms, lichens may need additional mechanisms to enable them to survive in the highly competitive wet forests. Various substances unique to the symbiosis could be used as defensive allelochemicals, enabling a large number of species to survive in relative low abundance in the wet forests.

A number of studies suggest that the lichen symbiosis is significantly more tolerant of extreme conditions than its constituent algae and fungi. This resistance is likely to be attributable to the various morphological and physiological adaptations specific to the symbiosis such as a layered thallus structure, the presence of lichen compounds, and a physiology enabling survival in extremely dry conditions (Meessen et al., 2014). In addition, the alga and fungus appear to be able to induce increased regulation of protective systems in the other (Kranner et al., 2005).

Adaptations of lichens to extreme conditions often involve changes in morphology and physiology, and there is a close interrelationship between the two. Hence, the tomentum in some lichens of the wet forest (Kappen 1988) may be water-holding adaptation, preventing the thallus becoming saturated for long periods, thus enabling more optimal nPS for longer periods. In addition, the lower cortex may be sealed to prevent water uptake but permeable to CO2, a similar adaptation to that of the SO2-tolerant lichen *L. conizaeoides* (Shirtcliffe et al., 2006).

Some desert lichen species exhibit an ‘inversion’ of thallus structure in which the algal layer is located ventrally rather than dorsally, thus increasing protection of the alga and enabling photosynthesis at higher light intensities (Broady, 1986). Moreover, dark pigmentation or increased exposure of a black prothallus is found in most extremely cold environments and may be an adaptation to enable the thallus to absorb heat and melt covering snow, thus enabling photosynthesis to begin more rapidly.

In general, when poikilohydrous plants are dry, they become dormant and their metabolic processes are reduced to a minimum. In this state their reactivity to the environment is much reduced. They are physiologically and ecologically quasi-isolated from their surroundings and therefore more resistant to drought and high temperature. Because of their activation and inactivation cycles, desert thallophytes have limited periods during which the production of dry matter takes place. Therefore their rate of growth is extremely slow (Batanouny, 2001).

7.3.3. Ability to Use Water Vapor

An important adaptation of lichens to water shortage is their ability to use not only liquid water but also water in the form of vapor, fog, and dew. For reasons that are unclear, while lichens with chlorophycean photobionts can achieve net photosynthesis from atmospheric moisture alone, species with cyanobacterial photobionts need liquid water. However, interestingly, desiccated cyanobacteria isolated from lichens in axenic cultures can display net photosynthesis following uptake of water vapor alone (Jenks and Wood, 2007). Lange and his co-workers have elegantly demonstrated the remarkable ability of some desert lichens to achieve net photosynthesis with nonliquid water, for example, in the coastal fog zones of Chile and in Namibia (Lange et al., 1990). *Ramalina maciformis* from the Sina in Egypt can carry out net photosynthesis when the relative humidity exceeds 80%, and at a relative humidity of 95%, CO2 uptake is identical to that of a fully hydrated thallus. In *Teloschistes capensis* growing in the coastal fog zone of the Namib Desert, heavy dewfall, supplemented by fog, typically increases the thallus water to 60% by midnight. A small but significant amount of respiration occurs during the night. After sunrise, lichens can achieve net photosynthetic rates of up to 16 nmol CO2 $g^{-1}.sec^{-1}$ for a few hours until thalli dry out, and photosynthesis and respiration stop.

In very cold habitats such as mainland Antarctica, the metabolic activity of lichens is severely limited by water availability and low temperatures. Schroeter and Scheidegger (1995) have shown that desiccated lichens can take up enough water to photosynthesize from the sublimation (vapor phase) of snow. The lowest temperature measured for net photosynthesis was -17 °C for *Umbilicaria aprina* at a continental Antarctic site. Even if lichens are “hydrated,” at low temperatures they will be subjected to severe “physiological drought.” For example, if water-saturated thalli of *U. aprina* were slowly cooled at subzero temperatures, ice nucleation activity could be detected at -5°C, indicating extracellular freezing of water.

Extracellular ice formation leads to cytorrhysis (cell collapse) of the photobiont cells and cavitation of the mycobiont cells. However, both processes were reversible if the lichen thallus was rewarmed. Furthermore, even if lichens were frozen in a hydrated state, they could still photosynthesize at subzero temperatures. Later studies in Antarctica (Pannewitz et al., 2003) showed that although the snow cover represented the major water supply, lichens became active only for a short period when the snow melted. The snow did not provide a protected environment, as occurs in some alpine habitats, but appeared to limit lichen activity.

Under conditions of high relative humidity, lichen thalli slowly absorb moisture until they reach an internal vapour pressure that is in equilibrium with the atmosphere. Most lichens achieve a water content of 40-50 % in a saturated atmosphere, but a number of days are required for this stage to be reached. Exposure for several hours to relative humidities above 90 % is usually sufficient to bring thallus moisture contents above the photosynthetic compensation point. It is not surprising, therefore, to observe that areas of the world with consistent patterns of high humidity but low pre cipitation support rich lichen floras. This diversity and the associated ecological importance of lichens are particularly evident in desert fog zones (Batanouny, 2001).

7.3.4. Algae

Historical studies show that desiccation tolerance must have evolved at least two times independently, first, in the prokaryotic algae and, second, in the newly evolved eukaryotic algal lineages originating from either primary (green and red algae) or secondary endosymbiosis (brown algae). Desiccation-tolerant algae are found among the three major groups of the green land plants (Chlorobionta), the Chlorophyta, the Prasionophyta, and the Charophyta. Other desiccation-tolerant algae are found in the red algae (Rhodophyta) and the polyphyletic group of algae with heterokont flagellae, including the brown algae (Phaeophyceae). The lowest limiting values for the state of hydration of algae in terms of water potential, at which the first irreversible effects or necrotic injuries appear, are employed as the measure of desiccation tolerance (sublethal at 5–10% injury, 50% is desiccation lethally, DL[1]50) (Larcher 2001). Marine littoral algae are among the most sensitive algae that can survive desiccation without injury at -1.4 to -4 MPa (99–97% relative air humidity, lower sublittoral); -7 to -20 MPa[2] (95–86%, sublittoral), and -20 to -25 MPa (86–83%, eulittoral). Algae of exposed rocks or the bark of trees may even tolerate water potentials as low as -140 MPa to indefinite for certain periods of time, depending on the functional group they belong to.

7.3.4.1 Marine Coastal Algae

Marine macroalgae (seaweeds) comprise about 20,000 species of which a large number can be found in the intertidal zone (Einav and Israel 2007). The intertidal shoreline zone of the oceans is a habitat of dramatic changes (Fig. 7.2). Its upper regions are the beginning of terrestrial vegetation and are often sparsely inhabited by algae. There,

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[1] - Dessication Lethally (DL)

[2] - Mega Pascal (MPa)

scattered or abundant lichens occur and between them, patchy populations of macroscopic algae can be interspersed. In this upper intertidal zone and below, algae are found exposed on bare rock and not in rock pools. In terms of physiological constraints, this zone is the most stressful encountered by organisms in general, and by marine algae in particular. A recent review on this topic is that of Garbary (2007) for example. For marine intertidal algae, the benefits of drying out are often overshadowed by the stresses (e.g., light and salinity) involved (Hunt and Denny, 2008).

Figure 7.2 Marine algae in coastal habitats under low tide (courtesy of Lǘttge et al., 2011)

7.3.4.2 Hypolithic algae in desert

According to Baanouny (2001), desert algae can absorb water from the air when the relative humidity exceeds 70 %. They become photosynthetically active within 15-20 min after being wetted. The same author, as quoted from Orshan (1986), estimated the standing algal biomass to be 0.02 t/ha. The lower sides of semi-translucent flints in the desert represent a habitat for particular algae. They enjoy the relatively high humidity conserved below the flint and receive light through the flint window. These hypolithic algae can photosynthesize at lower light intensities than algae in the open desert. Slight showers moisten the thin soil film below the flint. Such moisture is protected from rapid evaporation and represents a reasonable water supply to the algae below the flint, which make use of the humidity of the air.

The hypolithic community was named “hypolithon” (Schlesinger et al. 2003) and occurs along a zone of sufficient light for positive net photosynthesis. Although the hypolithon is mainly composed by cyanobacteria, eukaryotic algae occur frequently.

From the Namib Desert, even diatoms were reported from the hypolithic habitat (Rummrich et al. 1989). Vogel (1955) was the first who gave a species list of four green algae and one diatom identified from the hypolithon of South Africa. In a later investigation, Friedmann et al. (1967) determined 11 hypolithic green algal species from the Sinai Desert.

However, Azúa-Bustos et al. (2011) findings strongly suggests that hypolithic microbial communities thriving in the seaward face of the Coastal Range can survive with fog as the main regular source of moisture. A model is advanced where the development of the hypolithic communities under quartz stones relies on a positive feedback between fog availability and the higher thermal conductivity of the quartz rocks, which results in lower daytime temperatures at the quartz–soil interface microenvironment.

7.3.4.3 Ferns

The relationship of leaf trichomes to water uptake has been studied in *Asplenium ceterach* (syn. *Ceterach officinarum*). On rehydration, respiration of this fern resumes at a level higher than in undesiccated controls and requires several days to return to control levels.

The poikilohydrous spikemoss *Selaginella lepidophylla*, the so-called resurrection plant of the southwestern United States, is well known for its rapid foliar uptake of liquid water. Desiccation of this fern results in a decline in RUBP[1] carboxylase activity by about 40%, but recovery of activity occurs within the first 24 h of rehydration - possibly by de novo synthesis of the enzyme. Thus recovery of photosynthesis after desiccation may be facilitated in this species by a high level of conserved RUBP carboxylase and the ability to quickly restore enzyme levels to normal (Batanouny, 2001).

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[1] - Ribulose-1,5-bisphosphate (RUBP)

7.3.4.4 Mosses

Mosses occur in all of the major biomes of the world. They dominate the ground layer in the boreal forest and are foundational species of northern peatlands. They are among the most abundant epiphytes in higher elevation tropical rainforests and with liverworts and algae form soil crusts in prairies and deserts. In alpine and montane areas they may form complete cover on boulders and dominate many cliff faces, ledges, and rock falls. In temperate and oceanic regions, they form conspicuous carpets on the forest floor and are epiphytic on tree trunks. Their canopies have a rich internal structure and are the homes for numerous insects, rotifers, tardigrades, and other invertebrates.

Morphologically, the major lineages of mosses are defined by features of the peristome (Vitt, 1984). The phylogeny as presently constructed shows eight major lineages (Fig. 7.3). Mosses have enhanced their physiological tolerance with a suite of morphological or life history features. These morphological adaptations increase the ability of some species of mosses to occupy even more desiccation prone habitats. In most cases, specific avoidance features have evolved convergently in two or more lineages.

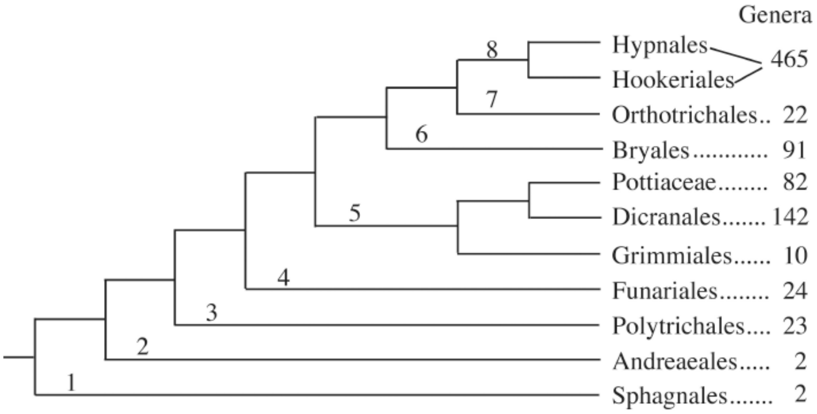

Figure 7.3 The major lineages of mosses (after Vitt, 1984)

Adaptation of Mosses to drought advanced either through increasing physiological desiccation tolerance or through morphological and life history changes leading to the ability to avoid desiccation.

Conceptually, many moss lineages have increased their physiological tolerance to drought, but also have developed morphological avoidance mechanisms that enhance habitat availability. Surprisingly, few mosses are truly aquatic and, as expected, those that are have little tolerance to drought, but even the aquatic *Fontinalis* (of streams and pools) can be induced if slowly dehydrated (Cruz de Carvahlo et al., 2014). A few species occur in deeply shaded, wet habitats such as seeps, beneath overhanging vegetation, and on exposed tree roots. These species also have little or no drought tolerance and occur sporadically through the moss lineages. Especially noteworthy are species in the Hookeriales that are characterized by flattened leaf arrangements and large thin-walled leaf cells (*Achrophyllum, Distichophyllum,* and *Hookeria*). In addition to these genera with multistratose leaves, a large number of mostly tropical moss genera have single-layered leaves with photosynthetically active green cells in the distal portion and dead porose hyaline cells (in one layer) in the proximal portion (e.g., Syrrhopodon, Leucophanella, and Mitthyridium). It appears that porose hyaline cells, in many cases surrounding active living green cells, have appeared in a number of distinct lineages, serving to extend the activity of a reduced number of photosynthetically active cells for a longer period of time under drought conditions.

References

Abe S., Kurashima A., Yokohama Y., Tanaka J. (2001) The cellular ability of desiccation tolerance in Japanese intertidal seaweeds. Bot Mar 44:125–131

Alpert P. (2000) The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecol
Angelovici R., Galili G., Fernie A.R., Fait A. (2010) Seed desiccation: a bridge between maturation and germination. Trends Plant Sci 15(4):211–218

Armstrong R.A. (2017) Adaptation of Lichens to Extreme Conditions, V. Shukla et al. (eds.), Plant Adaptation Strategies in Changing Environment. Doi: 10.1007/978-981-10-9744-0_1.

Bartels D., Singh M., Salamini F. (1988) Onset of desiccation tolerance during development of the barley embryo. Planta, 175:485–492.

Batanouny K.H. (2001) Adaptations of desert organisms. In: Cloudsley-Thompson J.L. (Eds) Plants in the deserts of the Middle East.

Bewley J.D., Krochko J.E. (1982) Desiccation tolerance. In: Pirson A., Zimmermann M.H. (Eds)
Broady P.A. (1986) In: Pickard J. (ed) Ecology and taxonomy of the terrestrial algae of the Vestfold Hills. Antarctic oases. Academic, Sydney, pp 165–202.

Cruz de Carvalho R., Bernardes da Silva A., Soares R., Almeida A.M., Coelho A.V., da Silva J.M., Cristina Branquinho C. (2014) Differential proteomics of dehydration and rehydration inbryophytes: evidence towards a common desiccation tolerance mechanism. Plant, Cell and Environment, 1499–1515.

Dalla Vecchia F., Asmar T.E., Calamassi R., Rascio N., Vazzana C. (1998) Morphological and

Einav R., Israel A. (2007) Seaweeds on the abrasion platforms of the intertidal zone of eastern
Encyclopedia of plant physiology, vol 12b, New series. Springer, Heidelberg, pp 325–378

Evenari M, Shanan L, Tadmor N (1971) The Negev, the challenge of a desert. Harvard Univ Press, Cambridge, 345 pp

Farrant J.M. (2000) A comparation of mechanisms of desiccation tolerance among three angiosperm resurrection plant species. Plant Ecol. 151:29–39

Farrant J.M., Brandt W., Lindsey G.G. (2007) An overview of mechanisms of desiccation tolerance in selected angiosperm resurrection plants. Plant Stress 1(1):72–84

Farrant J.M., Vander Willigen C., Loffell D.A., Bartsch S., Whittaker A. (2003) An investigation into the role of light during desiccation of three angiosperm resurrection plants. Plant Cell Environ. 26:1275–1286

Farrar J.F. (1973) Lichen physiology, In: Ferry BW, Baddeley M.S., Hawksworth DL (eds) Progress and problems in lichenology. Athlone Press, University of London, London, pp 238–282

Friedmann E.I., Lipkin Y., Ocampo-Paus R. (1967) Desert algae of the Sinai. Phycologia 6: 185-200

Garbary D.J. (2007) The margin of the sea: survival at the top of the tides. In: Seckbach J. (Eds) Cellular origin, life in extreme habitats and astrobiology, vol. 11. Springer, Dordrecht, pp 175-191

Hunt L.J.H., Denny M.W. (2008) Desiccation protection and disruption: a tradeoff for an intertidal marine alga. J. Phycol. 44:1164–1170

Illing N., Denby K.J., Collett H., Shen A., Farrant J.M. (2005) The signature of seeds in resurrection plants: a molecular and physiological comparison of desiccation tolerance in seeds and vegetative tissues. Integr. Comp. Biol. 45:771–787.

Jones L., McQueen-Mason S. (2004) Role for expansins in dehydration and rehydration of the resurrection plant Craterostigma plantiganeum. FEBS Lett. 559: 61–65

Kappen L. (1988) Chapter II.B.2: Ecophysiological relationships in different climatic regions. In:
Galun M. (ed) Handbook of lichenology, vol 2. CRC Press, Boca. Rato Kappen L., Valladares F. (1999) Opportunistic growth and desiccation tolerance: the ecological success of poikilohydrous autotrophs. In: Pugnaire FI, Valladares F (Eds) Handbook of functional plant ecology. Marcel Dekker, New York, pp 10–80

Kranner I., Cram W.J., Zorn M., Wornik S., Yoshimura I., Stabentheiner E., Pfeifhofer H.W. (2005) Antioxidants and photoprotection in a lichen as compared with its isolated symbiotic partners. Proc. Natl. Acad. Sci. U S A 102:3141–3146. Doi: 10.1073/pnas.0407716102

Lange O.L., Meyer A., Zellner H., Ullmann I.,Wessels D.C.J. (1990) Eight days in the life of a desert lichen: water relations and photosynthesis of *Teloschistes capensis* in the coastal fog zone of the Namib Desert. *Madoqua* 17:17–30.

Larcher W. (2001) Physiological plant ecology and stress physiology of functional groups. Springer-Verlag, Berlin, pp. 1–513.
Larsen D.W. (1984) Thallus size as a complicating factor in the physiological ecology of lichens.
localised glycine-rich protein plays a role in dehydration tolerance in the resurrection plant *Boea hygrometrica*. Plant Biol. 12:1–13

Lű̈ttge et al. (Eds.), Plant Desiccation Tolerance, Ecological Studies 215, Doi: 10.1007/978-3-642-19106-0_5, Springer-Verlag Berlin Heidelberg (2011)

Mc Queen-Mason S.J., Cosgrove D.J. (1995) Expansin mode of action on cell walls – analysis of wall hydrolysis, stress-relaxation, and binding. Plant Physiol. 107: 87–100

Meessen J., Backhaus T., Sadowsky A., Mrkalj M., Sanchez F.J., de la Torre R., Ott S. (2014) Effects of UVC254 nm on the photosynthetic activity of photobionts from the astrobiologically relevant lichens *Buellia frigida* and *Circinaria gyrosa*. Int. J. Astrobiol. 13:340-352. Doi. org/10.1017/S1473550414000275

Moore J.P., Farrant J.M., Lindsey G.G., Brandt W.F. (2007a) An overview of the biology of the desiccation tolerant resurrection plant Myrothamnus flabellifolia. Ann. Bot. 99: 211–217.

Moore J.P., Vicre-Gibouin M., Jill M., Farrant, Driouich A. (2008) Adaptations of higher plant cell walls to water loss: drought vs desiccation. Physiologia Plantarum 134: 237-245. 20

Mundree S.G., Baker B., Mowla S., Peters S., et al, (2002) Physiological and molecular insights into drought tolerance. Afr. J. Biotechnol. 1:28–38

Munns R., Passioura J.B., Guo J.M., Chazen O., Cramer G.R. (2000) Water relations and leaf expansion: importance of time scale. J. Exp. Bot. 51:1495–1504

Neg H.R. (2000) Onthe patterns of abundance and diversity of macrolichens of Chopta-Tunganath in the Garhwal Himalaya. J. Biosci. 25(4): 367–378.

Oliver M.J., Bewley J.D. (1997) Desiccation-tolerance in plant tissues. A mechanistic overview.
Hortic. Rev. 18:171–214

Oliver M.J., Tuba Z., Mishler B.D. (2000) The evolution of vegetative desiccation tolerance in land plants. Plant Ecol., 151:85–100

Orshan G. (1986) Plant form as describing vegetation and expressing adaptation to environment.

Ann. Bot. (Roma) 44:7-38

Pannewitz S., Schlensog M., Green T.G.A., Sancho L.G., Schroeter B. (2003) Are lichens active under snow in continental Antarctica? Oecologia 135:30–38.

Plant desiccation tolerance, (Eds), Matthew A. Jenks and Andrew J. Wood. 2007, pp 399. Blackwell Publishing Ltd, Oxford OX4 2DQ, UK.

Porembski S., Barthlott W. (2000) Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. Plant Ecol. 151:19–28

Rahmanzadeh R., Muller K., Fischer E., Bartels D., Borsch T. (2005) The Linderniaceae and Gratiolaceae are further lineages distinct from the Scrophulariaceae (Lamiales). Plant Biol. 7:1-12

Rascio N., La Rocca N. (2005) Resurrection plants: the puzzle of surviving extreme vegetative desiccation. Crit Rev Plant Sci 24:209–225

Rummrich U., Rummrich M., Lange-Bertalot H. (1989) Diatomeenals “Fensteralgen” in der
Schilderung. Beitr Biol. Pflanz., 31: 45–135

Schlesinger W.H., Pippen J.S., Wallenstein M.D., Hofmockel KS, Klepeis DM, Mahall B.E. (2003) Community composition and photosynthesis by photoautotrophs under quartz pebbles, Southern Mojave Desert. Ecology 84: 3222–3231

Schroeter B., Scheidegger C. (1995) Water relations in lichens at subzero temperatures: structuralchanges and carbon-dioxide exchange in the lichen *Umbilicaria aprina* from continental Antarctica. *N.* Phytol. 131: 273–285

Shirtcliffe N.J., Pyatt F.B., Newton M.I., McHale G. (2006) A lichen protected by a super-hydrophobic and breathable structure. J. Plant Physiol. 163:1193–1197.

Doi.org/10.1016/jplph.2005.11.007

Shen-Miller J., Mudgett M.B., Schopf J.W., Clarke S., Berger R. (1995) Exceptional seed longevity and robust growth – ancient sacred lotus from China. Am. J. Bot., 82:1367–1380.

Trainor F.R., Gladych R. (1995) Survival of algae in a desiccated soil: a 35-year study. Phycologia, 34:191–192

Vander Willigen C., Pammenter C.N.W., Jaffer M.A., Mundree S.G., Farrant J.M. (2003) An ultrastructural study using anhydrous fixation of Eragrostis nindensis, a resurrection grass with both desiccation-tolerant and sensitice tissues. Funct. Plant Biol., 30:1–10

Vecchia D.)1998) Ultrastructural aspects of dehydration and rehydration in leaves of Sporobolus stapfianus. Plant Growth Reg. 24: 219–228

Vicre´ M., Lerouxel O., Farrant J., Lerouge P., Driouich A. (2004) Composition and desiccationinduced alterations of the cell wall in the resurrection plant Craterostigma wilmsii. Physiol. Plant, 120:229–239

Vitt D.H. (1984) Classification of the Bryopsida. In: Schuster, R.M. (Ed.), The New Manual of Bryology. Hattori Botanical Laboratory, Nichinan, Japan, pp. 696–758.

Wang L., Shang H., Liu X., Wu R., Zheng M., Phillips J., Bartels D., Deng X. (2009) A role for a cell wall localized glycine-rich protein in dehydration and rehydration of the resurrection plant Boea hygrometrica.

Chapter 8

Water loss control

Introduction

The efficient control of water loss to the atmosphere is one of the foremost prerequisites for plant survival and competitiveness in any environment but particularly in deserts. As in any ecological system, the balance sheet of the water economy of desert plants has a debit and a credit side. The credit side is represented by the water sources available to the plant and its ability to absorb this water, while the debit side is the water lost by the plant. In order to survive under drastic edaphic and atmospheric droughts, desert plants must intensify water absorption, as already explained, and reduce water loss.

Before discussing the mechanisms of the adaptations of desert plants that reduce water loss, let us first consider the processes by which plants lose water. Transpiration is the main process through which water is lost. It occurs through the green parts, which have stomata (in the case of stomatal and cuticular transpiration), or from older parts over which cork has been laid down (in the case of lenticular transpiration). The latter type is, however, of limited value. From a physical point of view the rate of transpiration depends on the vapour-pressure gradient from the transpiring surface to the surrounding air. One can imagine how very steep this gradient must be under desert conditions of high vapour pressure deficit (VPD) and high temperature.

All climatic conditions that affect evaporation influence transpiration across this vapour pressure gradient. Transpiration takes place rather as one would expect it, especially during the dry season and when the plant has green organs, which may be stems, leaves, or both. The greater the surface of these green organs, the higher the water loss of the whole plant will be. Reduction of the transpiring surface is an effective means by which many desert perennials cut down their water loss and keep a positive water balance. Reduction of the rate of transpiration, both daily and seasonal, is another mechanism of adaptation that decreases water loss. In this case, the total water output from the whole plant is also less (Batanouny, 2001). Stomata and cuticle together enable plants to maintain a favourable water status. All above-ground primary parts of terrestrial higher plants are covered by a cuticle. This structure (Jeffree, 2006) consists of a matrix of polymeric cutin with cuticular waxes embedded within or deposited onto its surface.

Coatings of wax or hairs also help prevent water loss in plants. Waxy layers can give either a sheen or dull, grayish or bluish cast to a leaf surface. Century plant (*Agave americana*) has a dull, waxy coating that adds a gray color to its long leaves. A shiny wax and a coating of hairs are on the leaves of carob tree (*Ceratonia siliqua*), a native of the Eastern Mediterranean. The hairs help slow air movement over the tree's leaves, reducing transpiration and water loss. Brittlebush (*Encelia farinosa*) has silvery white leaves covered with reflective, white hairs that can reduce the plant's temperature by several degrees.

Some desert plants are able to conserve water because of their reduced leaf size. Less leaf surface area results in reduced water loss through the epidermis. Small leaves have fewer stomata than larger leaves, and that adaptation also reduces water loss. Some dry-land plants have stomata only on the bottom epidermis, which further reducing water loss, and some have several layers of epidermal cells. An example of a plant with small leaves is "Rosy Dawn" manzanita (*Arctostaphylos edmundsii* "Rosy Dawn"), which has gray-green leaves tinged with pink and pink flowers. Prickly pears (*Opuntia* spp.) have very reduced cylindrical, fleshy leaves that occur on only new growth.

8-1 Water loss adjustment

The most effective single adaptation by which desert plants reduce their water loss and adjust to variations in the amount of available water involves changing in the size of the transpiring body. In other words, the plasticity of the responses of desert plants to the changing soil water conditions is achieved mainly by changing the area of the transpiring surface. When a plant is confronted with a severe decline in the available soil moisture, it reduces its transpiring surface. This response can be continued until, in some cases, only a few living buds remain enclosed in dry dead leaves. When the plant is supplied with water in the next wet season, it produces new growth (Fig. 8.1). The growth and death of various organs of the shoot system, accompanied by this type of shedding, correlate with the availability of moisture to the plant (Batanouny, 2001).

In desert ecosystems, leaf shedding during severe water deficit (i.e. drought deciduousness) may represent a critical response that protects stems as predicted by the hydraulic fuse hypothesis (Wolf et al., 2016). In these environments water deficit adversely alters leaf longevity. Water stress reduces leaf area by early on setting of senescence or by accelerating its rate (Knapp et al., 1999).

Many deciduous trees and shrubs shed their leaf during water scarcity season Lower leaf absorption reduces water consumption and extends leaf longevity. These adaptations may buffer against the unpredictability of growing conditions in some arid regions (Darren et al., 1998). Dry soil conditions may favour early leaf senescence to reduce water requirements and avoid low water potentials deleterious for normal xylem dysfunctioning (Casper et al., 2001). Leaf shedding in response to drought stress occurred sequentially from older to younger leaves. In Mediterranean climate, plants confront with unpredictable precipitation during wet period and long hot dry summer extending up to subsequent autumn. The native plants developed a range of physiological and morphological adaptations to withstand such climatic conditions. The perennial species of this region have 3 major adaptations as evergreen sclerophyllous shrubs, drought deciduous shrubs and drought semi deciduous shrubs (Grammatikopoulos et al., 1995). The evergreen sclerophyllous shrubs possess compact small heavily cutinized leaves with well-developed stomatal regulation to check excessive water loss (Lange, 1988). This adaptation, however, reduced photosynthetic efficiencies (Hussain and Ali, 2015), but had extended longevity (Grammatikopoulos et al., 1995).

Leaf shedding depends on the species and the drought severity. When drought was severe, plants should need to rebuild the entire canopy (branches and leaves), while in other cases; only new leaves need to be grown. Vulnerability to drought should affect the investment needed to recover after drought episode, i.e., the amount of carbon needed to rebuild the canopy. Thus, a plant’s ability to preserve functional meristems under drought should substantially affect its capacity to withstand intense and recurrent droughts (Hoffmann et al., 2011). In some semiarid and arid regions the drought deciduous shrubs of this region lack stomatal regulation against water loss and other xeromorphic features. These shrubs shed their leaves in dry season as a result of desiccation. The drought semi-deciduous groups have intermediate strategy. The leaf senescence in this group is drastic but not complete during summer. The extreme drought stress is avoided partially by leaf shedding and partially by withstanding drought through remaining leaves. The leaves of this group are seasonally dimorphic (Grammatikopoulos et al., 1995).

Seasonal reduction in the transpiring surface is an important factor in maintaining the water balance of certain xerophytes stated that seasonal dimorphism is a common feature among the chamaephytes and is generally associated with a seasonal (Fig. 8.1). Among the chamaephytes reduction in their transpiring surface growing in deserts of the Middle East and specially in Iran that exhibit seasonal dimorphism, one might mention *Zygophyllum dumosum, Z. coccineum, Artemisia siebery, A. monosperma, Thymus capitatus,* and *Convolvulus lanatus.* Orshan and Zand (1963) stated that seasonal dimorphism is actually a special kind of drought - evading mechanism through which an increasing part of the transpiring plant's shoot is gradually shed as water shortage becomes accentuated during the long and dry summer, although the plant as whole retains its normal activity. They proposed the term "partial drought evasion" for this phenomenon. It has been found that the values of the relative seasonal reduction, i. e. the transpiring parts shed during summer, expressed as a percentage of the plant's transpiring area in late spring are greater among desert species than in the Mediterranean ones. Some desert plants, e. g. the bean caper *(Zygophyllum dumosum),* reduce their transpiring surfaces by up to 96 %.

Figure 8.1 Seasonal dimorphism in two desert species (a) *Artemisia siebery* and (b) *Zygophyllum dumosum* (Orshan and Zand, 1963; Batanouny, 2001)

The nature of plant organs which are seasonally renewed or shed was suggested as a suitable criterion of a plant's adaptation to seasonal drought stress (Orshan 1953). The following four types were recognized:

1- *Whole plant shedders*

Plants which are seasonally renewed from seeds, i.e. annuals (PS),

2- *Shoot shedders* - plants seasonally renewing their whole shoot (SS),

3- *Branch shedders* - plants seasonally shedding and renewing the upper parts of their branches (BS)

4- *Leaf shedders* - plants shedding only their leaves and inflorescences (LS).

8-1-1.Cortex shedding (part or whole)

In arid and Mediterranean ecosystems leaf and cortex shedding is usually associated with water deficit such as summer drought. The leaf or green cortex is the transpiring and photosynthesizing tissue and is shed by a number of species, e. g. *Haloxylon salicornicum* (Figure 8.2a), *Anabasis setifera* (Figure 2b), *Arthrocnemum macrostachyum* (Fig 8.2c), *Zygophyllum coccineum* (Fig. 8.2 d), and many succulent xerophytes and halophytes.

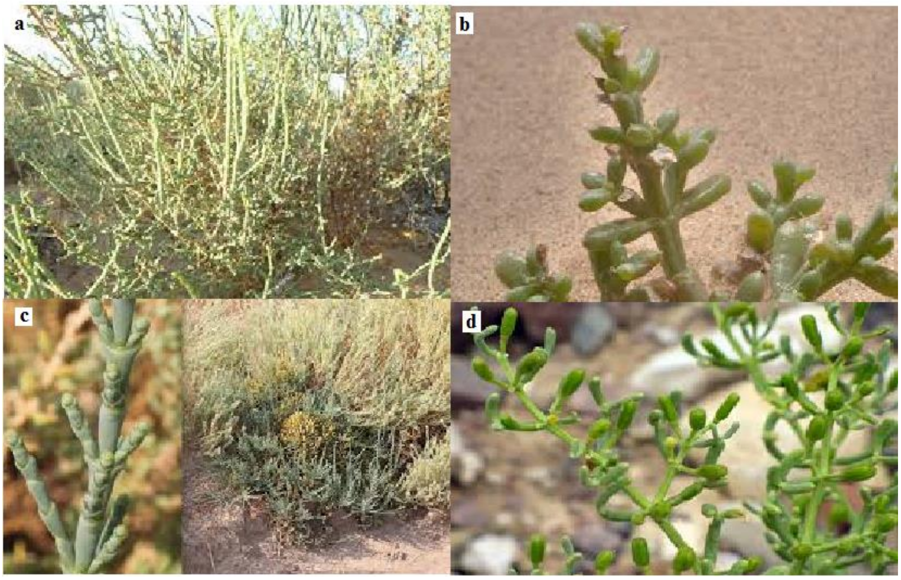

Figure 8.2 The green cortex is the transpiring in some desert species; (a) *Haloxylon salicornicum*; (b) *Anabasis setifera*; (c) *Arthrocnemum macrostachyum* and (d) *Zygophylum coccineum.* In *H. salicornicum* (Persian name: *Tarat*) branches show decortication of old parts under drought stress. This species is widespread in the central deserts of Iran (Semnan provine). Decorticated branches of *Anabasis setifera;* growing in the coastal plains along the Persian Gulf. Decorticated branches of *Anabasis setifera* (Persian name: *Jāfteh-shoor*) growing in Khozestan and the coastal plains along the Persian Gulf (Iran). *Zygophyllum qatarense* (Persian name: *Ghych*) exhibits cortex shedding from the old parts of the branch under water scarcity. This species grows in arid regions of Iran, particularly along the Persian Gulf and in coastal provinces such as Hormozgan.

Since cork is impermeable to water, the whole cortex is cut off from its water supply, dries out and is shed, and only the youngest internodes of the branches retain their photosynthesizing cortex. Without their green cortex the internodes cannot photosynthesize, but since they are also covered by cork they do not lose water by transpiration either. Only the few younger internodes that retain their green cortex continue to perform both functions. The seasonal reduction in the transpiring surface and the consequent decrease of water output brought about by cortex shedding is very considerable. It enables plants to survive the summer drought in an active state without becoming completely desiccated. Chenopodiaceae, which shed their cortex as well as some of their branches, produces flowers in autumn, at the end of the dry season.

8.1.2. Branch shedding

Branch shedding occurs in many members of the goose-foot family Chenopodiaceae and in other families that are also cortex shedders. When the water available to the plants becomes very scarce, the whole plant does not die, rather only some of its branches. The branches that remain alive continue to carry out photosynthesis and transpiration through the activity of their various green tissues. With progressive drying of the soil, more and more branches die, leaving only a few or sometimes just living buds protected by dry leaves.

Figure 8.3 *Calligonum comosum*, a desert plan illustrates how partial death is an important adaptation in the life of desert plants

After the rains in the subsequent wet season, the plant regenerates itself from these dormant renewal buds. This is evident in the case of *Cymbopogon shoenanthus*. According to Batanouny (2001), branch shedding is an important adaptation in the life of desert plants for survival.

8.1.3. Summer Leaf Shedding

Leaf shedding is an effective device which xerophytes that remain active during the dry season have developed to balance their water economy. Some desert plants are leafless almost all the year-round (e.g. *Retama raetam* and *Leptadenia pyrtechnica*; *Calligonum comosum,*). Many other desert plants are leafless in the dry season (e.g. *Zilla spinosa*). Leaf shedding may be accompanied by branch shedding in some species. In such cases, the weight of the plant may be considerably reduced. The white broom *(Retama raetam)* provides an example of leaf shedding. This plant produces tender green shoots carrying a few small leaves that are soon shed under moisture stress, while the shoots remain as the only photosynthetic organ of the plant. All other broom-like xerophytes, such as *Leptadenia pyrotechnica,* behave in the same manner. When leaf shedding is combined with branch shedding, as in the thorny saltwort *(Noaea mucronata),* a 90 % or greater loss may vastly reduce the weight of the plant. *Zilla spinosa,* a desert undershrub growing in desert environments, provides a good example of the effect of water supply on the persistence or shedding of leaves (Fig. 8.4) Batanouny, 2001).

Figure 8.4 Leaf shedding may be accompanied by branch shedding in some desert species (*Noaea mucronata*)

8.1.4. Winter leaf shedding

Some plants only shed their large winter leaves and retain their small summer ones. For example, at the beginning of the rainy season *Artemisia herba-alba* carries large winter leaves. These are shed at the beginning of the dry season and the new smaller leaves form as the season advances. *Artemisia monosperma* has the ability to produce small simple leaves. Winter and summer leaves differ not only in size and shape but also in their anatomical structure. The bean caper (*Zygophyllum dumosum*) has developed an effective method to reduce its transpiring surface (96%). By increasing summer drought it lose its leaf blades, leaving only the petioles. In another species, Z. *coccineum*, the leaflets are shed and the petioles are left, which can also be shed when conditions become drier.

Water loss through leaves is reduced in a wide variety of different ways including:

1. Reduced leaf area

The plasticity exhibited by some desert plants. For instance, *Lycium shawii* in wet habitats produces broad, thin leaves, while in dry sites it produces small leaves. Aggravation of drought results in the complete disappearance of leaves. Even the spines, which are weak and soft under conditions of ample water supply, become stiff and woody under dry conditions. It is noteworthy that for more than 1500 years, the Arabs have been able to distinguish between the two ecotypes of *Lycium* and *Ziziphus* that grow in dry and wet habitats.

2. Leaf abscission

In some grasses, the leaves become desiccated from their tips in a basipetal direction when the plant is subjected to severe drought. This reduces the transpiring surface. Many grasses are also capable of persisting throughout the dry season, or even for several rainless years, with just green stems covered by green sheaths and dry laminas (Danin 1996).

If the period of drought is extended, the leaf sheath may also die. *Cymbapagan schaenanthus* may dry out almost completely except for a few buds protected by dead organs and situated near the ground surface. After it rains, the plant starts to grow from these perennial buds and green circles of vegetative growth appear.

3. Investing the leaf surface with a covering of hairs or trichomes

Desert plant often have few, tiny or no leaves, which reduces transpiration. The epidermis of their leaves is often ornamented outgrowths called trichomes or hairs and a thick waxy cuticle. Hairs on the leaf surface trap humidity in dry climates and waxy leaf surfaces reduce water loss. According to the results obtained by Liu et al. (2014) the epidermis cover of most desert plants can be divided into five categories: (i) Trichomes with different forms covered completely on the adaxial and abaxial surfaces of leaf, and any other epidermal appendages could not been observed. (ii) Epicuticular wax crystals with different forms almost completely covered in the epistomatal chambers as well as on the surrounding epidermis, and there were no other appendages on the leaf surface. (iii) A lot of warty hairs arranged neatly on the surface and the stomatal index was too low. (iv) several or even dozens of papillary epidermal cells covered with waxy crystals enclosed a sunken stomata chamber; therefore the stomatal density is very low. (v) Like ordinary terrestrial plants, epidermal cells and cell outline are clear, with epidermal hairs or not, and the stomata and waxy crystals are visible. Several studies showed that desert plants have different thickness of cuticle, from 0.2μ m, up to 5.4μm on the adaxial surface, excluding the data of soluble waxy. Even the same plant has a varied thickness of cuticle in different habitats. These features and data reflect the adaptation mode and the ability of different desert plants in response to extreme environment, and will provide a theoretical basis for the selection of plant species in artificial vegetation reconstruction in sandy areas of arid and semi-arid regions.

Positioning of the stomata such that they avoid the direct impact of the climate; this can be achieved by rolling the leaf up under conditions of water stress. In this way, the abaxial side of the leaf, which is protected by a thick cuticle and is devoid of stomata, faces the harsh conditions of the desert atmosphere. The stomata are on the inner surface of the tightly inrolled leaf. This phenomenon can be observed in many desert grasses, e. g. *Ammophila arenaria, Lasiurus sindicus* (syn. *L. hirsutus), Pennisetum divisum, Stipagrostis* spp., *Halopyrum mucronatum,* and *Sporobolus arabicus*.

Investment of the leaf surface with covering of hairs has been regarded as an effective mechanism to control of water loss through leaf. Hairs have been credited with performing various functions; they can be regarded as an adaptation to strong solar radiation (Liu et al., 2014). Many desert plants have a thick covering of hairs, e.g. *Arnebia hispidissima, Echiochilon fruticosum, Anchusa* spp., *Moltkiopsis ciliata,* other species of Boraginaceae, and *Aerva tomentosa*.

Figure 8.5 Hairs have been credited with performing various functions; they can be regarded as an adaptation to water loss control and strong solar radiation in some desert plants like *Arnebia hispidissima*. This species grows in natural environments of Iran, and it is used as a Persian medicine (Hosseini et al., 2018)

4. Orienting the leaves vertically to minimize the direct radiation they receive. Erodium glaucophyllym is a leafy perennial herb with broad leaves that are fully exposed to the sun's rays in the morning. Before noon, when the evaporative power of the atmosphere becomes high, the leaves are oriented so that their blades are parallel to the sun's rays. The same phenomenon is to be observed in the different *Senna* species like *Senna alexandrina* growing in the desert environments.

8.2. Water efficiency at community level

Desert plants have unique morphological and anatomical structure and drought adaptation-related physiological characteristics, such as lower surface area to volume ratios, very low water potential and reduced transpiration rate (Du, 2006). For instance, Roderick et al. (2000) showed that the surface area to volume ratio of leaves generally decreases with soil water along the aridity gradient to reduce transpiration rate and keep higher water use efficiency (WUE); Horton et al. (2001) reported that saltcedar (*Tamarix chinensis* Lour) with low predawn shoot water potential in Arizona has greater tolerance of soil water deficits than the native species; shrubs and grasses in Hunshandak Sand Area lower their transpiration rates at the expense of photosynthesis rate to survive in dry habitats (Niu et al., 2003); and Caragana took a water-saving strategy with higher photosynthesis rate and lower transpiration rate in order to use water more efficiently (Ma et al., 2003). These drought-adaptive mechanisms help desert plants to explore water sources, reduce water losses and increase water-use efficiency.

In arid ecosystems, coexisting plant species may utilize water from different sources (Ehleringer and Dawson 1992). For example, most shallow- rooted grasses are opportunistic, utilizing the short-term availability of water in the upper soil layers, while shrubs rely on a deeper soil water resource that is more stable over the long term. This concept coincided with the vertical distribution of roots in different plants (Dodd et al., 1998).

Different rooting patterns among species have resulted from long-period evolution and served as adaptation mechanism to minimize competition for water in a particular habitat (Dawson 1996). The total water efficiency from a sample of desert vegetation depends mainly on the fresh weight of plants, their density, the climatic factors, the floristic composition, and the availability of soil moisture; and these factors may interact with each other. The ratio of water output per day to the total fresh weight of plants in a definite area is widely variable. It is worthy to consider water output on the community level in the same habitat all year-round. The diversity of the various components of the desert plant community, as related to the transpiration rate, affects water output. These components can be explained as follows:

8.2.1 Species Diversity

Water efficiency varies in different plant species. Desert vegetation consists of a permanent framework of perennials, filled in during wet years by annuals. The density of these annuals depends on the amount and distribution of both rainfall and runoff water to the habitat. The plant cover during the rainy season can be considerable in wet years and is composed mainly of ephemeral plants, whose transpiration rate is high under such conditions (Batanouny 2001).

According to Abdel Rahman and Batanouny (1964a) transpiration values varies between annuals and perennial plants. For instance in perennials during March transpiration values were much lower than those in annuals. However, they found that in *Zilla spinosa*, the transpiration rate ranged from a minimum of 32 mg g^{-1} h^{-1} at 04.00 h to a maximum of 273 mg g^{-1} h^{-1} at 13.00 h. In *Pennisetum divisum* (syn. *P. dichotomum),* the values ranged from a minimum of 36mg g-l h-l to a maximum of 295 mg g-l h-l at the same times. The transpiration rate of succulent plants such as Z. *coccineum* is very low compared with that of nonsucculent species. In *Zygophyllum,* the transpiration rate ranged from a minimum of l0 mg g^{-1} h^{-1} at 04. h to a maximum of 102 mg g^{-1} h^{-1} at 16.00h.

Species diversity is reflected in water efficiency, due to the fact that every species has its own level of water loss at a particular time of the year. High water efficiency levels from some species coincide with low levels from others. This normally ensures a continuous supply of water throughout the year. The disappearance of some species or the diminution of their transpiring surface and transpiration rate reduces the water efficiency. Thus, as the water supply decreases, some plant species disappear while others reduce their water efficiency (Batanouny, 2001).

8.2.2. Physiological Diversity

Numerous species with different photosynthetic pathways in desert plant communities. The majority of desert plants communities include both C3 and C4 plants. CAM plants may also be present. The occurrence of plants with different photosynthetic pathways can be regarded as a means by which the community maintains positive water relationships. C3 photosynthesis is the most common type and predominates among winter-active taxa. They are usually active at times when the temperature is low (winter season). C3 plants flourish during this period, and their foliage and vegetative growth are optimal (if there is any optimum in the desert). They have a high rate of transpiration during this period. By means of different adaptations, the rate of transpiration decreases in the dry season.

Figure 8.6 Photosynthesis pathways in desert plants: (C3), *Rhazya stricta;* (C4), *Haloxylon salicornicum*; *(CAM), Sedum album*

The C4 pathway is mostly found in summer ephemerals, short-lived summer active perennials, and halophytic shrubs. Its predominance in hot and/or saline desert environments supports the purported advantages of the C4 pathway: (1) high photosynthetic temperature optima; (2) high light-saturation points; and (3) high water-use efficiencies (WUEs) (Ehleringer and Monson 1993). Unlike C3 plants, C4 plants, such as *Panicum turgidum* and *Pennisetum divisum,* flourish during the hot weather, which starts in April and persists until the end of summer.

C4 plants, such as *Haloxylon salicornicum* and other chenopods, prosper and flower at the end of the dry season (Fig. 8.6). They are arido-active plants (Evenari et al., 1971), and withdrawal of water from the soil takes place during the hot season (in the Middle Eastern deserts this is the dry season). These C4 plants possess high water efficiency and are more economical in their water use than are C3 plants, so their water requirements are lower.

Crassulacean acid metabolism (CAM) is abundant in leaf and stem-succulents of the warm deserts, but CAM plants are rare in the cold deserts. The overall distribution of CAM plants in North America is highly correlated with aridity. This pattern reflects the high photosynthetic WUEs that are possible with nocturnal stomatal opening and CO2 assimilation of CAM plants (Smith and Winter, 1996). Water loss is also limited when CAM plants (8.6).

8.2.3. Life form diversity

Discrimination should be made between the term growth form and the term life form, as defined by Raunkiaer. According to, Growth form is distinct from life form. Life form refers to an inherent characteristic of a plant, while the growth form refers to a characteristic acquired by the plant under the prevailing environmental conditions (Kassas and Imam, 1959). This distinction is made with respect to several species that grow as deciduous plants under un-favourable habitat conditions, e. g. during the summer drought, whereas under favourable conditions they are evergreens. Growth form presents a complete morphological and physiological picture of the plant as regards its response to climatic factors. The growth forms of desert plants include ephemerals, evergreen perennials, summer-deciduous perennials, winter deciduous perennials and succulents. Plants in these categories vary in their response to the seasonality of the climate, especially temperature and rainfall.

The desert plant community consists of different species with different growth forms. Each of these growth forms has a special response to the prevailing conditions, especially soil water. Such responses vary from one species to the other. The responses of a few species result in reduced water efficiency when the water supply is low. There is always a balance between the amount of water available and water output. This balance keeps the community, with all its components, performing its functions satisfactorily Batanouny (2001).

8.2.4. Seasonal diversity

In desert ecosystems, two groups of annual plants have been recognized. One group, the winter annuals, consists of species that germinate and complete their life cycles during the winter and spring months; the other group, the summer annuals, includes species that germinate and complete their life cycles during the summer and early fall months (Mulroy and Rude, 1977). Normally, the seasonal occurrences of these two groups of species are highly predictable and are determined by specific temperature and moisture combinations required for germination.

In arid and semiarid regions, waves of different species appear at different periods of the wet season. Those species appearing in the early winter (December-January) are C3 annuals, which are adapted to the relatively low temperature prevailing in these months. Annuals appearing in the late winter (February) live till late spring (May to June); they are mainly C4 plants. These waves of diversity are usually obvious in good rainy years. Thus the temporal distribution of annuals in the arid zone allows the various species to exploit the uppermost soil water at different times of the wet season. This is known as intra-seasonal diversity. It assists in both the distribution of water and its withdrawal, as well as in the distribution of the accompanying fauna. Of these, the insects, which perform the function of pollination, are especially important to plants. Different insect species are also distributed temporally and thereby avoid competition (Batanouny, 2001).

8.2.5. Diversity of Transpiration Rates

Environmental factors affecting transpiration in plants. These factors are described as "environmental" to distinguish them from those genetic factors which are inherent in the plants. They are also described as external factors, that is, outside of or external to plants. Specifically climate factors which are called as the climate elements. These factors are the same climatic factors which can either promote or inhibit plant growth and development and. In general, plants transpire fastest under the following climatic conditions: (a) bright day, (b) dry air, (c) moist soil, (d) warm temperature, and (e) windy day.

Environmental conditions influence the transpiration rate of the same species in different habitats; in this case, Abdel Rahman and Batanouny (1965b) measured the transpiration rates of two species in different microhabitats. The diurnal fluctuations in the evaporation and transpiration rates of *Zilla spinosa* and *Zygophyllum coccineum* in three different microhabitats in the dry season were measured. The results showed that the daily rhythms of transpiration in both species vary from one habitat to the other. This shows the plasticity of the transpiration response of desert plants depending on prevailing conditions. The early decline in the transpiration rate in the plateau and the first terrace represent an economy in the use of water during a time of high transpiration. In the shade, it may be a result of to a general decline in the evaporating factors.

Plants are naturally subjected to different environmental conditions in the desert, namely: (1) humid atmospheric and edaphic conditions that usually occur in the rainy season, (2) humid atmospheric conditions combined with soil drought, that prevails in years with late winter rains and a prolonged drought period extending through the early winter, and (3) combined soil and atmospheric drought prevailing in summer when the temperature is high, the air is dry, and no rain falls. Atmospheric drought and favourable soil moisture represent a fourth combination. With respect to the mentioned conditions, Batanouny (2001) reported the daily changes in the transpiration rates of *Pennisetum divisum (P. dichotomum)* and *Zilla spinsa*. He mentioned that desert plants are not necessarily obliged xerophyte, in the case of supplied water, during the summer months, have very high transpiration rates consequently high growth rate. The attainment of high transpiration rates under these conditions is caused by the high evaporation rate. This, in turn, is due to favourable conditions for water absorption, namely abundant supply and high soil temperature. Comparison of the maximum and mean transpiration and evaporation rates for the two species under different conditions showed that, when atmospheric drought is associated with soil drought, i. e. in the July experiment in which irrigation was not applied, maximum transpiration rates in the two species are much lower than in the irrigated plants, being 455 mg g^{-l} h^{-1} in *Pennisetum,* and 307 mg g^{-l} h^{-1} in *Zilla.* The means transpiration rates under natural conditions were 210 mg g^{-l} h^{-1} in *Pennisetum* and 140 mg g^{-l} h^{-1} in *Zilla.* In the watered plants, the mean rates were 275 mg g^{-l} h^{-1} in *Pennisetum* and 242 mg g^{-l} h^{-1} in *Zilla*. This indicates that soil drought in the rainless season restricted the transpiration rate to a low level. In other words, well-watered desert plants transpire more freely than non-watered ones. One can see that desert plants are not characterized by low transpiration rates, but rather by their ability to lower the rate of transpiration under soil moisture deficits.

References

Abdel-Rahman A.A., Batanouny K.H. (1965b) Transpiration of desert plants under different
environmental conditions. J. Ecol., 53:267-272

Batanouny K.H. (2001) Adaptations of desert organisms. In: Cloudsley-Thompson J.L. (Eds) Plants in the deserts of the Middle East.

Casper B.B., Farseth I.N., Kempenich H., Xavier K. (2001) Drought prolongs leaf life span in the herbaceous desert perennial *Cryptantha flava*. Functional Ecology 15 740-747.

Danin A. (1996) Plants of desert dunes. In: Cloudsley-Thompson J.L. (Eds) Biotic interactions in arid lands. Springer, Berlin Heidelberg New York

Dawson TE, Pate J.S. (1996) Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia

Dodd M.B., Lauenroth W.K., Welker J.M. (1998) Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. Oecologia, 117:504–512

Du J.Z. (2006) The water physiological characteristics and drought tolerance of desert plants. Gansu Sci. Technol. 22:169–170

Ehleringer J.R., Dawson T.E. (1992) Water uptake by plants: perspectives from stable isotope composition. Plant, Cell Environ 15:1073–1082

Ehleringer J.R., Monson R.K. (1993) Evolutionary and ecological aspects of photosynthetic pathway variation. Ann. Rev. Ecol. Syst., 24: 411-439.

Evenari M., Shanan L., Tadmor N. (1971) The Sinai (Negev), the challenge of a desert. Harvard Univ. Press, Cambridge, 345 pp

Grammatikopoulos G.A. Kyparissis, Manetas Y. (1995) Seasonal and diurnal gas exchange characteristics and water relations of the drought semi deciduous shrub *Phlomis fruticosa* L. under Mediterranean field conditions. Flora, 190: 71-78.

Hoffmann W.A., Marchin R.M., Abit P., Lau O.L. (2011) Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. Glob Chang Biol. 17:2731–2742

Horton J.L., Kolb T.E., Hart S.C. (2001) Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species. Tree Physiol. 21: 233–241.

Hosseini A., Mirzaee F., Davoodi A., Jouybari H.B., Azad-bakht M. (2018) The traditional medicine aspects, biological activity and phytochemistry of Arnebia spp. Med Glas (Zenica), 15(1): 1-9. Doi: 10.17392/926-18

Hussain B., Ali B. (2015) Leaf longevity in plants under water stress – a review. Indian Journal of Plant Sciences, 4 (4): 127-133.

Jeffree C.E. (2006) The fine structure of the plant cuticle In: Riederer M., Müller C., eds. Biologof the plant cuticle. Oxford, UK: Blackwell Publishing, 11–125.

Knapp A.K., Bargmann N., Laura A., Christine A.M., Mc Allister A, Dale J.B., Ham M. and Owensby C.E. (1999) Elevated CO2 and leaf longevity in the C4 grassland dominant *Andropogon gerardii*. International Journal of Plant Science 160 1057-1061.

Liu Y., Li X., Li M. (2014) Leaf epidermal appendages of desert plant: an ecological perspective. Geophysical Research Abstracts, 16, EGU2014-2034.

Ma C.C., Gao Y.B., Guo H.Y., Wang J.L. (2003) Interspecific transpiration among Caragana microphylla, C. davazamcii and C. korshinskii along geopraphic gradient. II Characteristics of photosynthesis and water metabolism. Acta Botanica Sinica 45:1228–1237.

Mulroy T.W., Runde P.W. (1977) Annual Plants: Adaptations to Desert Environments. BioScience, 27(2): 109-11.

Niu S.L., Jiang G.M., Gao L.M., Li Y.G., Liu M.Z. (2003) Comparison of gas exchange traits of different plants pecies in Hunshandak Sand Area. Acta Phytoecologica Sinica 27:318–324

Orshan G., Zand G. (1963) Seasonal body reduction of certain desert halfshrubs. Bull. Res. Counc, IID, (1):35-42

Physiological Ecology of North American Desert Plants, edited By S.D. Smith, R.K. Monson, and J.E. Anderson (1997), Springer-Verlag Berlin Heidelberg 1997.

Roderick M.L., Berry S.L., Noble I.R. (2000) A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. Funct. Ecol. 14:423–437

Smith J.A.C., Winter K. (1996) Taxonomic distribution of crassulacean acid metabolism. Pages 427–436 *in* K Winter, J.A.C. Smith, Eds. Crassulacean acid metabolism: biochemistry, ecophysiology and evolution. Springer, New York

Wolf B.T., Sperry J.S., Kursar T.A. (2016) Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. New Phytologist, 212:1007-1018. Doi: 10.1111/nph.14087

Chapter 9

Water absorption adaptation

Introduction

Water is a limiting factor for survival and growth of desert plants (Ranjbar-Fordoei, 2019). The flow of water in the soil–plant–atmosphere continuum is a passive process driven by water potential differences and enabled by the continuity of the liquid phase of water between the soil and the leaf mesophyll (Li et al., 2018). To adapt to the arid environment, plants formed multiple morphologic and physiologic adaptation strategies to resist the drought stress environment of the outside world, including plant morphology and structure, growth rate, water use efficiency, antioxidant system, and developed root system (Li et al., 2009).

The ability of any plant to keep its tissues turgid depends on a balance between the external relationships of water uptake and water loss, as well as on the internal osmoregulation of the plant cells. Water uptake from the soil, especially in deserts, is a crucial function of every root system and largely determines the water status of the shoot. The most obvious starting point for research in such a case is to examine whether drought-tolerant plants have any special means of obtaining water that are denied to drought-sensitive species. The root systems of desert perennials have particular characteristics and adaptations that favour water absorption from as large a volume of soil as possible (Batanouny, 2001).

The root system is an organ that absorbs water from the soil and is the site where the plant initially perceives drought (Mu et al., 2005), and the morphology characteristics, such as root length (RL), specific root length (SRL), root surface area (RSA), specific root surface area (SRSA), and root diameter (RD), are important parameters affecting water and nutrients uptake of plants (Eissenstat, 1999), which is closely related to the drought resistance of plants.

In addition to its function in water uptake, the root can communicate changes in the soil environment to the shoot. Freitas (1997) stated that roots seem to be the primary sensors of water deficits, and biochemical signals transported from the roots cause many of the physiological perturbations observed in the shoots of plants subjected to drought. He also mentioned that these signals are probably related to changes in the kind and concentration of hormones exported to the shoots, possibly in the transpiration stream.

Soil water stress forced the root diameter of *Reaumuria soongarica* seedlings to become smaller, the root volume decreased, and the specific surface area and specific root length increased (Shan, 2013). Cortina et al. (2008) held that the fine root was an important part of the root system of plants, with important physiological and ecological characteristics, and was very sensitive to the changes of water, thus many plants could adapt to drought stress by increasing both the numbers of fine roots and surface area.

Under water stress, the factors leading to the decrease of the root radial flow conductance include the decrease of the diameter of the central catheter of the xylem of the root system, and the increase of the diameter of the root system and the cortical thickness (Running et al., 1980).

9.1. Root system adaptations

Plant root systems are essential for adaptation against different types of biotic and abiotic stresses. The primary functions of root systems of terrestrial plants are anchorage and acquisition and conduction of water and nutrients from soil; other functions such as storage, synthesis of growth regulators, propagation and dispersal may be viewed as secondary (Gibbens and Lenz, 2001). Because roots are an indispensable pathway for water and nutrients much has been learned about the anatomical and physiological aspects of root systems, particularly those of crop plants (Fitter, 1991). Roots have been evolved to be responsive and extremely adaptive to the environment conditions, their morphology, growth and physiology are closely related with plant genotype and growth medium properties (Wasaya, 2018). For example, elongation rate and number of lateral roots can be decreased by high soil water content or soil density and this can also be associated with shoot growth reduction (Bengough et al., 2011). The type of root distribution required for different crops depends on the target environment, as abiotic stresses experienced by roots have a significant effect on the crop yield (Wang and Frei, 2011. Strong root development is essential for survival of seedlings in soils which undergo rapid surface drying, while sufficient moisture remains available in deeper soil layers. Therefore, good understanding about plant responses to abiotic stresses might be helpful in the selection of more resistant crop varieties (Den Herder et al., 2010).

The root system architecture (RSA) is affected by various factors such as soil temperature, moisture, nutrients and soil pH (Robbins and Dinneny, 2015) which greatly affects crop growth and yield (Price et al., 2013). Several root characters such as morphological plasticity (Lynch, 2007), root tip diameter (Haling et al., 2013), gravitropism, and rhizosheaths allow the plants to adapt and respond to various environmental factors and they might be quite useful for improving water use efficiency in crop species (Fenta et al., 2014). Therefore, it is very important to understand the RSA regulating mechanisms for crop improvement (Lynch, 2007). Different types of roots have special features such as primary root length (Forde, 2014), length and number of lateral roots (Zhan et al., 2015), crown root number (Saengwilai, 2014) and cortical cell file number and cell size (Chimungu et al., 2014), which help in determining water absorption/uptake ability among various root types as an adaptation strategy under dry conditions.

Root traits are more related to drought tolerance compared with above ground plant parts and are key factors to maintain plant surviving under water deficit. Root system is as important as shoot system, because plant’s ability to uptake moisture and nutrients mainly depends on root architecture and function.

Based on anatomical characteristics, the root systems of plants for adaptations to desert conditions can be categorized as:

1. The form of the root system
2. The succulence of the roots
3. Development of thick bark
4. Sclerification of the cortical cells
5. Isolation of the vascular cylinder by periderm formation or by necrosis of the cortical parenchyma (Fahn, 1989).

The root systems of desert plants possess various characteristics, which represent adaptations to the prevailing dry conditions in the desert. The presence of such characteristics and adaptations helps the plants to absorb water in quantities at least sufficient to compensate for that lost during transpiration. The main characteristics of the root systems of desert perennials that act as adaptations increasing water intake are described in the following sections (Batanouny, 2001).

9.1.2 Seedlings establishment

Seed germination and seedling establishment are the most critical stages in the plant life cycle (Mayer and Poljakoff-Mayber, 1989). Germination behaviors play a key in the persistence and dynamics of desert plants. Most germination studies on desert plants have been concerned with the proportion of seeds that could germinate in a growing season and the effects of specific environmental factors on seed germination (Baskin et al., 1993). Water stress is a major factor limiting the establishment and regeneration of desert species. Another factor that may be important in seed germination in desert environments is temperature (Baskin and Baskin, 1998).

The capacity of the root system for rapid and early development is an important factor in drought resistance (Batanouny, 2001).

Saidi et al. (2010) reported that, with decreasing water availability, root growth is enhanced at the cost of the accumulation of above-ground biomass. The results obtained by Reader et al. (1992) confirm that the rooting depth of seedlings may increase significantly in response to drought. Several reports have confirmed that plasticity in seedling rooting development may differ among species for different reasons (Park 1990; Rhizopoulou and Davies 1991; Reader et al., 1992).

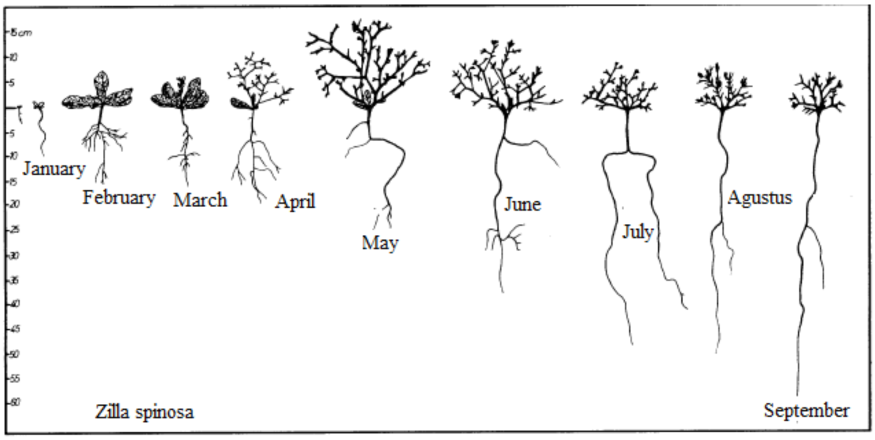

Figure 9.1 Root systems of *Zilla spinosa* seedlings over the period from January to September. Note the rapid growth of the root system during the growing season (Courtesy of Batanouny, 2001)

Variuos studies suggest that morphological plasticity facilitates growth in heterogeneous environments (Jackson and Caldwell 1989; Campbell et al. 1991; Reader et al., 1992). Plasticity in the maximum rooting depth may be helpful to allow plants to sustain growth as soil dries during drought periods (Fig.9.1). For instance, the root of the newly germinating seedlings of *Zilla spinosa* exhibit continuous growth at a moderate rate till the water is available in the soil. By the initiation of soil water deficit (beginning of dry season), the seedling roots exhibited considerable growth (Batanouny, 2001).

9.1.3. Root morphological plasticity (extension)

In terrestrial ecosystems, the root system can change its morphological structure in response to the environmental conditions (Rent et al., 2011). Such strong plasticity is an important survival strategy in certain environments. Root morphological plasticity is also closely related to plant growth strategies and the ability to exploit environmental resources (Wang et al. 2017). Any change in plasticity will therefore have an effect on plant growth (Wang et al., 2012), playing an important role in environmental adaptation (Zhang and Xu, 2010). For example, morphological plasticity of the root system determines the position and extension ability of the roots (Malamy, 2005). Moreover, it also affects the utilization of soil resources as well as the efficiency of water and nutrient uptake, and therefore, the plants' adaptability (Wang et al., 2017). Thus, horizontal and vertical distribution of the roots (root extension) is the basic manifestation of a plant's ability to gain water and nutrition (Zhang et al., 2005). According to Kassas and Batanouny (1984), root extension is a common feature of desert perennials. Various studies on desert environments, especially in the deserts of the Middle East have revealed that perennial desert plants have extensive root systems (Batanouny and Abdel Wahab 1973; Kassas and Batanouny 1984; Batanouny, 2001).

Root extension consists of different features including: (a) deep penetration of the roots, enabling plants to absorb water from deep permanent wet layers; (b) root extension to pockets in the soil between stones, which helps in providing the plant with available water; and (c) lateral extension, both extensive and intensive, to exploit large soil volumes. All these features ensure a high root/shoot ratio and represent adaptations that increase water uptake by the plants (Changjun et al., 2015). In desert systems, due to high capacity of evapotranspiration and absorption of water by ephemerals, the surface soil layer is dry almost throughout the year, except on a few days during the rainy season. However, these plants represent dry mulch, protecting the deeper layers from further evaporation. At layers deeper than 50 cm, soil moisture might be sufficient for other plant life forms like as shrubs and Phanerophytes.

Root systems are important in the collection of scarce soil resources. A review of rooting depth on a world-wide basis (Canadell et al., 1996) showed that maximum rooting depth ranged from 0.3 m for some tundra species to 68 m for a species in African deserts. Various studies of vegetation along a rainfall gradient revealed that total biomass decreased with decreasing precipitation but below-ground biomass decreased at a slower rate than above-ground biomass.

The extent and plasticity of shrub root systems is a contributing factor to the success of this life form in arid environment. The root systems of saxaul, mesquite, and tarbush, all of which have increased their area of dominance, have several common characteristics. (1) Roots spreading horizontally from a few to many meters are abundant at shallow soil depths and can access soil water resulting from the common small rainfall events; (2) A small but significant number of roots penetrate through calcic and petrocalcic horizons, accessing soil water from soil horizons where recharge is infrequent but may be crucial in sustaining plants during extended droughts; (3) Exhibitig similar root systems in a wide variety of soils although mesquite is the most ubiquitous of the three in this respect (Gibbens et al., 2005).

In the Gurbantonggut Desert of China, Xu and Li (2008) found that the root system of Haloxylon ammodendron reaches a depth of more than 10m. However, information obtained from local farmers in Yazd province (the people who dig deep wells and long underground channels by hand (qanat) to supply water for agricultural crops), saxaul roots (black/white saxaul) reach a depth of 60 m.

9.1.3 Low shoot/root ratio

When respect to different plants life forms, it is apparent that annual plants and succulents exhibit relatively low root/shoot ratios (based on above ground biomass) compared to non-succulent perennials. In fact, the root/shoot ratios of desert annuals are at the low extreme of those found among herbaceous plants from temperate mesic environments. This ratio pattern reflects a general response in desert annuals to selection for rapid growth and completion of the life cycle during periods following a critical amount of precipitation and before the onset of drought. The low root/shoot ratios in succulents reflect a pattern of moisture acquisition that depends upon opportunistic absorption of moisture in the soil surface layers and subsequent aboveground storage. Because of their large capacity to store moisture between precipitation events, succulents need not allocate biomass to the continuous exploration of deeper soil layers. It should be noted, however, that low root/shoot ratios based on biomass do not adequately reflect root/ shoot ratios based on surface area (succulents have massive aboveground structures, often with low surface area). With no large perennial roots, a given allocation of biomass to roots can result in a substantial absorptive area in these plants. Higher root/shoot ratios for non-succulent perennials reflect a requirement to acquire moisture longer into the dry season, compared to annuals (which are dormant as seeds) and succulents (which maintain considerable stores of water).

The moisture collected by the extensive root system is drawn upon for the consumption of a reduced shoot. The preponderance of the root system over the above-ground shoot system facilitates adjustment of the water balance of desert plants. The transpiration rate of desert plants is very high when calculated on the basis of the fresh weight or the area of transpiring shoot, but it is very low when calculated on the basis of the fresh weight or the area of the absorbing root (Batanouny 2001). Each unit of transpiring surface is supplied with water by many more roots than is usual in mesophytes. Hence, a positive water balance is more likely to prevail. In other words, the low shoot to root ratio (S: R) must be advantageous to ensure an adequate supply of water, which is the major limiting resource in deserts. The low S: R ratio is established as early as the seedling stage. The ratio of shoot height to root axial length (length of the root excluding lateral branches) is 1:7 in *Schismus barbatus* (Fig. 9.2).

In order to obtain a larger portion of one resource, plants must allocate more biomass to structures involved in the acquisition of that resource at the expense of allocation of biomass to structures involved in the acquisition of another resource. Morphological plasticity may increase the competitive ability of a plant over a range of different resource availabilities (Aerts et al., 1991).

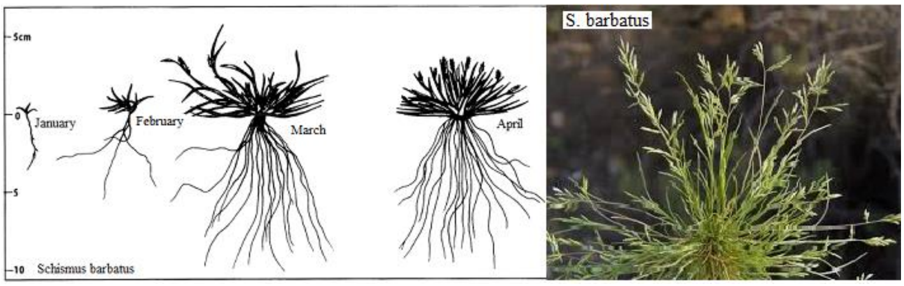

Figure 9.2 Development of the root system of *Schismus barbatus* (an annual desert grass) from the seedling in January to the fruiting stages in April (Courtesy of Batanouny, 2001)

9.1.4 Exploitation of different layers above and underground by different species

Deserts contain a vast array of different plant functional groups that display different ecological strategies and consequently they exhibit different root demographics. Trees and shrubs in deserts maintain above-ground biomass throughout the year, whereas herbaceous perennials maintain their root system but grow a new shoot every year. It is therefore possible that perennial desert species also exhibit different strategies with regard to their root demography (Liu et al., 2016).

Different species in a plant community exploit different layers above and below ground. Ephemerals differ from perennials regarding the strata exploited by their roots. Some plants that form mounds exploit the soil water resources from the body of the mound above the ground surface. This results in a distribution of the layers that are exhausted. Uneven water penetration results in a heterogeneity of the water contents of the soil. This is reflected in the distribution of root systems within the soil profile.

The root systems of some of the plants growing on the coastal dunes along the Mediterranean Sea exploit different strata. These plants have roots that penetrate deeply into the soil in addition to roots extending horizontally and parallel to the soil surface. The deep vertical roots extract water from the deep layers, whereas the horizontal roots make use of the dew that condenses during nights. The occurrence of roots of the same or different species in the various strata of the soil provides an opportunity for reducing competition for water and for obtaining water from various strata. Specific differences in the distribution of the root system exploit the lack of homogeneity of the water in such soils and thereby reduce spatial competition (Rundel and Nobel 1991).

9.1.4.1 Openness and sparsity of root system

The depth, lateral spread and degree of overlap of plant root systems are important for plant’s adsorption of water and nutrients. Plants in arid areas have particularly large underground biomass. For instance, Ma and Fang (2006) reported that, belowground biomass of plants in Inner Mongolian grasslands is six to ten times greater than aboveground biomass. Studying the distribution of plant roots is useful to predict different responses of plants under future drought conditions, and in order to develop strategies to protect local ecological environment and maintain ecological functions in the grassland.

One of the main characters in desert vegetation is openness. This characteristic results in the absence of competition between perennials, which show the permanent framework of the vegetation. The withdrawal of moisture from the soil depends on the density, cover and openness of the vegetation. The low density of roots per unit volume of soil reduces root competition which, in turn, minimizes the amount of water withdrawn by the root per unit volume of soil. These characteristics ensure less withdrawal and better conservation of the soil moisture.

The dry season lasts, in some places, for up to 9 months. During this time the uppermost soil layers are dry and form a protective layer that prevents water loss from the soil through evaporation. Water loss from the soil in the dry season takes place only through absorption by roots and its subsequent transpiration (Batanouny, 2001).

Study of the vertical and horizontal distribution of roots is ecologically important. Most of plant root biomass occurs in the 0-50 cm soil layer, and only a small portion reaches deep soil (Canadell et al., 1996). Therefore, it has commonly been assumed that study of plant roots in the 50 cm soil layer can allow to fully understanding the function and structure of the root systems on the ecosystem level. However, more and more research has shown the significant role of deep roots, especially for water, carbon and nutrient cycling (Douglas, 2011; Yu et al., 2015).

Elongation of lateral roots of adjacent plants can affect the amount of available resources in an ecosystem and thus determine the competitive advantage between plants (Jose et al., 2003; Ruta et al., 2010). Data on root depth and lateral root spread can help predicting functional differences between plants with different growth under future climate change scenarios. However, the absolute root depth or horizontal extension of roots may even be greater in humid environments, because plants shoots can be relatively large in these regions (Schenk and Jackson, 2002). Study of the vertical and horizontal distribution characteristics of plant roots can provide important reference values for plant root sampling techniques, and can be useful in building models related to roots; and in calculating the carbon retention rates in global grasslands.

Wang et al (2017) classified the plant roots of 430 species, mainly in arid and steppe into 6 root types including: Rhizome-rooted plants have a subterranean stem (Fig.9.3a). Creeping rooted plants are characterized by a horizontal root with branches coming from the horizontal root (Fig.9.3c), while fasciculate rooted plants have many branches of the same size coming from both the root and shoots (Fig.9.3b). Fibrous rooted plants have a single long stem with many of thin roots of the same thickness (Fig.2d). Tap-rooted plants exhibit a significant difference between the diameter of the main root and lateral roots (Fig.9.3e). The bulb-corm-tuber rooted type refers to plants that have roots with abnormal organs such as tubers, corms or bulbs (Fig.9.3f).

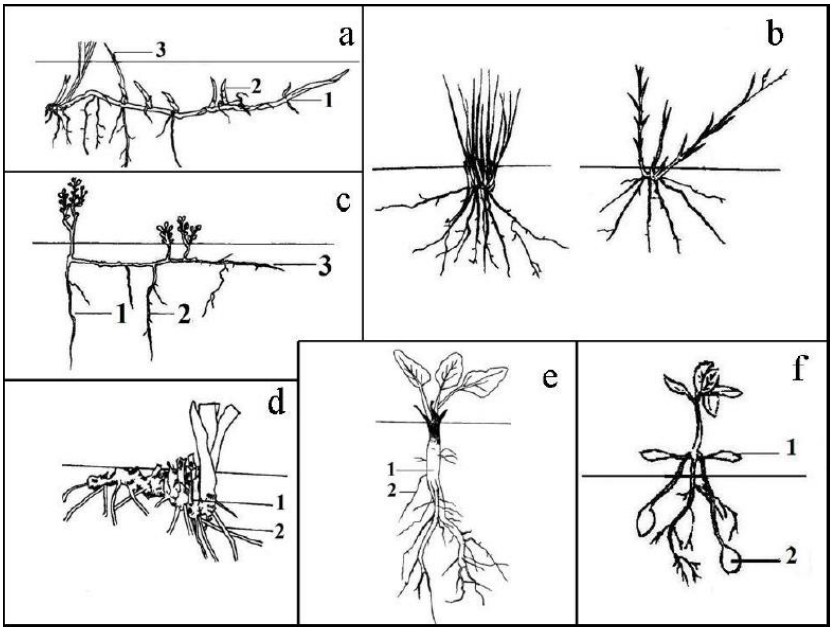

Figure 9.3 The different root types of plants found in grassland and desert steppe of northern China. note: a. Rhizome-rooted plant (1, subterranean stem; 2,bud; 3, shoot); b. Fasciculate rooted plants; c. Creeping rooted plants (1, main root;2, vertical root;3, horizontal root); d. Fibrous rooted plants; e. Tap-rooted plants (1,main root; 2, lateral roots); f. The bulb-corm-tuber rooted type (1, shoot; 2, abnormal organs) (after Wang et al, 2017).

Tap rooted plants can reach very deep into the soil. Creeping rooted plants have a strong capability to spread roots horizontally. Creeping rooted and tap rooted plants were mainly distributed in the desert steppe.

9.1.4.2 Root responses to various soil conditions

Root plasticity is the plant’s ability to alter its root phenotype in response to changing environmental conditions, plays a significant role in plant adaptation (Wang and Yamauchi 2006). A number of soil physical stresses, acting independently or in combination, can limit root plasticity. The physical stresses operating vary markedly between different soils with, for example, roots growing in poorly drained clay soils being subject to hypoxia to a much greater extent than on a well-drained sandy loam. Soil strength increases generally as the soil dries, often by an order of magnitude between matric potentials of -5 kPa and -1.5 MPa. Large strength increases on drying can occur for a wide range of soil textures, including soils that are predominantly sandy, silty, or clayey. Such strength increase is particularly marked in hard-setting soils that slump to a massive structure (Bengough et al., 2006).

Morphological plasticity facilitates the growth of plants in heterogeneous environments. Halophytes growing in sites with a shallow water table have their root systems confined to the layers above it. In sites where the water table is far below the surface, these plants have deep roots. When the soil is stony the rooting habits of desert plants are influenced accordingly. The layer of soil below large embedded stones is protected from evaporation and the water content is consequently higher than in other parts of the same horizon. This leads to the formation of dense tufts of thin roots, especially in the wet season, when the surface layers are enriched with the permeating water. The formation of these tufts adds greatly to the absorbing surface.

Soil layers with different physical attributes have various water holding capacities and support growth of different types of roots. The roots of desert shrubs and dwarf shrubs are specially adapted to the moisture conditions in their habitats. The root systems of shrubs growing on hilltops, slopes, or loess plains are very shallow and do not penetrate to more than 30-50 cm.

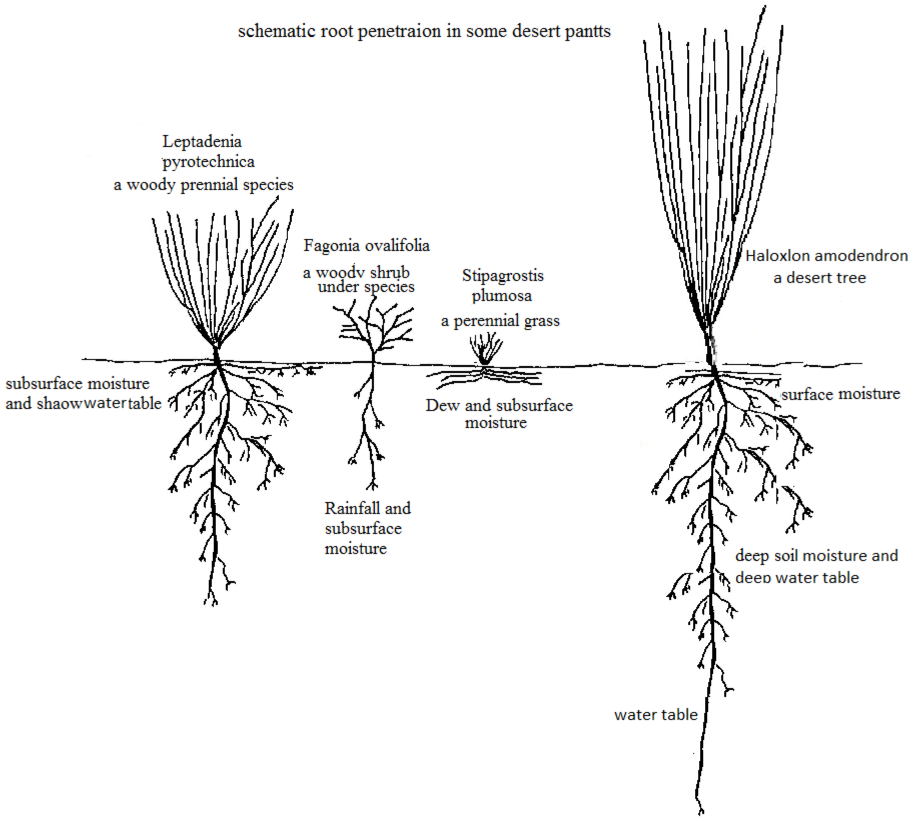

Figure 9.4 Penetrability of root system in different desert life forms. From left to right, *Leptadenia pyrotechtica*, *Fagonia ovalifolia*, *Stipagrostis plumose* and *Haloxylon amodendron* (redrawn from Batanouny, 2001).

9.1.5. Adventitious roots in desert plants

The dynamics of vegetation in arid environments and particularly regions where having drifting sand primarily on dunes regions have been investigated. Plants growing where the sand is mobile must become adapted to a number of constraints in order to survive. (a) They have to be able to germinate under highly unfavorable soil moisture conditions (low quantity and or transience) and at depths which may alter greatly. Once it has germinated, a seedling must, in turn, be able to grow sufficiently quickly to become established. (b) Seedlings must have a very fast rate of initial root elongation to compensate for the rapid drainage of water. (c) They must remain emergent above sand which tends to bury them. Local accumulations of the order of a decimeter are not unusual in a matter of days, or even hours. (d) Plants have to withstand the blast of sand particles which cause lesions, especially in plantlets. (e) They must withstand unearthing of the roots. (f) They must have a flexible root system enabling them to take advantage of water availability at all depths. (g) They have to be able to make very rapid use of slight, transitory water, and to tolerate water scarcity over very long periods. (h) They must be able to tolerate very low levels of nutrients in order to meet the low trophic level of the substrate (Bendali, et al., 1990).

In these regions vegetation are often swept by violent winds. Obstacles that check the velocity of the wind may cause some of its load to be deposited, and mounds or ridges are formed. The gradual building-up of these mounds is usually a physical process only partly due to plant growth, as wind-blown sand, dust and waterborne sediments may accumulate around the plant which then traps the sediments.These regions (desert and marshlands) have been explained well by Batanouny (2001) as the following:

1. They are able to produce adventitious roots from vegetative organs that become buried under the collected sediments. These roots may be long and thread-like, travelling horizontally at a shallow depth over long distances, as in *Arthrocnemum macrostachyum.* They may be in the form of tufts of very fine roots as in *Anabasis articulata.* Tufts of fine adventitious roots cover the thick buried stems.

Figure 9.5 The Mount and Nebkha dunes in: (a) miniature Nebkhas formed behind grass clumps in the Mojave; (b) the Chihuahuan Desert around mesquite plants (the Nebkha in the centre is about 1.5-m tall and 3.5-m in diameter – note also the evidence of fluvial activity in this landscape in the form of the rill running to the left of this Nebkha and towards the bottom left of the image) (courtesy of Parson and Abrahams, 1994) and (c) Iran the Nebkha in Lut Desert the foreground is approximately 3 meters tall and 10 meters in length.

These roots may be responsible in great measure for the total water absorption. Production of these newly formed roots is enhanced by the accumulation of sand.
2. They are capable of producing new shoots to replace those buried by on-blowing sand. In this way, plant growth copes with the sand accumulation: plant growth keeps abreast of the sand inundation.
3. They usually have intricately branching shoot systems, thus effectively intercepting wind-borne and water-borne materials and causing their deposition around the plant body.
4. They have perennating organs buried in the soil, or shoot and bud close to or near the soil surface. In other words, they have definite life forms:

(a) Geophytes with rhizomes, e.g. *Ammophila arenaria, Sporobolus virginicus, Pennisetum divisum, Sprobolus spicatus* and *funcus acutus.*

(b) Hemicryptophytes, especially *Hemicryptophyta caespitosa* or the tussock-forming species, e. g. *Stipagrostis plumosa,* S. *ciliata, Lasiurus* and *Frankenia revoluta*.

(c) Chamaephytes:
(i) *Chamaephyta pulvinata* (cushion plants), e.g. *Halocnemum strobilaceum, Arthrocnemum macrostachyum* (syn. *A. glaucum), Suaeda vermiculata,* S. *fruticosa,* S. *pruinosa, Salsola tetrandra, Haloxylon scoparium* (syn. H. *articulatum), Anabasis articulata, A. setifera, Cornulaca monacantha, Zygophyllrim album* and *Limoniastrum monopetalum.*
(ii) *Chamaephyta graminida* (hard grasses), e. g. *Lygeum spartum.*
(iii) *Chamaephyta suffrutiscentia* (semi-shrubs), e.g. *Ephdera alata* and *Calligonum comosum.*

(d) Phanerphytes: Only some nanophanerophytes have the ability to form mounds. The lower branches of these plants are usually prostrate, and consequently able to trap moving sand and other materials close to the surface of the ground. *Lycium shaw ii, L. europaeum, Nitraria retusa* and *Tamarix* spp. afford examples. The most common example in the Sahara is *Zizyphus lotus,* which forms Nebkas. These are rounded dune structures that can reach 10 m in diameter and 3 m in height. The formation of *Nebkas* in great number in cornfields can be considered to be an important indicator of an advanced state of desertification.

9.1.6. Resistance to sand deflation

Sand dunes can be divided into three categories: active, semi-stabilized and stabilized sand dune. Active dunes, characterized by sand burial, aeolian erosion and sand abrasion (García Novo et al., 2004; Ripley and Pammenter, 2004), are unfavorable for survival of most plants, but favorable for psammophytes. Evidently, species that can become established under such conditions conceivably have special adaptations in anatomy, morphology, reproduction and physiology (Danin, 1991; Hesp, 1991; Maun, 1994, 1998, 2004). Regenerative strategies are found to be extremely important for plants inhabiting active dunes.

It is believed that psammophytes deal with burial much better than with excavation (Bowers, 1982), and previous studies on psammophytes have paid much more attention to sand burial than that to wind erosion (Bowers, 1982; Danin, 1991; Hesp, 1991; Maun, 2004). Nevertheless, reports show that psammophytes may adapt to wind erosion by means of not only anatomical and morphological ways but also regenerative ways, as shown by *Cakile edentula* (Hesp, 1991) and *Artemisia monosperma*.

Plant adaptation and distribution in the dune field are closely linked to sand abundance, sand properties (accumulation or deflation) and intensity of sand mobility, which are relevant with dune position (García Novo et al., 2004). For instance, for a dune field composed of barchan dunes or barchan chains, the inter-dune lowland and the lower windward side of the dune are the erosion-prone zone, but the top and the leeward side of the dune are sand accumulation-prone zone. Different psammophytes may be distributed over different zones in response to different sand properties (Fig. 9.6).

Figure 9.6 Burial of the plant of *Artemisia wudanica* in response to wind erosion and their consequences, formation of a cluster on the active sand dune, (a)the plant eroded by wind, (b) buried by sand and (c) eroded first and then berried), China, (courtesy Liu, 2014).

Since sand abundance is different between the active and the stabilized sand dune, and the same aeolian process (burial or erosion) may occur at the different zones of an active sand dune, it is necessary to explore if there is a position effect in regenerative strategies when psammophytes deal with wind erosion. However, current knowledge is not enough to explain why different psammophytes are distributed over different dune positions.

Psammophytes have roots that tolerate exposure for a long time under the harsh desert conditions. They may produce vegetative growth when moistened. Examples of such plant species that grow in the deserts of the Middle East include *Moltkiopsis ciliata*, *Convolvulus lanatus*, *Polycarpaea repens*, *Echiochilon fruticosum*, *Scrophularia hypericifolia*, *Artemisia monosperma* and *Cornulaca monacantha.* Danin (1991) recorded cases in which the exposed roots of C. *monacantha* are 1-2-m long. That the plant tolerates exposure of its rootsmay be explained by the internal structure of the root. Roots of C. *monacantha* have internal active phloem and xylem elements, enabling transport to take place even when the roots are exposed. Danin (1991) suggested that protection of the xylem and phloem from external desiccation enables these drought-resistant species to withstand the principal stress of this habitat (Fig. 9.7).

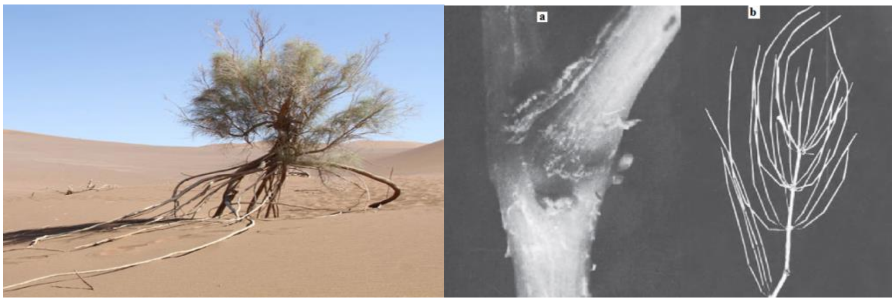

Figure 9.7 A shrub of *Haloxylon persicum* after being subjected to sand deflation for a long time (left). Accessory buds at the nodal area of a vegetative stem (a) and generative branches of *Caligonum comosum* (b) arranged in two groups at each node as a result of the sprouting of accessory buds (right) (after Danin, 1996)

9.1.7. Higher osmotic pressure and absorption from a relatively dry soil

Osmotic potential (Ψs) represents the potential ability of plants to absorb water from environments, which is an important indicator of drought tolerance. The value of Ψs can be regulated by many factors, which characterize the plant's attempt to minimize difference in water potential between the plant body and its environment (Batanouny, 2001). To cope with the prolonged annual dry period, which occurs in most arid areas, different plant functional types have evolved different survival mechanisms, which might be reflected by the leaf Ψs (Evenavi et al. 1971). Plants exhibiting osmotic regulation can normally lower their own internal water potentials by the synthesis or accumulation of osmotically active substances, e.g., carbohydrates (Oleksyn et al., 2000; Lawlor and Cornic, 2002), lipid composition (Sutinen 2000), and protein accumulation (Taulavuori et al., 1999; Kontunen-Soppela et al., 2000). Osmotic potential is regarded as a good criterion of the ability of desert plants to extract water (Fernndez and Reynolds 2000)

Absorption of dew by several desert plants growing was regarded by Vaadia and Waisel (1963) in a sandy area. They assumed that xerophytes, because of their thick cuticles, are less efficient than mesophytes in rapid foliar absorption of water during the night. *Trianthema hereroensis*, growing on sand dunes in the fog zone of Namibia, is one of the few desert plants shown to use fog efficiently.

Xerophytes have higher osmotic pressure values than mesophytes. The high osmotic pressure of the root and shoot tissues may be considered as a special physiological asset that adds to the efficiency of absorption. Osmotic values may serve as an exact indicator of the water balance and, therefore, of the total water economy of the plant (Walter, 1974). The osmotic pressure values are closely related to the water supply and decrease with increasing water supply (Batanouny, 1980).

The relatively high osmotic pressure of desert plants enables their roots to overcome the high total soil moisture stress that develops under xeric conditions and to withdraw more water than plants with low osmotic pressures. Zohary (1962) considered osmotic value to be one of the chief factors affecting drought resistance. The osmotic pressure values are closely related to water supply and decrease with increasing availability of water (Batanouny, 2001).

9.1.8. Hydraulic Lift

One of the mechanisms that plants have to overcome during drought stress is the redistribution of water from wetted to dried zones of the soil. This mechanism is called hydraulic lift (Liste and White 2008). In fact, a correlation between the capacity of plants to transfer water from deeper wet zones of the soil to dryer ones and tolerance to drought has been observed in different maize genotypes. This hydraulic lift not only achieves better water status of drought tolerant plants, but also increases the transpiration rate and therefore, can increase both CO2 assimilation rate and plant growth (Wan et al., 2000). In the same way, increase of hydraulic lift under arid conditions has been observed in several crop species and such an increase was related with the maintenance of photosynthesis rate unchanged under drought conditions (Zegada-Lizarazu and Iijima, 2004).

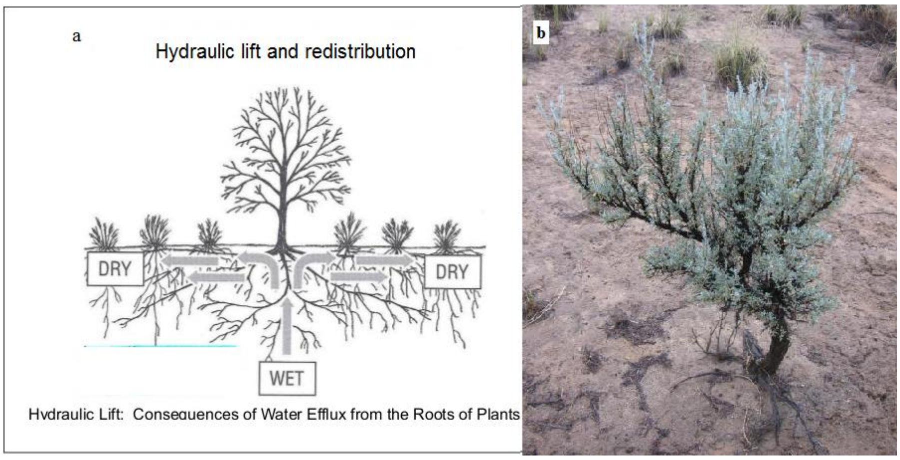

Figure 9.9 (a) Pattern of water flow through the root system during the day and night periods according to the hydraulic lift hypothesis and (b) *Artemisia tridentata* which uses hydraulic lift and grows in arid and semiarid conditions, throughout a range of cold desert and steppe habitats (after Caldwell 1988).

Hydraulic lift not only contributes to absorption of water by the same plant that is moving the water, but also by adjacent plants. Hence, the use of plants with deeper roots systems, reaching groundwater planting aside of the interested crops may delay adverse drought effects in such crops. Also, this agronomical technique can be improved by shadowing of the plant doing the hydraulic lift (Sekiya and Yano, 2004). Finally, water redistribution from wet to dryer soil layers can also operate from top to bottom soil layers after raining events (Oliveira et al., 2005). In spite of the great importance of hydraulic lift for drought stress tolerance, the molecular mechanisms behind this process are totally unknown. Hydraulic lift depends on soil and root conductivities, water potential gradients, and the intensity of transpiration. Up-to-date, how these factors are interconnected is not completely understood (Neumann and Cardon, 2012) (Fig. 9.9).

9.1.9. Root anatomical properties to tolerate aridity

In woody plants drought stress decreases diameter of vessel and tracheid, thickness of vascular cambium, and delays formation of xylem and phloem, or division of cambium cell (Lovisola and Schubert, 1998). Under drought stress, xylem cavitation is induced, resulting in the formation of embolism and disruption of the transpiration stream one of the key features affecting plant survival and productivity under drought stress (Swidrak et al., 2014).

Under prolonged drought, there is an increase in osmotic potential (change in chemical potential of water by solutes) of xylem sap. Similar changes in both leaf and root extracts have been observed in some species, such as grapevine (*Vitis vinifera* L.). This could help contribute to the maintenance of proper water flow, which can be calculated based on the volume flow rate and the force of water flow, including water movement from soil into the roots, under water deficit (Barrios-Masias et al., 2015). Severe drought can lead to complete loss of hydraulic conductance and, in turn, to the desiccation of aboveground tissues and plant mortality (Martínez-Vilalta et al., 2014).

Drought can suppress cambial cell division and inhibits turgor-driven cell enlargement (Swidrak et al., 2014). In dry conditions, plants increase suberization of root apoplastic barriers; for example, root suberization, which is important for water retention, increased in the endodermis but decreased in the sclerenchyma, cells of rice **(**Henry et al., 2012). Increased suberization is observed under a number of stress conditions. In the drought-sensitive cultivars of grapevine, more rapid root suberization occurs even under control conditions, as opposed to root suberization in drought-insensitive cultivars of grapevine. Also, under drought stress, suberization occurs closer to the root tip in both cultivars, indicating a faster maturation of root tissue (Wasson et al., 2012). Hydrotropism can result in deeper roots, with access to deep-water (Eapen et al., 2005). When deep-water is available, plants have longer root systems with increased root density at such depths, increasing capacity for water transport from soil to shoot as a result of higher frequency of root hairs and increased vessel diameter.

The supply of soil moisture to plants is very poor and variable as a consequence of severe climatic aridity. Subsurface layers of deep soils may have limited available water. However, in dry years the soil at different depths may be dry and have no available water for plants. Dryness of the soil around plant roots is not rare. Consequently, one might expect that the root moisture could be affected. The presence of internal active phloem and xylem elements protects the roots from the harsh atmospheric conditions when they are exposed.

According to Bahardwaj and Gopal (1979) even during the summer when the soil moisture content at various depths decreases considerably, root moisture is not as much affected. For instance in *Haloxylon articulatum*, the peripheral layer may become hard and corky, thus protecting the plant from the pressure of hard soil and from desiccation. The inner cortex may instead become spongy, forming dead sleeves that function as water storage tissue.They also noted that the width of cortex increases along with secondary growth in older plants. The authors postulated that water stored in the root cortex can be utilized for growth and reproduction during the dry period, when other climatic conditions are favourable.

References

Aerts R., Boot R.G.A., van der Aart P.J.M. (1991) The relation between above and belowground biomass allocation patterns and competitive ability. Oecologia (Berlin) 87:551-559

Barrios-Masias F.H., Knipfer T., McElrone A.J. (2015) Differential responses of grapevine rootstocks to water stress are associated with adjustments in fine root hydraulic physiology and suberization. J. Exp. Bot., 66: 6069–6078.

Baskin C.C., Baskin J.M. (1998) Seeds ecology, biogeography, evolution of dormancy and germination. Academic Press, San Diego, 666 p.

Baskin C.C., Chesson P.L., Baskin J.M. (1993) Annual seed dormancy cycles in two desert winter annuals, J. Ecol., 81: 551-556.

Batanouny K.H., (2001) Adaptations of desert organisms. In: Cloudsley-Thompson J.L. (ed) Plants in the deserts of the Middle East.

Batanouny K.H., Abdel Wahab MA (1973) Eco-physiological studies on desert plants. VIII. Root penetration of *Leptadenia pyrotechnica* (Forssk.) Decne. in relation to its water balance. Oecologia (Berl) 11:151-161

Bendali F., Floret C., Le Floc'h E., Pontanieri R. (1990) The dynamics of vegetation and sand mobility in arid regions of Tunisia. Journal of Arid Environments, 18: 21-32

Bengough A.G., Bransby M.F., McKenna S.J., Robers T.J., Valentine T.A. (2006) Root responses to soil physical conditions; growth dynamics from field to cell. Journal of Experimental Botany, 57(2): 437–447

Bengough A.G., Mc Kenzie B.M., Hallett P.D., Valentine T.A. 2011. Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. J. Exp. Bot. 62: 59–68.

Bowers, J. The plant ecology of inland dunes in western North America, J. Arid Environ., 5: 199–220, 1982.

Caldwell M.M. (1988) Plant root systems and competition. In: Greuter W., Zimmer B. (eds) Proceedings of the XIV international botanical congress. Koeltz, KoÈ nigstein/Taunus, pp 385-404

Campbell B.D., Grime J.P., Mackey J.M.L. (1991) A trade off between scale and precision in resource foraging. Oecologia, 87: 532-538.

Canadell J., Jackson R.B., Ehleringer J.R., et al., (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia, 108: 583–595.

Changjun L., Fanjiang Z., Bo Z., Bo L., Zichun G., Huanhuan G., Tashpolat T. (2015) Optimal root system strategies for desert phreatophytic seedlings in the search for groundwater, J. Arid Land, 7(4): 462–474, doi: 10.1007/s40333-015-0006-3.

Chimungu J.G., Brown K.M., Lynch J.P. 2014. Large root cortical cell size improves drought tolerance in maize. Plant Physiol. 166: 2166–2178.

Cortina J., Green J.J., Baddeley J.A., Watson C.A. (2008) Root morphology and water transport of Pistacia lentiscus seedlings under contrasting water supply: A test of the pipe stem theory. Environ. Exp. Bot., 62: 343–350.

Danin A. (1991) Plant adaptations in desert dunes, Journal of Arid Environments, 21: 193–212

Danin A., Plants of Desert Dunes. Springer-Verlag Berlin Heidelberg (1996) P. 181. DOl: 10.1007/978-3-642-60975-6

Den Herder G., Van Isterdael G., Beeckman T., De Smet I. 2010. The roots of a new green revolution, Trends Plant Sci. 15: 600–607.

Den Herder G., Van Isterdael G., Beeckman T., De Smet I. (2010) The roots of a new green revolution. Trends Plant Sci. 15: 600–607.

Douglas B.K. (2011): Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. Annals of Botany, 108: 407–418.

Eapen D., Barroso M.L., Ponce G., Campos M.E., Cassab G.I. (2005) Hydrotropism: Root growth responses to water. Trends Plant Sci., 10: 44–50100.

Eissenstat D.M. (1991) On the relationship between specific root length and the rate of root proliferation: A field study using citrus rootstocks. New Phytol., 118: 63–68

Evanavi M., Shanan L., Tadmor N. (1971) The Negev, the challenge of a desert. Harvard University Press, Cambridge

Fahn A. (1989) Plant anatomy, 3rd edn. Pergamon Press, Oxford, 544 pp

Fenta B.A., Beebe S.E., Kunert K.J., Burridge J.D., Barlow K.M., Lynch J.P., Foyer C.H. (2014) Field phenotyping of soybean roots for drought stress tolerance. Agronomy, 4: 418–435.

Fernndez R.J., Reynolds J.F. (2000) Potential growth and drought tolerance of eight desert grasses: lack of a trade-off. Oecologia, 123:90–98

Fitter, A.H. (1991) Characteristics and functions of root systems. In: Waisel Y., Eshel A., Kafkafi U. (Eds), Plant Roots: The Hidden Half, pp. 3–25. New York, NY: Marcel Dekker Inc. 948 pp.

Forde B.G. (2014) Nitrogen signalling pathways shaping root system architecture: An update. Curr. Opin. Plant Biol., 21: 30–36.

Freitas (1997) Drought. In: Prasad M.N.V. (Eds) Plant ecophysiology. Wiley, New York, pp 129-149

García N., Díaz Barradas M.C., Zunzunegui M., García Mora R., et al, (2000) Comparison of germination strategies of Artemisia ordosica with its two congeners from deserts of China, Acta Bot. Sin., 42: 71–80.

Gibbens R.P., Lenz J.M. (2001) Root systems of some Chihuahuan Desert plants. Journal of Arid Environments, 49: 221-263 Doi:10.1006/jare.2000.0784

Gibbens R.P., MCNeely R.P., Havstad K.M. (2005) Vegetation changes in the Jornada Basin from1858 to 1998. Journal of Arid Environments 61: 651–668

Gupta P.K., Balyan H.S., Gahlaut V., Kulwal P.L. (2012) Phenotyping, genetic dissection, and breeding for drought and heat tolerance in common wheat: Status and prospects. In Plant Breeding Reviews; Janick, J., Ed.; John Wiley and Sons: Hoboken, N.J., USA, pp. 85–168.

Haling, R.E.; Brown, L.K.; Bengough, A.G.; Young, I.M.; Hallett, P.D.; White, P.J.; George, T.S. (2013) Root hairs improve root penetration, root-soil contact, and phosphorus acquisition in soils of different strength. J. Exp. Bot., 64: 3711–3721.

Henry A., Cal A.J., Batoto T.C., Torres R.O., Serraj R. (2012) Root attributes affecting water uptake of rice (*Oryza sativa*) under drought. J. Exp. Bot., 63: 4751–4763.

Hesp P. (1991) Ecological processes and plant adaptations on coastal dunes, J. Arid Environ., 21: 165–191

Jackson R.B., Caldwell M.M. (1989) The timing and degree of root proliferation in fertile-soil microsites for three cold desert perennials. Qecologia, 8: 149-153

Jose L.B., Alfredo C. R., Luis H.E. (2003) The role of nutrient availability in regulating root architecture. Current Opinion in Plant Biology 6: 280–287.

Kassas M., Batanouny K.H. (1984) Plant ecology in Sahara desert. In: Cloudsley-Thompson J. (Eds) Sahara desert. Pergamon Press, Oxford, pp 77-90

Kontunen-Soppela S., Laine K. (2001) Seasonal fluctuation of dehydrins is related to osmotic status in Scots pine needles.Trees 15: 425–430

Kontunen-Soppela S., Taulavuori K., Taulavuori E., Lhdesmki P., Laine K. (2000) Soluble proteins and dehydrins in nitrogenfertilized Scots pine seedlings during deacclimation and the onset of growth. Physiol. Plant 109: 404–410

Lawlor D.W., Cornic G. (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ. 25: 275–294

Li S., Su P., Zhang H., Zhou Z., Shi R., Gou W. (2018) Hydraulic Conductivity Characteristics of Desert Plant Organs: Coping with Drought Tolerance Strategy. Water, 10(8): 1036. Doi: 10.3390/w10081036.

Liu B., Liu Z., et al (2014). Sand burial compensates for the negative effects of erosion on the dune-building shrub Artemisia wudanica. Plant and soil, 374(1-2): 263-273.

Li X.R., Tan H.J., He M.Z., Wang X.P., Li, X.J. (2009) Patterns of shrub species richness and abundance in relation to environmental factors on the Alxa Plateau: Prerequisites for conserving shrub diversity in extreme arid desert regions. Sci. China-Earth Sci., 52: 669–680.

Liste H.H., White J.C. (2008) Plant hydraulic lift of soil water: implications for crop production and land restoration. Plant Soil 313:1–17

Liu B., He J., Zeng F., Lei J., Stefan K. Arndt S.K. (2016) Life span and structure of ephemeral root modules of different functional groups from a desert system. New Phytologist, 211:103–112

Liu Z., Liu B., Qian J. (2014) Some mechanisms in reproduction of psammophyte to adapt to wind erosion on the active sand dune. Adv. Geosci., 1: 1-8. Doi: 10.5194/adgeo-1-1-2014

Lovisola C., Schubert A. (1998) Effects of water stress on vessel size and xylem hydraulic conductivity in Vitis vinifera L. J. Exp. Bot., 49: 693–700.

Lynch J.P. (2007) Roots of the second green revolution. Aust. J. Bot., 55: 493–512.

Ma W. H., Fang J. Y. (2006) Root to shoot ratios of temperate steppe and the environmental controls in Inner Mongolia. Acta Scientiarum Naturalium Universitatis Pekinensis 42(6):774-778.

Malamy J.E. (2005) Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ. 28: 67–77. Doi: 10.1111/j.1365-3040.2005.01306.x

Martínez-Vilalta J., Poyatos R., Aguadé D., Retana J., Mencuccini M. (2014) A new look at water transport regulation in plants. New Phytol. 204: 105–115.

Maun M.A. (2004) Burial of plants as a selective force in sand dunes, Coastal dunes, ecology and conservation, edited by: Martinez, M.L. and Psuty, N.P., Berlin, Springer, 119–135, 2004

Mayer A.M., Polijakoff-Mayber A., (1989) The germination of seeds, 4th ed. Pergamon Press, London, 270 p.

Mu Z.X., Zhang S.Q., Liang A.H., Liang Z.S. (2005) Relationship between maize root hydraulic conductivity and drought resistance. Acta Agron. Sin., 31: 203–208.

Newmann R.B., Cardon Z.G. (2012) The magnitude of hydraulic redistribution by plant roots: a
review and synthesis of empirical and modeling studies. New Phytol. 194: 337–352

Oleksyn J., Zytkowiak R., Karolewski P., Reich P.B., Tjoelker M.G. (2000) Genetic and environmental control of seasonal carbohydrate dynamics in trees of diverse Pinus sylvestris populations. Tree Physiol. 20: 837–847

Oliveira R.S., Dawson T.E., Burgess S.S.O., Nepstad D.C. (2005) Hydraulic redistribution in three Amazonian trees. Oecologia, 145:354–363

Park Y.M. (1990) Effects of drought on two grass species with different distribution around coastal sand-dunes. Functional Ecology, 4: 735-741.

Prince, S.J., Mutava R.N., Pegoraro C., Oliveira A.C.D., Nguyen H.T., Root characters. In Genomics and Breeding for Climate Resilient Crops; Kole, C., Eds.; Springer: Berlin, Germany, 2013; pp. 67–131.

Psuty M. L., N.P. Ecological Studies, 171, Springer, Coastal Dunes, Ecology and Conservation, 2004.

Ranjbar-Fordoei A. (2019) The Study of Different Water Regimes on Photosynthetic Performance and Leaf Water Status of Pistachio Trees (*Pistacia vera* L.). Journal of Nuts 10(1): 25-34

Reader R.J., Jalili A., Grime J.P., Spencer R.E., Matthews N. (1992) A comparative study of plasticity in seedling rooting depth in drying soil. J. Ecol. 81:543-550

Ren Y.Z., Xu Y.H., Ding J.P., Ma Y.S., Pei D.L., Li C.W., et al., (2011) Regulation of abiotic factors on the plasticity of plant root development. Chin. Agric. Sci. Bull., 27: 34–38.

Rhizopoulou S., Davies W.J. (1991) Influence of soil drying on root development, water relations and leaf growth of *Ceratonia siliqua* L. Oecologia (Berlin), 88: 41-47.

Robbins N.E., Dinneny J.R. (2015) The divining root: Moisture-driven responses of roots at the micro-and macro-scale. J. Exp. Bot., 10: 1–10.

Rundel P.W., Nobel P.S. (1991) Structure and function in desert root systems. In D. Atkinson, ed, Plant Root Growth: An Ecological Perspective, special publication No. 10 of the British Ecological Society. Blackwell Scientific Publications, Oxford, UK, pp. 349-378.

Running S.W. (1980) Field estimates of root and xylem resistance in Pinus contorta using root excision. J. Exp. Bot., 31: 555–569.

Ruta N., Liedgens M., Fracheboud Y., Peter S., Hund A. (2010) QTLs for the elongation of axile and lateral roots of maize in response to low water potential. Theoretical and Applied Genetics 120(3): 621–631.

Saengwilai P., Tian X., Lynch J.P. (2014) Low crown root number enhances nitrogen acquisition from low-nitrogen soils in maize. Plant Physiol., 166: 581–589.

Saidi A., Ookawa T., Hirasawa T. (2010) Responses of root growth to moderate soil water deficit in wheat seedlings. Plant Production Science, 13(3): 261-268, Doi: 10.1626/pps.13.261

Schenk H.J., Jackson R.B. (2002) Rooting depths, lateral root spreads, and belowground/aboveground allometries of plants in water limited ecosystems. Journal of Ecology 90: 480-494.

Sekiya N., Yano K. (2004) Do pigeon pea and sesbania supply groundwater to intercropped maize through hydraulic lift? Hydrogen stable isotope investigation of xylem waters. Field Crop Res. 86:167–173

Shan L.S. Studies on morphology and function of root of typical desert plant and its drought resistant physiology characteristics on northwest China. Ph.D. Thesis, Gansu Agricultural University, Lanzhou, China, June 2013

Sutinen M.L., Repo T., Sutinen S., Lasarov H., Alvila L., Pakkanen T.T. (2000) Physiological changes in Pinus sylvestris needles during early spring under sub-arctic conditions. Fore. Ecol. Manag., 135:217–228

Swidrak I., Gruber A., Oberhuber W. (2014) Xylem and phloem phenology in co-occurring conifers exposed to drought. Trees, 28: 1161–1171.

Taulavuori E., Taulavuori K., Laine K. (1999) Seasonality of glutathione dynamics in Scots pine and bilberry. Plant Biol 1:187–191

Walter J. (1974) A new approach to the water relations of desert plants. In: Brown GW J.R. (ed) Desert biology, vol. II. Academic Press, New York, pp. 213–310

Wan C.G., Xu WW, Sosebee R.E., Machado S., Archer T. (2000) Hydraulic lift in drought-tolerant and -susceptible maize hybrids. Plant Soil 219: 117–126

Wang H., Yamauchi A. (2006) Growth and function of roots under abiotic stress soils. In B. Huang ed., Plant-Environment Interactions 3rd ed. CRC Press, Taylor and Francis Group, LLC, New York. 271-320

Wang P., Mou P. (2012) Review of root nutrient foraging plasticity and root competition of plants. Chin. J. Plant Ecol. 36: 1184–1196. Doi: 10.3724/sp.j.1258.2012.01184

Wang Y., Frei M. (2011) Stressed food–The impact of abiotic environmental stresses on crop quality. Agric. Ecosyst. Environ., 141: 271–286.

Wang Y.L., Zhou M., Li P., Sun G.P., Shi S.L., Xu C.Y. (2017) Root morphological plasticity determing the adaptive strategies of *Cotinus coggygria* seedlings in barren soil environment. *J.* Beijing For. Univers. 39: 60–69.

Wang Z.Y., Hou J., Qu Z.Q., Guo J.Y., Li, J.R. (2017) Root distribution of 430 plants species in temperate grassland of northern China, Applied ecology and environmental research, 15(3): 1625-1651

Wasaya A., Zhang X., Fang Q., Yan Z. (2018) Root Phenotyping for Drought Tolerance: A Review. Agronomy, 8, 241; Doi: 10.3390/agronomy8110241

Wasson A.P., Richards R.A., Chatrath R. et al, (2012) Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. J. Exp. Bot., 63: 3485–3498.

Yu P., Li X., White, P. J., Li, C. (2015) A Large and Deep Root System Underlies High Nitrogen-Use Efficiency in Maize Production. PLOS ONE 10(5):1-17.

Zegada-Lizarazu W., Iijima M. (2004) Hydrogen stable isotope analysis of water acquisition ability of deep roots and hydraulic lift in sixteen food crop species. Plant Prod. Sci. 7:427–434

Zhan A. Lynch, J.P. (2015) Reduced frequency of lateral root branching improves N capture from low-N soils in maize. J. Exp. Bot. 66: 2055–2065.

Zhang S.Q., Xu B. C. (2010) Root and Plant Efficient Use of Water. Beijing: Science Press.

Zhang Y.Q., Zhu Q.K., Qi S., Zhang Y., Wang D.M. (2005) Root system distribution characteristics of plants on the terrace banks and their impact on soil moisture. Acta Ecol. Sin. 25: 500–506. Doi: 10.3321/j.issn:1000-0933.2005.03.017

Zhu J., Ingram P.A., Benfey P.N., Elich T. (2011) From lab to field, new approaches to phenotyping root system architecture. Curr. Opin. Plant Biol. 14: 310–317.

Zohary M. (1962) Plant life in Palestine and Jordan. Ronald Press, New York, 262 pp

Chapter 10________________

Seed dispersal aspects with emphasize on desert systems

Introduction

Each desert plant species has its own complex life history strategy that enables it to persist in its arid habitat. These strategies include seed dispersal and germination. In general, seed dispersal helps seeds escape sibling and kin competition, decreases predation, reduces the probability of offspring survival in unpredictable environments, and aids in reaching and colonizing new habitats for seed germination and population regeneration (Gutterman, 1993; Venable et al., 2008.) Different plants evolve different dispersal strategies in deserts. The escape strategy occurs when plants produce large numbers of small seeds with long viability and thus escape from seed-eating insects and other animals by entering cracks in the soil. The protection strategy occurs when mature seeds remain attached to the mother plant and must be dispersed by wind, animals, or rain and it reduces the potential of dispersal to uncertain conditions (Gutterman, 2002). In addition, seed structures and characters (seed mass and seed shape) affect the effectiveness of seed dispersal (Platt and Weis, 1997; Wemer and Patt, 1979). Hence, species with different structures form different dispersal syndromes, including anemochory (Augspurger, 1986 and Matlack, 1987), zoochory (Andersen, 1993), autochory (Ellner and Shmida, 1981; van Oudtshoorn and van Rooyen, 1999), ombrohydrochory (Sorensen, 1986) and barochory (Leishman et al., 1995). However, very little is known about the dispersal strategy in relation to dispersal syndromes in plant species of cold deserts.

Seed germination and dormancy are pivotal events in seedling establishment, and they are closely related to seed dispersal and population generation. Some researchers consider seed dormancy as an adaptive bet-hedging strategy in spatiotemporally varying environments (Snyder, 2006; Venable and Brown, 1988). In other words, desert plants depend more on dormancy than dispersal for survival, since timing of precipitation is uncertain and plants tend to delay germination until the occurrence of a favorable precipitation event rather than relying on dispersal (Venable and Lawlor, 1980). For this reason, seed dormancy and germination are important for desert plants. Species inhabiting deserts have developed different seed germination strategies via natural selection over a long period of time (Gutterman, 1994). Typically, these strategies are divided into two general categories: (1) opportunistic, that is, with fast germination rate, no or low seed dormancy, and high germination percentage; and (2) cautious germination strategies, with low germination rate, high seed dormancy, and low germination percentage (Gutterman, 1994). In addition, seed dispersal strategies seem to be related with germination strategies. Plants in the Negev Desert with seed protection strategies may develop cautious germination strategies with low risk to seedling survival, while plants with escape seed dispersal strategies may develop opportunistic germination strategies with high risk to seedling survival (Gutterman, 1994).

Dispersal spectra vary from place to place, presumably because the relative merits of different dispersal modes are affected by attributes of the plants in question (e.g. seed size, height) and because of the environmental circumstances under which seedlings establish or fail to establish (Hughes et al., 1994). Similar vegetation types in different geographic regions often have somewhat different dispersal spectra. The differences can be related to different biogeographic and evolutionary histories (Willson et a1., 1990).

10.1. Zoochory: the dispersal of plants by animals

Zoochory is the dispersal of diaspores (fruits, seeds or pollen) by animals. Animals can disperse plant seeds in several ways. Seeds can be transported on the outside of animals (through digestive tract), a process known as *epizoochor*y. Seed dispersal via ingestion by animals, or *endozoochory*, is the dispersal mechanism for most tree species.

The diaspores of endozoochorous plants are eaten by animals and humans and the hard seeds or fruit stones pass through the intestinal canal without damage (Smallwood, 1984). Synzoochory is the dispersal of seeds (nuts), which are an attractive long-term, storable food resource for animals (e.g., acorns, hazelnuts, and walnuts): the seeds are stored some distance from the parent plant, and some escape being eaten if the animal forgets them. Synzoochory is mainly performed by ants and some birds. The dispersal process that involves birds carrying plant propagules in their bills is called stomatochory, a type of synzoochory. Dyszoochory is the process whereby diaspores are destroyed (eaten and digested), but some of the seeds are accidentally dropped, thus contributing to regeneration (van der Pijl, 1982).

Endozoochory indicates the mutualistic relationship between animals and plants (Bascompte and Jordano, 2007). Synzoochory seems to indicate a predation relationship, but, in many cases, it has positive results on plants. In epizoochory, the plant benefits because its dispersal units are dispersed while the animal does not benefit but does not lose the seeds or fruits attached to its body; therefore, this relationship can be characterized as commensalism.

10.1.2. Epizoochory

Plant species transported externally by animals can have a variety of adaptations for dispersal, including adhesive mucus, and a variety of hooks, spines, and barbs, which are also used against predators. These fruits do not supply compensation and do not have means to exhibit and advertise (Fig. 10.1).

Figure 10.1 *Eremopyrum triticeum* an epizoochorous plant has diaspores that penetrate the soles of animals and is dispersed

10.1.3. Endozoochory

Endozoochory is generally a coevolved mutualistic relationship in which a plant surrounds seeds with an edible, nutritious fruit as a good food for animals that consume it. Birds and mammals are the most important seed dispersers, but a wide variety of other animals, including turtles and fish, can transport viable seeds (Corlett, 1998).

The exact percentage of tree species dispersed by endozoochory varies between habitats, but can range to over 90% in some tropical rainforests (Smallwood, 1984). Seed dispersal by animals in tropical rainforests has received much attention, and this interaction is considered an important force shaping the ecology and evolution of vertebrate and tree populations (Terborgh, 1986). In the tropics, large animal seed dispersers (such as tapirs, chimpanzees, and hornbills) may disperse large seeds with few other seed dispersal agents. The extinction of these large frugivores (fruit-eaten) from poaching and habitat loss may have negative effects on the tree populations that depend on them for seed dispersal (Chapman and Onderdonk, 1998). The high frequency of fleshy fruited species in tropical rainforests may generally be associated with large seeds, of which vertebrates are the most effective agents of dispersal.

In most cases, the fruits are consumed by the animals and birds and deposited in their droppings or feces. In some cases, passage through the digestive system serves to remove impermeable waxes and coatings as well as germination retardants, and the feces provide moisture and nutrients to the seedlings. Sometimes, fruit-eating improves germination, sometimes it prevents it, and sometimes it has no influence (Howe, 1986). In the marine plant, *Najas marina*, it was found that the eating of seeds with hard peels by Mallard ducks (*Anas platyrhynchos*) improves the germination amount of seeds not digested by increasing the grinding.

In Africa, many seeds of acacia species germinate from elephant droppings, and it seems that the acacia depends on the elephant eating for helping its germination. Also, in the Sinai, there is a positive influence on the germination of acacia species. Seeds passing through the digestive system of *Dorcas Gazelle* are essential and germination increases. Another benefit of acacia is that beetles (*Bruchidoe*) harm acacia seeds and the *Gazelle* eats them also. Digestive juices destroy larvae and prevent damage to embryos. The improvement and acceleration in germination are very essential to germination promise in conditions of not regular soil wetting in desert area. In the eastern North America, it was found that white-tailed deer represent a significant and previously unappreciated vector of seed dispersal across the North American landscape, probably contributing an important long-distance component to the seed shadows of hundreds of plant species, and providing a mechanism to help explain rapid rates of plant migration (Myers et al., 2004) (Fig. 10.2).

Figure 10.2 Endozoochory in southern Morocco (an arid environment), tree-climbing goats disperse seeds by spitting (after Dlibes, 2017)

10.1.4. Synzoochory

Seed predators, which include many rodents (such as squirrels) and some birds (such as jays) might also disperse seeds by hoarding them in hidden caches (Forget and Milleron, 1991). The seeds in caches are usually well protected from other seed predators and, if left uneaten, will grow into new plants. Finally, seeds may be secondarily dispersed from seeds deposited by primary animal dispersers. For example, dung beetles are known to disperse seeds from clumps of feces while in the process of collecting dung to feed their larvae (Andresen and Levey, 2004).

Best known in this respect are the nutcrackers (*Nucifraga*), which feed largely on the “nuts” of beech, oak, walnut, chestnut, and hazel trees; the jays (*Garrulus*), which hide hazelnuts and acorns; the

nuthatches; and the California woodpecker (*Balanosphyra*), which may embed literally thousands of acorns, almonds, and pecan nuts in bark fissures or holes of trees. Secondarily, rodents may aid in dispersal by stealing the embedded diaspores and burying them.
In Germany, an average jay may transport about 4,600 acorns per season over distances of up to 4 km (2.5 miles). Woodpeckers, nutcrackers, and squirrels are responsible for similar dispersal of *Pinus cembra* in the Alps near the tree line.

10.1.5. Myrmecochory

Myrmecochory is the dispersal of seeds by ants. Foraging ants disperse seeds that have appendages called elaiosomes (Terborgh, 1986) (e.g., bloodroot, trilliums, acacias, and many species of Proteaceae). Although myrmecochory is a type of synzoochory, it will be discussed as a separate animal-dispersal mechanism.

For myrmecochorous plants, the final location of seeds depends; basically, on which ants interact with the seed. Myrmecochorous plants have seeds that have caruncles or arils that act as elaiosomes. When ants find a seed, in most cases it is transported to the nest. They usually do this by using the elaiosome as a handle (Byrne and Levey, 1993). After eating the elaiosome, the seed may remain in the nest or be discarded on the midden or farther away. Thus, the pattern of final seed location is directly influenced by ant behavior. The consequences of seed and seedling distribution in relation to density-dependent selection, the juvenile plants' defenses and predation are well known (e.g. Howe, 1989). Myrmecochory is an example of true mutualism, which has arisen independently in so many groups of plants that there must be very strong pressures, which favor this type of dispersal mechanism (Handel and Beattie, 1990). Elaiosomes are soft, fleshy structures that contain nutrients for the animals to eat. The ants carry such seeds back to their nest, where the elaiosomes are eaten. The remainder of the seed, which is hard and inedible to the ants, then germinates either within the nest or at a removal site where the seed has been discarded by the ants (Chapman and Onderdonk, 1998).

There is also a well-documented body of evidence showing the advantages of seeds remaining in the nest, where they are protected against fire and/or predators (e.g., Christian and Stanton, 2004). The presence of an elaiosome may be important for the transport of the seed to the nest, but its absence after seed manipulation implies that the shape of the seed, its size, or the presence of surfaces that can provide a new handle for the ants, may be key factors in the outcome of the interaction, i.e., the final location of the seed. The final location of seeds with their elaiosomes (Fig. 10.3) removed was evaluated to assess the importance of possible handles in transporting ants during redispersal experiments of seeds from nests of six species of ants. The results indicate that seeds remained within the nest because the ants were not able to transport them out of the nest. As a consequence of the elaiosome being removed, small ant species could not take *Euphorbia characias* seeds out of their nests. Only large ant species could remove *E. characias* seeds from their nests. Attaching an artificial handle to *E. characias* seeds allowed the small ant species to redistribute the seeds from their nests. On the other hand, *Rhamnus alaternus* seeds that have a natural handle after elaiosome removal were removed from the nests by both groups of ant species.

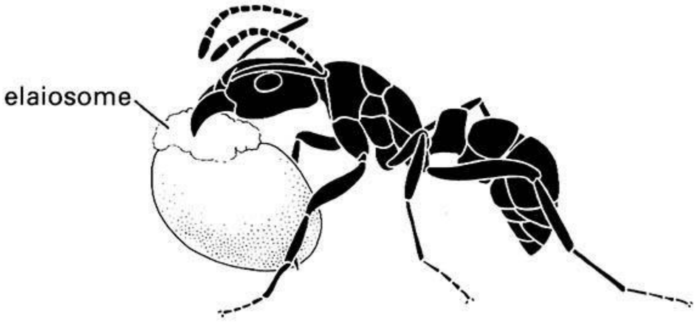

Figure 10.3 An ant carrying a seed of *Dillwynia juniperina* (Fabaceae) by its elaiosome (seed appendage) (after Gullan and Cranston, 2014)

If a seed has an element that acts as a handle, it will eventually be removed from the nest. The ant size and their mandible gap can determine the outcome of the interaction (i.e., the pattern of the final seed shadow) and, as a consequence, could influence the events that take place after the dispersal process (Gòmez et al., 2005). This dispersal relationship is an example of mutualism, since the plants depend on the ants to disperse seeds, while the ants depend on the plant seeds for food.

10.2. Anemochory

According to Van der Pijl (1982) anemochory, although extensive, is regarded as a derived dispersal mechanism and one that is not characteristic of primitive flowering plants.

Anemochorous species can be found all over the world in all vegetation types, but they are especially prominent among plant species of open habitats such as steppes, prairies, open heath lands, deserts, sand dunes and along road verges (Collins and Uno, 1985). In stratified plant communities, the contribution of anemochorous species usually increases in the lower layers, whereas zoochorous species are more abundant in the upper layers (Hilger and Schultka 1988).

A multitude of structural devices for dispersal by wind have evolved. These structures may be of varied origin, e.g. the testa, fruit coat, calyx, bracts, hypsophylls and even the whole plant (Fahn and Werker, 1972). The following classification based on the action of the wind during dispersal will be used to facilitate the discussion on anemochory.

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10.3. Accidental and indirect wind action dispersal diaspores modes

The accidental transport of diaspores by wind, without any particular features promoting anemochory, occurs more commonly than believed (Van der Pijl, 1982). Observations have shown that diaspores can be transported over large distances during storms or cyclones.

Diaspores falling among dead leaves can adhere to the leaves either because of stickiness of the leaves or of the diaspores and once they have beenattached, they can be blown along with the leaves. Although this manner of transport should not be regarded as the normal mode of dispersal, it can play an important role in arid regions with a high percentage of deciduous species, especially if those leaves are viscous. In Namaqualand (South Africa) the hairy diaspores of *Lasiospermum brachyglossum* as well as those of *Arctotheca calendula* often cling to leaves and twigs. It was also observed that diaspores of a variety of species adhered to the sticky leaves of *Tripteris* species (Rösch, 1977). This category includes those cases where wind does not exert its influence on the diaspores directly, but on the capsule or follicle enclosing the diaspores. Several terms have been introduced for this mechanism, for example anemoballism (Van der Pij L., 1982), jactitation and censer mechanism (Bansal and Sen, 1981).

Indirect wind action occurs predominantly among smaller herbaceous geophytic species. Flowers and fruit are borne on long peduncles, or the peduncles elongate during fruit maturation in order to expose the fruit maxim ally to wind action above the foliage. A horizontal wind induces the fruits to swing, thereby effecting diaspore dispersal. For effective anemoballism (*Greek: anemos = wind + ballistes = to throw*) several adaptations of the plant are essential. The negative influence of humidity on wind dispersal requires auxiliary mechanisms for exposure at the right time. Most anemoballists have dry fruits that dehisce due to a xerochastic mechanism.

Opening in dry air only (xerochasy) is apparent in many anemochorous species (Van der Pijl, 1982). For example, capsules of *Nemesia* species and *Wahlenbergia* species close again during rainy weather due to the absorption of water, thus preventing dispersal in a moist atmosphere. Another adaptation found among some anemoballists is the curving of the peduncle during seed maturation.

10.4. Direct Wind Action

According to Van der Pijl (1982) this mode of wind dispersal has two main categories. Diaspores that are transported by air are termed meteor-anemochores, whereas those transported along the ground are termed chamae-anemochores or anemogeochores.

The principal function of the structural modifications for wind dispersal are to increase the resistance between the air and the falling diaspore, so prolonging aerial flight and increasing the chances of the diaspore being carried away by wind currents. The two physical forces determining the dispersal distance of a wind dispersed diaspore in flight are drag and gravity. These forces act through the processes of gravitational settling, advection by wind and atmospheric turbulence (Greene and Johnson 1990a, b). A multitude of factors affect wind dispersal. Some of these factors, for example, seed mass, wing-loading, diaspore release height and morphology of the diaspore, are under the direct control of the parent plant (Andersen 1991, 1992). Others such as wind velocity, wind direction, topography and vegetation structure are not (Okubo and Levin 1989).

The chemical composition of seeds can even be affected by the dispersal mode in anemochorous species. Several studies showed that wind- and animal-dispersed species had significantly higher proportions of fat and less of protein and carbohydrates than those of passively-dispersed species (Lokesha et al., 1992). Although fats are more energy demanding in their synthesis than proteins and carbohydrates, fats have other associated benefits. Dispersal efficiency of anemochorous species is usually increased by a reduction in seed mass and, assuming that increased dispersal is advantageous, anemochorous species should select for a higher fat content.

10.5. Dust-like Diaspores

One of the simplest means of gaining access to the wind is by being extremely small, with a large surface to volume ratio (Willson, 1993). These small diaspores can be blown about like dust particles without any special devices for buoyancy (Van der Pijl, 1982). The "smallness" of dust diaspores is accomplished by reduction in the endosperm and/or testa and/or an underdeveloped embryo (Fahn and Werker, 1972). This reduction in seed size is often associated with the dependence on another organism for nutrition.

Dust diaspores are characteristic of lower plant species, such as mosses. Among higher plant species they occur predominantly within certain families that are rich in epiphytic, parasitic or saprophytic species, e.g. Orchidaceae, Pyrolaceae, Orobanchaceae and Droseraceae. In all these families, enormous numbers of seeds are produced at the cost of fewer, larger sized seeds (Stebbins, 1971). Because these species have such specific habitat requirements, the production of increased numbers of seeds is essential to enhance the probability that at least some seeds will reach a favourable germination site.

The Crassulaceae is one of the families which produce minute seeds. Several genera of the Crassulaceae, e.g. *Crassula, Tylecodon* and *Cotyledon,* with many species, occur abundantly in the arid areas of southern Africa. Within the Campa- nulaceae, many species have very tiny seeds, for example the successful winter annual species of *Wahlenbergia* in the Namaqualand desert (Rösch, 1977). Production of numerous dust-like seeds by desert species serves as an escape strategy to prevent mass consumption of seeds. Several species inhabiting the Sainai Desert are quoted by Gutterman (1993a) as having dust-like seeds: *Schismus arabicus* (Poaceae, 0.07 mg), *Spergularia diandra* (Caryophyllaceae, 0.018 mg), *Nasturtiopsis coronopifolia, Arabidopsis kneuckeri, Diplotaxis harra,* and D. *acris* (Brassicaceae). These tiny seeds are carried by the wind to cracks and furrows in the soil and are then covered with fine soil particles

10.6. Cystometeorochory (balloon)

An air filled structure lightens small seeds in cystometeorochory (balloon-like). This dispersal mode is little studied. Maximum calculated distances are below 2 m (Soons and Ozinga 2005), but extreme values were measured up to 80 m for *Calluna vulgaris* (Bullock and Clarke 2000). This mode is certainly less efficient in forests, as wind is weaker.

The tiny seeds of Orchidaceae, Pyrolaceae and Orobanchaceae also have a low falling velocity (0.2–0.31 m/s for Orchidaceae). But only a calculated dispersion distance is available (median 0.95 m and 99th -percentile14.7 m for *Cephalanthera damasonium*; Soons and Ozinga 2005). However, because it is thought that very light seeds (<0.05 mg), even without corresponding adaptation for anemochory, are as efficient in wind as plumed seeds (Bonn and Poschlod, 1998; Greene and Calogeropoulos, 2002). Ferns pores can be included incystometeorochory as well, but no data exist on their dispersal capacity except a calculated distance of 330 km for *Lycopodium* sp. based on its very low falling velocity based on its very low falling velocity.

10.7. Trichometeorochory

Plumed seeds are more efficient for wind dispersal. In trichometeorochory, seeds are completed with a hairy structure to reduce falling velocity. These organs have very variable efficiency, however, with falling velocity varying from 8 cm/s for *Epilobium angustifolium* to 165 cm/s for *Pulsatilla alpina* (Vittoz and Robin Engler, 2007). Forest species were classified with trichometeorochory for less efficient plumes (type 3).

10.8. Pterometeorochory (pterochory)

In Pterometeorochory or pterochory, seed dispersal is improved through wings. Trees are frequent in this category, but herbs are present as well, with a generally higher falling velocity. Reviewed maximum distances ranged mainly between 80– 314 m for trees and 1–12 m for herbs. Pterometeorochory was thus classified as dispersal type 3 for herbs and type 4 for trees.

10.9. Chamaechory

A much less studied dispersal mode is chamaechory, with diaspores rolling on the ground pushed by the wind. This diaspore can be either a circular-shaped fruit (*Astragalus alpinus*), the fruit with calyx (Anthyllis vulneraria) or the complete, dry, inflorescence. Chamaechory is especially common and efficient in steppes where nothing hampers dispersal (Vittoz, Robin Engler, 2007). Dispersal is usually restricted because seeds get stuck in irregularities. For chamaechory, we retained dispersal distance type 2 for fruits in grassland and type 3 for seeds on snow or carried by dry inflorescences.

10.10. Boleochory

Boleochory (semachory) is another mode used by anemochorous plants. The small seeds without particular features are spread when the fruit is shaken by wind. At maturity, the stem of such plants is often rigid but elastic and sways in the wind, acting like a catapult. As animals or others may shake the capsules as well, some classify this mode independently (Bonn et al. 2000). Although small, the seeds are dense and have a high falling velocity (Vittoz, Robin Engler, 2007). Consequently, Soons and Ozinga (2005) calculated very short dispersal distances, generally<0.5 m, but without considering the catapult effect.

10.11. Hydrochory

Water can disperse seeds in various ways. In wetland plants, seeds are often light enough to float and move on rivers, lakes or ponds (nautochory of *Alisma plantagoaquatica*, *Carex flava*, *C. elata*, *Iris pseudacorus*, *Sparganium* sp.). Some seeds can float and survive for one year or more (Vittoz, 2007). Similarly, running water may carry many different types of seeds with heavy rains (bythisochory), sometimes to rivers and down to lowland areas. Bythisochory is complementary to other dispersal modes and randomly affects many different species dwelling on slopes. It is through this vector that high mountain species are frequently observed on gravel areas along rivers (Bill et al., 1999). Although the dispersal distances may be important, it may not attribute dispersal types to hydrochorous dispersal modes because distances are highly unpredictable and never documented. Moreover, nautochory (*plant and plant seed spreading by swimming*) is geographically limited and the bythisochory downslope restricted. Rain may contribute to disperse seeds through the shock generated by the rain droplets hitting the fruits (ombrochory). Some species (e.g. *Caltha palustris*, *Veronica serpyllifolia*, *Prunella vulgaris*, *Thlaspi perfoliatum*) have developed fruit shapes and elastic fruit stalks in order to use this energy to eject seeds. Very few measurements are published for ombrochory, but they are all below or close to 1 m.

10.11.1. Ombrohydrochory (ombrochory)

The present review describes the ombrohydrochoric dispersal syndrome in plants, i.e. seed expulsion by raindrops. There are two different ombrohydrochoric dispersal modes – dispersal by rain wash and by ballistic forces. Both have been reported from the understory of tropical and temperate forests, from wetlands and from deserts, and from numerous families and genera. A special form of ombrohydrochoric dispersal is the jet-action rain-operated seed dispersal mechanism which is restricted to the semi-desert ice plants, Aizoaceae, one of the major families of the angiosperms. Within this family, 98% of the species possess hygrochastic capsules with an ombrohydrochoric seed dispersal mechanism which in part is also responsible for the remarkable speciation burst and radiation. The highly complex capsules open when wet and the seeds are expelled by a ‘jet action’ with the kinetic energy of raindrops. The halves of the covering membranes of a locule (each of a number of small separate cavities, especially in an ovary), origin form a nozzle near the center of the capsule which serves as a jet. Drops of water falling on the distal opening (after the locule has been filled with water) result in an explosive expulsion of water droplets and seeds through that jet. More seeds are dispersed further away from the capsule than in those capsule types without such a jet mechanism (Pia, 2006).

10.11.2. Hygrochasy

In contrast to xerochasy, hygrochasy is not very common in the plant kingdom, and is restricted to arid regions (Van der Pijl, 1982). The best known examples of hygrochasy have been described for the deserts of the Old World. Hygrochasy may be due either to a cohesion mechanism or an imbibition (shrinking or swelling) mechanism or a combination of both. Cohesion mechanisms are based mainly on the water content of the cell lumen as opposed to imbibition mechanisms that are based on the water content of cell walls. The active cell walls in the case of a cohesion mechanism are usually thin and when the cells lose water, the walls curve inward or wrinkle as a result of the cohesion between water molecules and their adhesion to cell walls.

A group of these cells may draw another organ with thicker cell walls along with it. The imbibition mechanism is based on the action of the walls belonging to cells of two antagonistic groups, or of different sections of the same cell. When a cell wall loses or imbibes water, it shrinks or swells, respectively, in a direction perpendicular to that of the cellulose microfibrils. The reaction of the cell walls is determined by the orientation of these microfibrils in different cells or the direction of the cells themselves. The walls of cells taking part in imbibition mechanisms are usually thick and the resulting movement is either bending or torsion (van Oudtshoorn, van Rooyen, 1999).

10.11.3. Trypanospermy

Anchorage in the case of trypanospermic species is caused by the presence of a long appendage on the upper side of the diaspore which is composed of two parts (van Oudtshoorn and van Rooyen, 1999); a basal part which is capable of spiral twisting by a hygroscopic mechanism, and an upper part which is always straight and at right angles to the basal part. A surface view of the spiral portion of *Erodium moschatum* shows three zones. On contact with water, the spiral portion untwists and lengthens while the upper portion is held in place by pressure against the ground or another object. The elongation of the spiral portion causes the penetration of the diaspore into the soil (van Oudtshoorn and van Rooyen, 1999).

Trypanospermy represents an example of adaptive convergence within two distinct families, the Poaceae and the Geraniaceae (Ghermandi 1995). In the Poaceae, the structure responsible for the rotating movement is the awn and in the Geraniaceae it is the part of the style that remains attached to the carpel. The geographical distribution of the genera containing trypanospermic diaspores indicates that these genera are widespread in semi-arid and desert areas. Genera such as *Aristida, Stipagrostis* and *Stipa* are abundant in open communities in arid areas (Haase et al. 1995; van Oudtshoorn and van Rooyen, 1999). Within the Geraniaceae, the *Pelargonium* species and *Sarcocaulon* species are found predominantly in the arid north-western portion of South Africa and in Namibia, while the genus *Erodium* occurs mainly in semi-desert and desert areas (van Oudtshoorn and van Rooyen, 1991).

Figure 10.4 *Stipagrostis plumose* (a), *Aristida penata* (b), *Sipa barbata* (c) and *Peganum harmala* (d) are widespread in semiarid and desert areas via trypanospermic diaspores.

10.11.4. Myxospermy

Mucilages can be classified on the basis of their physical appearance, origin, chemical composition or fine structure. A distinction is often made between (1) pure slime and pectin mucilage which is structureless (Hedge, 1970), and (2) cellulose mucilage which has more structural strength due to the presence of cellulose micro fibrils (van Oudtshoorn and van Rooyen, 1991). The capacity of the mucilaginous cell walls to swell considerably upon wetting indicates that these cell walls consist of large quantities of unesterified galacturonic acid with an exceptionally large capacity for hydration. Mucilage membranes are usually laid down in secondary cell walls and only rarely do they develop by metamorphosis from existing secondary cell walls (Mű̈hlethaler, 1950). In some instances, the mucilage can also constitute the primary cell wall. On the basis of the anatomical origin of the mucilage, the following different types can be distinguished (van Oudtshoorn and van Rooyen, 1991):

1. The entire cuticle is released as a mucilaginous mantle.
2. The outer cell wall of the epidermal layer of the testa becomes mucilaginous.
3. From the outer wall of each cell a threadlike outgrowth, consisting of a dense helix, protrudes into the cell. Upon wetting, a small lid in the outer wall above a thickening opens on one side and the inner substance of the threadlike outgrowth swells and is pushed out.
4. The mucilage is pushed out through slits in the epidermal cells.
5. Mucilage production is restricted to sub-epidermal layers. The epidermis is ruptured due to the swelling of these mucilaginous cells.
6. Only the epidermal cells in longitudinal ridges become mucilaginous or mucilage producing cells are restricted to the margins of the seeds.
7. Hairs or papillae on the pericarp produce the mucilage.

Myxospermy is especially common in certain plant families such as the Acanthaceae, Brassicaceae, Lamiaceae, Plantaginaceae and Asteraceae (Grubert, 1974). *Plantago* species, belonging to the Plantaginaceae, are examples of pure slimes containing no cellulose. Seed dispersal in a variety of *Plantago* species found in the Sinai Desert (van Oudtshoorn and van Rooyen, 1991).

10.12. Anthropochory

Seed dispersal by humans certainly always occurred, but it strongly increased during the last centuries, and became particularly important a few decades ago with the market globalization and the intercontinental transport of goods. Vittoz and Robin Engler (2007) distinguished three modes of anthropochory: plants or seeds being sold for agriculture and gardening (*ethelochory*), seeds being involuntarily mixed with the previous ones (speirochory), or seeds travelling hidden in goods, cars, soil under soles, with hay, etc. (*agochory*). All three means can potentially lead to very long dispersal distances and are, for example, responsible for the advent of neophytes in Switzerland and Europe. But while ethelochory and speirochory mostly concern urban and cultivated areas, agochory is probably more important in natural or semi-natural ecosystems. Seed dispersal distance through anthropochory is strongly dependent on the type of human activity but, in general, agricultural activities are the most susceptible to spreading seeds in semi-natural ecosystems due to movements between fields (McCanny and Cavers 1988). Anthropochory dispersal distance thus, limit to the approximate size of a farming property (Vittoz, 2007).

10.13. Autochory

Autochorous plants are equipped with an autonomous mechanism involved in seed dispersal. Some of these mechanisms provide for telechoric dispersal, whereas others prevent dispersal and are antitelechoric. Ballistic dispersal, a form of telechoric autochory, occurs when the diaspore is propelled explosively, by a fruit that opens suddenly or by a trip-lever (Willson et al., 1990). Autochory is commonly encountered in arid environments.

10.13.1. Telechoric Ballistic Dispersal

This dispersal mechanism is found in diverse taxonomic families' e. g. Scrophulariaceae, Fabaceae, Papaveraceae, Liliaceae, Caryophyllaceae, Campanulaceae, Euphorbiaceae, Capparidaceae, Rubiaceae and Acanthaceae. An ecological constraint of the ballistic dispersal mechanism is seed size, because neither very heavy nor very light seeds can be projected effectively. The production of numerous seeds per fruit may also interfere with effective ballistic dispersal. The distance achieved by this form of dispersal is inherently and directly limited by the physical mechanism itself (Hughes et al., 1994). The potential energy necessary for the explosive dispersal of plant propagules is most commonly accrued during the maturation of fruits which deform during drying to become structurally unstable.

10.13.2. Ballistic Dispersal and Turgor Mechanisms

The turgor mechanism is a telechoric mechanism in which living cells take part. Elastic tissue is stretched in a certain direction by another tissue with a very high turgor pressure, or the tissue with high turgor pressure is itself stretched in a certain direction as a result of being set against a tissue that offers a resistance. Great tension develops and when the tension exceeds a critical value, a barrier is removed by opening of the fruit along an abscission tissue which reaches its final stages of development at the same time. As a result, the stretched tissue suddenly contracts and the seeds are ejected with great force. The direction of stretching of the elastic tissue and the form and location of the abscission tissue determine the way the seeds are ejected when tension is released.

Turgor mechanisms are almost always situated in the fruit walls. The only example, in which the seed coat takes part, is found in the Oxalidaceae (Phillips, 1922). In this family, the thick elastic cuticular membrane is excessively stretched in girth by the growth of the seed and the parenchyma cells of the outer integument become strongly turgescent by enzymatic degradation of starch immediately before the maturation of the seed. Finally, the counteracting forces in the cuticular membrane and those exerted by the parenchymatous cells become so excessive that the seed coat bursts at the antiraphal side. Another example of the turgor mechanism is encountered in the squirting cucumber (*Ecballium elaterium*) occurs in dry areas on Mediterranean coasts. As the fruit ripens, the tissue surrounding the pedicel breaks down and the seeds are surrounded by semi-liquid mucilage.

10.13.3. Ballistic Dispersal by Imbibition Mechanisms

The site of action of this mechanism is in the walls of dead cells. This mechanism is based on the antagonistic actions of the walls belonging to cells of two antagonistic groups or of different walls of the same cell. When a cell wall loses or imbibes water, it either shrinks or swells, respectively, in a direction perpendicular to that of the cellulose microfibrils. If the angle of the cellulose micro fibrils in different cells varies or the direction of the cells themselves varies, their reaction towards moisture will be different. The movement will be bending or torsion.

An example of dispersal by imbibition mechanisms can be found in *Tephrosia purpurea* (Fabaceae). The pod of his species is flat but slightly curved at the tip. When mature, it is dry and remains attached to the parent plant by a small pedicel. The enclosed seeds are dispersed when the pod suddenly breaks into two halves.

The imbibition mechanism is very common in the Euphorbiaceae e. g. *Euphorbia mauritanica* and *E. dregeana,* two species from Namaqualand, South Africa. Their small fruits, usually a capsule, burst open suddenly at maturity and expel the seeds with a considerable force approximately 1 m away from the parent plant (McCann 1959; Dyer 1973).

The capsules of the Acanthaceae, when ripe, burst and eject the seeds in a similar manner. The two-valved seed case opens with an audible report and hurls the seeds out to a considerable distance (McCann, 1959). The seed is subtended by a short woody hook (the indurated funicle) and this aids in flinging the large seeds away from the mother plant.

The imbibition mechanism can also aid dispersal of diaspores which creep or leap on the ground. Bristles, involucre bracts, calyxes, awns, or other rigid organs of the diaspores which are capable of hygroscopic movements can cause the whole diaspore to move on the ground. These organs are sensitive to atmospheric moisture and accordingly change their direction in response to the environment and by their movement propel the diaspore in a definite direction (McCann 1959). Creeping is achieved by outward and inward movements of the bristles or bracts equipped with short hairs or teeth by which they adhere to the ground (van Oudtshoorn and van Rooyen 1999).

In the Dipsacaceae, Asteraceae, Geraniaceae and Poaceae, movements of the bristles of the pappus or the awn produce creeping of the whole diaspore. In the Poaceae, the awns exert torsion movements as a result of changes in their moisture content. These movements cause pressure of one awn of the spikelet upon the other, thus turning the whole diaspore over and inducing a leap. The layers of sclerenchymatous tissue responsible for the torsion occupy most of the awns' tissue (van Oudtshoorn and van Rooyen, 1999).

10.13.4. Trypanospermy

The imbibition mechanism is also responsible for different types of antitelechory e.g. trypanospermy. Trypanospermic or boring fruits are equipped with a hygroscopic drilling apparatus or with a sharply pointed tip which enables them to penetrate the soil. The main advantage of trypanospermy is the enhancement of water uptake due to increased seed-soil contact. It also affords anchorage against surface runoff, while the risk of predation is decreased as soon as the diaspores of trypanospermic species are buried (Van Rooyen et al., 1990). Approximately 7% of the species of Namaqualand are trypanospermic and belong to the Poaceae and Geraniaceae (Van Rooyen et al., 1990).

A long appendage on the upper side of the diaspore is divided into two parts; the lower part is capable of spiral twisting by a hygroscopic mechanism whereas the upper part is always straight and at a right angle to the lower one. Changes in moisture cause the spiral portion to twist and untwist, while the upper portion is held in place by pressure against the ground. The movement of the spiral portion causes the penetration of the diaspore, which is pointed and stiff at its base, into the soil. Hairs present on the diaspore are directed upward so that they prevent return of the diaspore to the soil surface when the appendage starts to twist up again as the atmosphere dries out (van Oudtshoorn and van Rooyen, 1999). Trypanospermy is found in Poaceae, *Stipa capensis* and *Aristida* genus.

References

Andersen A.N. (2006a) Predispersal seed losses to insects in species of *Leptospermum* (Myrtaceae). Aust. Ecol. 14: 13–18.

Andersen U.V., (1993) Dispersal strategies of Danish seashore plants, Ecography, 16(4): pp. 289-298.

Augspurger C.K. (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees, The American Journal of Botany, 73(3): 353–363

Bansal R.P., Sen D.N. (1981) Dispersal strategies in plants of the Indian Desert. J. Arid Environ. 4:3-14

Bascompte J., Jordano P. (2007) Plant–animal mutualistic networks: The architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst. 38: 567–593.

Bill H.C., Poschlod P., Reich M., Plachter H. (1999) Experiments and observations on seed dispersal by running water in Alpine floodplain. Bull. Geobot. Inst. ETH 65: 13 – 28.

Bonn S., Poschlod P. and Tackenberg O. (2000) ”Diasporus” – a database for diaspore dispersal.

Bullock J.M., Clarke R.T., (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 124: 506 – 521.

Byrne M.M., Levey D.J. (1993) Removal of seeds from frugivore defecations by ants in a Costa Rican rain forest. Vegetatio, 107/108:363–374

Canada. II. Dispersal by combines. Weed Res. 28: 67-72.

Chapman C.A., Onderdonk D.A. (1998) Forests without primates: primate/plant codependency. Cons. Biol. 45: 127–141.

Christian, C.E. and Stanton, M.L. (2004) Cryptic consequences of a seed dispersal mutualism: seed burial, elaiosome removal, and seed bank dynamics. Ecology 85: 1101–1110.

Corlett R.T. (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. Biol. Rev. 73: 413–448

Delibes M., Castañeda I., Fedriani J.M. (2017) Tree-climbing goats disperse seeds during rumination**.** Front Ecol. Environ. 15(4): 222–223, doi:10.1002/fee.1488

Ellner S., Shmida A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants?" Oecologia, 51(1): 133–144, 1981.

Forget P.M., Milleron T. (1991) Evidence for secondary seed dispersal by rodents in Panama.
Oecologia 87: 596–599.

Ghermandi L (1995) The effect of the awn on the burial and germination of Stipa speciosa (Poaceae). Acta Oecol.16:719-728

Gòmez C., Espadaler X., Bas J.M. (2005) Ant behaviour and seed morphology: a missing link of myrmecochory. Oecologia, 146: 244–246.

Greene D.F., Calogeropoulos C. 2002. Measuring and modelling seed dispersal of terrestrial plants. In: Bullock J.M., Kenward R.E. and Hails R.S. (Eds) Dispersal ecology. The 42nd Symposium of the British Ecological Society held at the University of Reading 2 – 5 April 2001. Blackwell, Oxford, 3 – 23.

Greene D.F., Johnson E.A. (1990a) The dispersal of winged fruits and seeds differing in autorotative behavior. Can. J. Bot. 68: 2693-2697.

Greene D.F., Johnson E.A. (1990b) The aerodynamics of plumed seeds. Func. Ecol. 4:117-125.

Grubert M. (1974) Studies on the distribution of myxospermy among seeds and fruits of Angiospermae and its ecological importance. Acta Bioi Venez 8: 315-551

Gutterman Y. (1994) Strategies of seed dispersal and germination in plants inhabiting deserts, Botanical Review, 60(4): 373–425.

Gutterman Y., Seed Germination in Desert Plants, Springer, Berlin, Germany, 1993.

Gutterman Y., Survival Strategies of Annual Desert Plants, Springer, Heidelberg, Germany, 2002.

Haase P., Pugnaire P.I., Incoll L.D. (1995) Seed production and dispersal in the semi-arid tussock grass Stipa tenacissima L. during masting. J. Arid Environ. 31:55-65

Handel S.N., Beattie A.J. (1990) Seed dispersal by ants. Sci. Am. 263: 76–83.

Hedge I.C. (1970) Observations on the mucilage of Salvia fruits. Notes Roy. Bot. Gard. Edinb.
30:79-95

Howe H.F. (1986) Seed dispersal by fruit-eating birds and mammals, In: D.R Murray (ed.) *Seed Dispersal*. Academic, New York, pp. 123–190.

Hughes L., Dunlop M., French K., Leishman M.R., Rice B., Rodgerson L., Westoby M. (1994) Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. J. Ecol. 82: 933-950

Leishman M.R., Westoby M., Jurado E. (1995) Correlates of seed size variation: a comparison among five temperate floras, Journal of Ecology, 83(3): 517–530, 1995.

Lokesha R., Hedge S.G., Shaanker R.U., Ganeshaiah K.N. (1992) Dispersal mode as a selective force in shaping the chemical composition of seeds. Am. Nat. 140: 520-525

Matlack G.R. (1987) Diaspore size, shape, and fall behavior in wind-dispersed plant species, American Journal of Botany, 74(8):1150–1160, 1987.

McCanny S.J., Cavers P.B. (1988) Spread of proso millet (Panicum miliaceum L.) in Ontario,

Mű́hlethaler K (1950) The structure of plant slimes. Exp Cell Res 1:341-350

Myers J.A., Vellend M., Gardescu S., Marks P.L. (2004) Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139: 35–44.

Okubo A., Levin S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology 70:329-338

Pia P. (2006) Ombrohydrochory: Rain-operated seed dispersal in plants - With special regard to jet-action dispersal in Aizoaceae. Flora, 201: 511-511

Platt W.J., Weis I.M. (1997) “Resource partitioning and competition within a guild of fugitive prairie plants. American Naturalist, 111: 479–513.

Rösch MW (1977) Enkele plantekologiese aspekte van die Hester Malan-natuurreservaat. MSc. thesis. University of Pretoria, Pretoria

Smallwood J. (1984) Ecology of seed dispersal Annu. Rev. Ecol. Syst., 13: 201–228.

Snyder R.E., (2006) Multiple risks reduction mechanisms: can dormancy substitute for dispersal? Ecology Letters, 9(10): 1106–1114.

Sorensen A.E., (1986) Seed dispersal by adhesion, Annual Review of Ecology and Systematic, 17: 443–463

Stebbins G.L. (1971) Adaptive radiation of reproductive characteristics in angiosperms. Seeds and seedlings. Annu. Rev. Ecol. Syst., 2:237-260

Terborgh J. (1986) Community aspects of frugivory in tropical forests, In: A. Estrada and
T.H. Fleming (Eds.) Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 371–384.

The Insects: An Outline of Entomology. An outline of entomology, Gullan P.J. and Cranston
P.S. (2014) pubished by John Wiey and Sons

Van der Pijl L. (1982) Principles of dispersal in higher plants, 3rd edn Springer, Berlin Heidelberg New York

Van der Pijl L. (1982) Principles of Dispersal in Higher Plants, Third Edition. Springer, New York.

Van Oudtshoorn K.V.R., van Rooyen M.W. Dispersal Biology of Desert Plants, Springer, Berlin, Germany, 1999.

Van Rooyen M.W., Theron G.K., Grobbelaar N. (1990) Life form and dispersal spectra of the flora of Namaqualand, South Africa. J. Arid Environ. 19: 133-145

Venable D.L. and Brown J.S. (1988)The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments, American Naturalist, 131(3): 360–384.

Venable D.L., Flores-Martinez A., Muller-Landau H.C., Barron-Gafford G., Becerra J.X., (2008) Seed dispersal of desert annuals. Ecology, 89(8): 2218–2227.

Venable D.L., Lawlor L., (1980) Delayed germination and dispersal in desert annuals: escape in space and time, Oecologia, 469(2): 272–282.

Vittoz P., Robin Engler R. (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. Bot. Helv. 117 (2007): 109-124 0253-1453/07/020109-16. DOI 10.1007/s00035-007-0797-8

Werner P.A., Platt W.J., (1979) Ecological relationships of co-occurring goldenrods (Solidago: compositae),The American Naturalist, 110: 959–971

Willson M.F. (1993) Dispersal mode, seed shadows, and colonization patterns. Vegetatio, 107/108*:* 261-280

Willson M.F., Rice B.L., Westoby M. (1990) Seed dispersal spectra: a comparison of temperate plant communities. J.Veg. Sci. 1: 547-562

Chapter 11

High temperature and heat stress

Introduction

There are three cardinal points for the types of temperatures that are vital for plant activity:

-Minimum temperature below which no plant growth and development occurs

-Optimum temperature at which maximum plant growth and development occurs

-Maximum temperature above which plant growth and development stops

The sudden increase in ambient maximum temperature, in a matter of few days, by 5–7°C with corresponding increase in the minimum temperature, creates ‘heat stress’ on plants. The normal physiology of the plant gets affected and plant maturity is accelerated. In some cases, plants shed leaf/flower/fruit or dry-up non-productive tillers and even become sterile to overcome the unprecedented stress. In practical agriculture, such heat stress inflicts enormous crop losses. Due to global weather change, the frequency of heat stress is predicted to increase in different parts of the world.

Rates of photosynthesis and respiration increase with an increase in temperature until a threshold maximum photosynthesis level is achieved. Generally, it is around 22–24°C and remains that way, up to 30–32°C. In rice, it was found that grain yields declined if mean seasonal temperature increased above 33°C. Surpassing the high temperature peak, various enzymes get inactivated, decreasing the photosynthetic efficiency. The high temperature coupled with high respiration and evaporation pushes the plant to permanent wilting when the temperature exceeds 46°C. The extent of crop loss inflicted by heat stress can ruin the income for poor farmers in heat prone areas. In many cases, there may be adequate soil moisture but the negative water balance created by heat stress lead to withering of plants in a matter of few days. Under the natural habitat, plants have been exposed to more than one stress at a time; consequently they have evolved strategies against a combination of stresses by responding to them in different ways. Often high temperature, high transpiration rate and high light intensity occur together affecting the plant productivity (Wardlaw and Wrigley, 1994).

Plants experience high temperature in many different ways and adaptation or acclimation to high temperature occurs over different time scales and levels of plant organization. Exposure to high temperature can be chronic and long term, as experienced in hotter habitats, or it can be more acute, as a result of seasonal or daily temperature extremes. It is also clear that different plant tissues and organs at different growth stages will be damaged in different ways depending on the heat susceptibility of the dominant cellular processes that are active at the time of the stress. Altogether, this means that 'heat stress' (and therefore, 'heat tolerance') is not a single phenomenon, but rather a varying set of complex perturbations of organismal homeostasis.

At the cellular level, heat affects a wide range of structures and functions. High temperatures alter lipid properties, causing membranes to become more fluid and thereby disrupting membrane processes. All proteins have an optimal temperature window for activity, so increased temperatures alter enzyme activity leading to imbalance in metabolic pathways, and eventually at high temperature proteins denature. Membrane and protein damage leads to the production of active oxygen species (AOS). This may not be effectively controlled through antioxidants at high temperatures, resulting in heat-induced oxidative damage in addition to the direct effects of heating. At the physiological level, this damage translates into reduced efficiency of photosynthesis, impaired translocation of assimilates and loss of carbon gain. These factors in turn combine to cause altered phenology, reproductive failure and accelerated senescence.

Heat stress may also be accompanied by high irradiance stress. Other environmental stresses also result in similar types of damage as those caused by heat. Therefore, it is expected that the responses of plants to different stresses might overlap, and that exposure to any one stress may affect subsequent reactions to another stress (cell or tiusse hardening).

Molecular studies are beginning to illuminate processes that are involved in sensing, responding and acclimating to heat over a short time scale. In addition to the summary presented here, readers are also referred to other recent reviews (Sung and Guy, 2003; Wang et al., 2004). One, now classic, response to acute heat stress is the production of heat shock proteins (HSPs), which function, at least in part, as molecular chaperones in cellular protein quality control.

Leaf senescence is one of the inimitable symptoms of heat injury characterized by structural changes in the chloroplast followed by a vacuolar collapse, and thereafter a loss of plasma membrane integrity and interference of cellular homeostasis (Khanna-Chopra, 2012).

11.1. Heat stress (HS)

Heat stress is one of the major limiting factors for plants all over the world. As a consequence of climate change and global warming, heat stress has an increasingly negative impact on crop growth, survival, and overall productivity. Heat shock proteins (HSPs), also known as molecular chaperons, are present in all organisms and are important for maintaining and restoring the homeostasis of proteins. Heat shock proteins are named according to their molecular weight such as HSP101, HSP70, HSP90, HSP60, HSP40, and small heat shock protein (HSP) (Swindell et al., 2007; Li et al., 2015a). Apart from heat shock proteins, the role of several other heat responsive genes which are mainly transcription factors has been investigated (Wahid et al., 2012). Since complex mechanism is involved toward the development of heat stress resistance in plants, developing thermotolerant crops seem to be a difficult task.

Several genes like quantitative trait locus/es (QTLs) have been identified for tolerance against heat stress. QTLs associated with heat tolerance in plants have been reviewed in detail by Driedonks et al. (2016).

Gene ontology and Genomes analyses determined that the identified DEGs were involved in heat shock protein, heat shock transcription factors, hormone, as well as calcium and kinase signaling. Some of the ethylene-responsive element binding proteins have been found to be up-regulated by heat stress. Binding protein (BiP) is also contributing to abiotic stress by reducing ROS accumulation and by increasing the water retention ability, by enhancing un-translated region (UTR) pathway, and also by expression of stress-related genes (Wang et al., 2017).

Association of endophytic fungus with plants enhanced the tolerance against heat stress. Khan et al. (2013) found that P. resedanum infestation led to increase in the plant growth during heat stress. Plants having infestation were found to have enhanced the survival rate and produce higher number of leaves as compared to control plants with or without stress excursion.

Garruna-Hernandez et al. (2014) reported that the increase in diurnal air temperature raised both stomatal conductance and transpiration rate in habanero pepper (Capsicum chinense) causing an increase in temperature deficit (air temperature–leaf temperature). Leaf temperature decreased by 5 °C, allowing a higher CO2 assimilation rate in plants at diurnal maximum air temperature (40 °C), and showed that the thermal optimum range in a tropical crop such as Habanero pepper is between 30 and 35 °C (leaf temperature, not air temperature).

11.2. Physiological responses to heat stress

High temperature limits the optimal plant performance plants can experience wide fluctuations of temperature on a daily or seasonal basis. It is to be expected, therefore, that plants have evolved mechanisms through which cellular activity could be maintained at varying temperatures. The ability of plants to cope with extreme temperature is a complex process and is determined by environmental factors and also by the genetic capability of the plant. In general, stability of life processes in most plants is comparatively wide which ranges from several degrees above zero to around 35°C (Zróbek-sokolnik, 2012). The increase of temperature up to a certain level increases plant growth, photosynthesis, respiration and enzyme activity and after that these parameters tend to decline.

The increase of temperature up to a certain level increases plant growth, photosynthesis, respiration and enzyme activity (Fig. 11.1) and after that these parameters tend to decline process has its own referred critical or lethal temperature after that it cannot proceeded and causes permanent damage to cell structures and ultimately the cell, plant death as well (Zróbek-sokolnik, 2012).

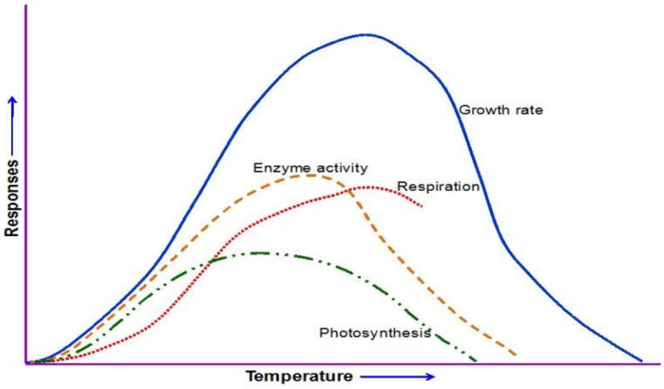

Figure 11.1 Schematic illustration of the effect of temperature on major physiological processes of plants (after Fitter and Hay, 2002)

11.2.1. Photosynthesis

Temperature plays one of the most important roles in the rate and ability of a plant to photosynthesize effectively. In general, there is a positive correlation between change in temperature and photosynthesis. But when temperatures exceed the normal growing range (15°C to 45°C) of plants heat injury takes place and heat temperature hurts the enzymes responsible for photosynthesis. Even in the absence of heat stress injury, photosynthesis would be expected to decline as temperature increases because photorespiration increases with temperature faster than does photosynthesis (Schuster et al., 1990). Photosynthesis is highly sensitive to high temperature stress and is often inhibited before other cell functions are impaired (Berry and Bjorkman, 1980).

11.2.2. Heat stress and photoinhibition

Other major abiotic stress which is often accompanied with high temperature is light intensity. Light varies in intensity both temporally (as a result of the diurnal cycle) and spatially (as a result of shading by clouds and other organisms and objects) throughout the day. Excess light leads to photoinhibition, a sustained decline in photosynthetic efficiency, associated with damage to P680 (Powles, 1984).

Photoinhibition occurs when the demand from the carbon reduction cycle for ATP and mainly reductive power is decreased and thereby not enough NADP+ is available to act as the terminal electron acceptor of the linear photosynthetic electron transport chain. Under increasing light intensity, the photosynthetic reaction centers become progressively saturated (closed), resulting in a reduction in the fraction of energy utilized in photosynthesis and the subsequent build-up of ‘‘unused’’, potentially harmful, excitation energy in the photosynthetic membrane. Since photoinhibition has a potential to lower productivity and plant growth, avoidance of photoinhibition is critical for the fitness and survival of plants in natural habitats (Takahashi et al, 2002).

11.2.3. Effect of heat stress on photosynthetic apparatus

High temperature stress leads to impairment of Chl[1]. biosynthesis in plastids (Dutta et al., 2009). Lesser accumulation of Chl. in high temperature stressed plants may be attributed to impaired Chl. synthesis or its accelerated degradation or a combination of both. The inhibition of Chl. biosynthesis under high-temperature regimes results from a destruction of numerous enzymes involved in the mechanism of Chl. biosynthesis (Efeoglu and Terzioglu, 2009). In response to high temperature stress (38/28 °C), a decrease in total Chl. content (18%), Chl. *a* content (7%), Chl. a/b ratio (3%), sucrose content (9%) and an increase in reducing sugar content (47%) and leaf soluble sugars content (36%) (Hasanuzzaman et al., 2013) was observed in soybean.

11.2.4. Effect of heat stress on photosystem II

Photosystem II (PSII) is considered to be one of the most thermosensitive components of photosynthetic apparatus (Srivastava et al., 1997). The two key factors that make PSII electron transport most susceptible to heat stress are: (i) increase in fluidity of thylakoid membranes at high temperature which causes dislodging of PSII light harvesting complexes from thylakoid membrane and (ii) dependence of PSII integrity on electron dynamics. The sensitivity of PSII to stress

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1 - Chlorophyll

depends on the organization level of the system in question (e.g. cyanobacteria, monocot, dicot, etc.) and there is also variation in the extent of the acclimation of PSII to heat stress (Baker, and Rosenqvist, 2004; Janka et al., 2013).

High temperature stress leads to downregulation of the quantum efficiency of PSII through a decrease in the rate of primary charge separation, a reduction in the stabilization of charge separation and the disconnection of some minor antenna from PSII (Janka et al., 2013).

Various fluorescence parameters have proven to be an excellent high temperature stress indicators. An increase in energy dissipation at high temperature reduces the energy available for photochemistry under stress conditions (Mathur et al., 2011). Oxidized plastoquinone molecules are known non-photochemical quenchers of chlorophyll excited states of both PSII and PSI antennas due to thermal dissipation (Joly and Carpentier, 2007).

11.2.5. Effect of heat stress on photosystem I

Many investigations have shown that PSI activity is much more heat stable than PSII (Sayes et al., 1989). Results of moderately high temperatures stimulate PSI activity in vivo and in vitro and caused increased thylakoid proton conductance and increased cyclic electron flow around PSI (Pastenes and Horton, 1996). Under conditions when PSII activity is severely diminished, this stimulation of proton conductance of cyclic electron flow (CEF) around PSI could be an adaptive process, producing ATP[1]. Heat stress also significantly increases the dark reduction of PQs (Bukhov et al. 2000; Havaux et al., 1991; Bukhov and Carpentier, 2004) and enhances the transthylakoid proton gradient which was interpreted through a stimulation of CEF around PSI (Havaux, 1996).

Yamane et al (2000) reported a flow of electrons from the stroma to the plastoquinone pool in the dark at 36 °C. PSI was more reduced by heat stress (Pastenes and Horton, 1996; Havaux, 1996) while PSII and the stroma become more oxidized at high temperature, which indicates that the redox balance of different components of photosynthetic electron transport can change in opposite directions

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[1] - Adenozine triphosphate (ATP)

and heat significantly alters the redox balance of the components of electron transport away from PSII and toward PSI.

11.2.6. Effect of heat stress on stomatal conductance

Transpiration is a physical process in plants in which part of the net radiation energy is converted into latent heat, under physiological control by changes in stomatal aperture. Plant photosynthesis and stomatal conductance shares a strong relationship. A decrease in soil and root hydraulic conductance as a result of soil drying may be an important control mechanism of stomatal closure. Low leaf water potential which is caused by high transpirational rates results in midday reduction in stomatal conductance. The capability of plant to sustain leaf gas exchange and CO2 assimilation rates under heat stress is directly concomitant with heat tolerance. High temperature noticeably affects the leaf water status, leaf stomatal conductance (gs) and intercellular CO2 concentration (Greer and Weedon, 2012). Closure of stomata under high temperature is another reason for impaired photosynthesis that affects the intercellular CO2 (Ashraf and Hafeez, 2004). Stomatal conductance (gs) and net photosynthesis (Pn) are inhibited by moderate heat stress in many plant species due to decreases in the activation state of Rubisco (Wahid et al., 2007). Temperature changes not only directly affect vapour pressure density (VPD) but can also result in changes in plant hydraulic conductance and water supply to the leaf surface (Yang et al., 2012).

11.2.7. Effect of heat stress on membrane properties

The plasma membrane and cytoplasmic membranes of plants are composed of lipids and proteins; components of cell membranes, especially the lipid may change in response to environmental conditions such as temperature. Change in physical characteristics of membrane structures is sometimes considered a necessary physiological task when environmental factors change. But changes in membrane structure beyond a certain limit result in gross structural changes that might be phase separation of the membrane constituents or disturbances of function, including the loss of selective permeability and transport processes. These phenomena might occur in all membranes, including cytoplasmic, chloroplast, and mitochondria, which results in a disruption in major and basic physiological processes. Injuries to cell membranes, organization of microtubules and cytoskeleton, and changes in membrane permeability induced by heat stress (HS) alter cell differentiation, elongation, and expansion (Potters et al. 2008; Nahar et al., 2015). Maintenance of cellular membrane function is essential for a sustained photosynthetic and respiratory performance under HS (Chen et al., 2010). High temperatures induce photosynthetic membrane damage resulting in subsequent swelling of grana stacks and aberrant stacking, which significantly increase ion leakage from leaf cells and change the energy allocation to the photosystems (Nahar et al., 2015). According to Silva et al. (2010), in *Jatropha curcas* the leaf electrolyte leakage increased by 28 % and lipid peroxidation increased by 50 % when subjected to HS of 43 °C. High-temperature-induced membrane lipid peroxidation and aggravated membrane injury found in cotton, sorghum and soybean (Djanaguiraman et al., 2011).

11.2.8. Effect of heat stress on water relations

Water status of the plant is one of the most important components that should be in balance under changing ambient temperatures, otherwise physiological processes will be severely affected by environmental stresses (Mazorra et al., 2002). Although plants under stress conditions try to maintain balance in their water status, it is often altered due to alteration of water relations between growing media and plant tissue or between different components of the plant under different stress conditions including HS. High temperature stress disrupts the balance between symplastic and apoplastic loading of the phloem. This might be the reason for reduced water transportation.

Sugarcane leaf water potential and its components change upon exposure to HS. During HS, although soil, water supply, and relative humidity conditions are optimal, irrespective of this optimal condition HS affects the root hydraulic conductance and water status of the plant (Wahid and Close 2007). High temperature decreases water-use efficiency in wheat (Shah and Paulsen 2003). Elevated night temperatures reduce leaf water potential of *Lotus creticus* to a great extent (Bannon et al., 2004). In tomato, HS adversely affected hydraulic conductivity due to reduced stomatal movement that significantly decreased the water status of the plant (Morales et al. 2003).

The ecological importance of heat tolerance in plants is clearly observed in terrestrial cryptogams with relatively low heat tolerance in the soaked state. Their ecological adaptation is due to their poikilohydric nature, which allows them to lose water rapidly under the sun, and their extreme tolerance to desiccation. The difference in the heat-tolerance limits of dry and soaked terrestrial cryptogams differs much; the annual amplitude of dry bryophytes is much larger than moist ones (Nahar et al., 2015). The degree of heat tolerance in the dry state is frequently more closely related to the thermal conditions of the natural habitat than the heat tolerance of the soaked specimen as such; terrestrial cryptogams are adapted to exist in hot, but arid environments. In some hydrophytic lichens the heat tolerance reaches upto 90 °C when dry; however, wet cultivation decreases their heat resistance. The membrane stabilization resulting from thermoadaptation is different due to adaptation to desiccation. The species of some highly desiccation tolerant Poikilohydric connophytes become as heat tolerant as cryptogams in the dry state. The tolerance limit strongly depends on the water deficit of the leaves and the range increases nearly constantly on an annual basis. In sclerophyllous and mesophytic plants the heat tolerance limit increases with the saturation deficit of the leaves, the reason being tolerance increases only in wilted xerophytes and not in mesophytes and 62 °C appears as the absolute upper heat tolerance limit for cormophytes (Vertovec et al., 2001; Sakcali and Škute, 2010). Osmotic agents also increase heat tolerance, such as desiccation, although no close correlation exists between heat tolerance and desiccation tolerance.

11.2.9. Stress-induced proteins

To cope with environmental stress, plants activate a large set of genes leading to the accumulation of specific proteins, which are generally considered stress induced proteins. Some stress-induced proteins, such as heat shock proteins (HSP) and late embryogenesis abundant proteins (LEA) are required for stress tolerance, and their accumulation has a role in protecting plant tissues from possible damages caused by environmental stresses (Sachs, 1996). The alteration of the protein level is a reflection of both transcriptional and translational regulation. The current section discusses the effect of environmental stress conditions on HSPs and LEAs, which function in protecting cells from stress injury and are the two major types of stress-inducible proteins that accumulate upon extreme temperature, water and salinity stress (Wang et al., 2003).

11.2.10. Heat shock proteins (HSPs)

When juvenile plants are subjected to temperatures above their optimal growth temperature, synthesis of most proteins and mRNAs are repressed, and the transcription and translation of a small set of proteins, which are named heat shock proteins (HSPs), are initiated by exposure to other environmental stress conditions, such as drought, cold, salinity, and hypoxia (oxygen deprivation). Consequently, HSPs are also referred to as stress proteins and their upregulation is sometimes described more generally as part of the stress response (Sabehat et al*.,* 1998). Heat shock proteins also occur under non-stressful conditions, simply "monitoring" the cell's proteins. Some examples of their role as "monitors" are that they carry old proteins to the cell's "recycling bin" and they help newly synthesized proteins fold properly. These activities are part of a cell's own repair system, called the "cellular stress response." One of the important roles of HSPs involves stabilization of proteins in a particular state of folding.

Through this mechanism, HSPs such as HSP90 and HSP70 facilatate a wide diversity of important processes including folding and transport of proteins across membranes and therefore these HSPs are also called "molecular chaperones" (Vierling, 1991). The molecular masses of HSPs range from 15 to 104 kDA (atomic mass *unit,* and kilo Dalton). Among five conserved families of HSPs—HSP100, HSP90, HSP70, HSP60, and small HSP (sHSP)—the small HSPs are found to be most prevalent in plants. sHSPs vary in size, with a molecular weight between 15 to 42 kDa (Sun, 2002). Small heat schock proteins (sHSPs) are produced ubiquitously in prokaryotic and eukaryotic cells upon environmental stresses such as temperature, light, salinity, and drought (Wang *et al.*, 2003). Under unstressed growth conditions, most sHSPs cannot usually be detected in most plant tissues, however, upon stress there is an accumulation of sHSPs. The induction of sHSPs depends on the severity of the stress and its duration (Howarth, 1991).

High levels of sHSPs, as a result of overproducing HSF's, increased the basal level of thermotolerance in Arabidopsis (Lee, 1995). The correlation between sHSP synthesis and stress response led to the hypothesis that sHSPs protect cells from detrimental effects of stress, however, the mechanisms in which they are involved in cell protection are still not fully understood (Sun, 2002). Hamilton and Heckathorn, 2001 suggested that sHSPs might act as antioxidants in protecting complex-I electron transport in the mitochondria during salinity stress. sHSPs as well as other HSPs are regarded as stress proteins with a potential to protect cells from stress damage. An increasing number of studies show the existence of cross tolerance in plants, where an exposure of tissue to moderate stress induces tolerance to other stresses. Although cross-tolerance has been demonstrated in several plant species, a common mechanism has not yet been found; however, HSPs have been demonstrated to play an important role in cross protection (Sabehat, 1998). Many publications have highlighted the importance of the molecular chaperone HSP90 complex in plant development and responsiveness to external stimuli. In particular, HSP90 is crucial for R-protein-mediated defense against pathogens. Other facets of the HSP90 function in plants include its involvement in phenotypic plasticity, developmental stability, and buffering of genetic variation (Sangster and, Queitsch, 2005).

11.2.11. Chaperones

There are five well-characterized classes of HSPs that have been defined in both plants and other organisms: HSP100 (ClpB), HSP90, HSP70 (DnaK), HSP60 (GroE) and small HSPs (sHSPs). Chaperones facilitate a range of processes including protein folding, transport of proteins across membranes, modulation of protein activity, and regulation of protein degradation and prevention of irreversible protein aggregation. The latter activity is believed to be critical to survival of high temperature stress and to explain the induction of these proteins by high temperature.

11.2.11.1. Hsp100 (ClpB)

Interestingly, the Hsp100 (ClpB) class of chaperones is found in bacteria, yeast, certain parasitic protozoans and plants, but not in other higher eukaryotes (Agarwal et al., 2002). Perhaps plants have retained this class of chaperones through evolution because of their unique exposure to the environment compared to other higher eukaryotes. Plants have both cytosolic and chloroplast-targeted Hsp100 (ClpB) proteins, both of which have been shown to strongly induced by heat (Keeler et al., 2000). These proteins are hexameric members of the AAA proteins, which couple ATP binding and hydrolysis to a variety of protein-remodeling activities (Lupas and Martin, 2002).

According to Mogk et al. (2003b), an interaction of the Hsp100/ClpB and sHSP chaperone systems in protein disaggregation. Although it is well accepted that Hsp100 (ClpB) proteins are involved in protein disaggregation, no critical cellular substrates have been identified in plants or any other organism. The cytosolic Hsp100 (ClpB) proteins are the only HSPs for which direct genetic evidence supports a significant role in acquired thermotolerance in plants. The important role of plant Hsp100 in thermotolerance was predicted from previous experiments demonstrating that the homologous gene is required for thermotolerance in Saccharomyces cerevisiae, cyanobacteria and Escherichia coli and from the observation that plant Hsp100 (ClpB) could restore thermotolerance to a yeast hsp104 mutant (Wells et al., 1998). Surprisingly, the cytosolic HSP100 (ClpB) null mutants in Arabidopsis and maize show no obvious developmental defects or growth rate disadvantage under optimal temperature conditions. Further, while essential for acquired thermotolerance to severe heat stress, there is no evidence that the protein confers any advantage to plants suffering from chronic, milder heat stress (Hong and Vierling, 2001). This observation emphasizes the point that different forms of heat stress require different protective responses.

11.2.11.2. HSP90

The Hsp90 chaperones are highly abundant proteins that are essential for viability in a number of eukaryotes, most likely including plants. Studies in animals and yeast have demonstrated that Hsp90 has a key role in modulating the activity of metastable client proteins involved in signal transduction, either by facilitating interactions with ligands, trafficking clients to membranes or altering client interactions with other cellular components. These activities depend on HSP90 function within a dynamic multi-protein complex that includes HSP70, HSP40.

Arabidopsis has seven Hsp90 genes, encoding four cytosolic forms, and forms targeted to the chloroplast, mitochondrion and endoplasmic reticulum (Krishan and Gloor, 2001). Although some of these genes show significant heat induction, no direct connection between HSP90s and heat tolerance has been defined. Hsp90 in plants and animals has also been postulated to buffer genetic variation, and loss of Hsp90 function is proposed to release genetic variation for selection in evolution (Sangster et al., 2004).

11.2.11.3. HSP70/ DnaK

The Hsp70/DnaK chaperone family is probably the best understood of the molecular chaperones (Mayer et al., 2002). Genomic analysis of Arabidopsis defined 14 Hsp70 proteins, five cytosolic forms, three targeted to the endoplasmic reticulum (BiP), three targeted to the chloroplasts, two localized to mitochondria and one potential pseudogene (Lin et al., 2001). Detailed expression analysis in Arabidopsis revealed complex developmental and stress responsiveness of these different genes; all but one mitochondrial and one chloroplast.

HSP70 showed significant induction in response to heat (Sung et al., 2001). The number of Hsp70 genes in plants complicates genetic analysis of their role in plant heat tolerance. Lee and Schoffl (1996) used heat-inducible Hsp70 antisense RNA to demonstrate a requirement for Hsp70 in thermotolerance. Another attempt to alter the levels of Hsp70-1 in transgenic Arabidopsis with a constitutive promoter led to negative effects on plant growth and viability (Sung et al., 2003).

Overexpression of Hsp70-1 did, however, result in enhanced heat tolerance under specific test conditions. Overexpression of an endoplasmic reticulum Hsp70, BiP, has been demonstrated to abrogate ER stress and enhance drought, but not heat tolerance (Alvim et al., 2001). In Chlamydomonas the chloroplast Hsp70 has been implicated in photoprotection of PSII during photoinhibition (Schroda et al., 1999). Overall, Hsp70s are important for plant heat tolerance, but manipulating expression of these essential proteins to enhance plant heat tolerance may be difficult.

11.2.11.4. HSP60/GroE

The HSP60, or chaperonin, family of chaperones have not been directly implicated in the acclimation of plants to heat stress. However, the drastic phenotypic consequences seen at normal temperatures when their expression is attenuated or eliminated suggest that their participation is essential in such fundamental processes as protein assembly and transport. These pleiotropic effects include defects in embryonic development (Apuya et al., 2001) and slow growth and may complicate experimental approaches aimed at demonstrating a specific role in stress responses.

Despite these difficulties, some evidence suggests that Group I chaperonins, which are found in plastids, mitochondria and eubacteria (Wang et al., 2004) may function in the context of temperature stress. For example, heat induces expression of the mitochondrial chaperonin (Cpn60) (Prasad and Stewart, 1992). The chloroplastic family member Cpn60-b3 is not heat-regulated, but plants carrying a T-DNA insertion in this gene display heightened heat sensitivity as well as a tendency to form lesion mimics (Ishikawa et al., 2003). Cyanobacteria may prove to be more tractable than vascular plants in determining a role for the chaperonins during heat stress as reports have found the chaperonin GroEL in these organisms to be heat inducible and to play a role in thermotolerance (Asadulghani and Nakamoto, 2003).

11.3. Morphological responses to heat stress

The most observed effect of heat stress on plants is the retardation of growth. As heat stress often occurs simultaneously with drought stress, the combination of drought and heat stress induce more detrimental effect on growth and productivity of crops than when each stress was applied individually (Prasad P.V.V. Staggenborg and Ristic, 2008).

In higher plants, heat stress significantly alters cell division and cell elongation rates which affect the leaf size and weight. However, it was reported that heat stress resulted in significant increases in leaf numbers, particularly when reproductive development was arrested without any decrease in leaf photosynthetic rates. Exposure of plants to severe heat stress decreased the stem growth resulting in decreased plant height (Prasad PVV et al., 2006).

Ahamed (2010) observed that in *T. aestivum* sowing time mediated heat stress negatively influenced the plant height and number of tillers of 4 different genotypes. In a recent study, Al-Busaidi et al. (2012) observed that high atmospheric temperature cause significant water loss which negatively influenced the growth and biomass production in biofuel plant, *Jatropha curcas*. Parallel to shoot growth heat stress often decreases root growth, number of roots and root diameter (Porter and Gawith, 1999).

High temperature decreased shoot dry weight, relative growth rate (RGR) and net assimilation rate in maize, millet and sugarcane (Wahid, 2007; Ashraf and Hafeez, 2004). According to Wahid (2007) heat stress can cause considerable pre- and post-harvest damages, including scorching of leaves and twigs, sunburns on leaves, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage. High temperature also alters the internal morphology (anatomy) of plants and these changes are generally similar to those under drought stress (Fig. 11.2).

Under heat stress, there is a general tendency towards reduced cell size, closure of stomata and curtailed water loss, increased stomatal density and trichomatous densities, and larger xylem vessels in both roots and shoots (Wahid, 2007).

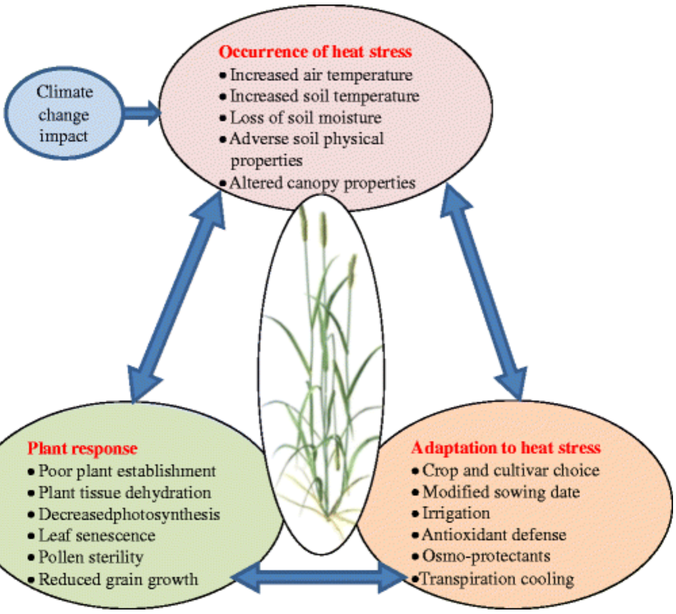

Figure 11.2 Environmental stresses have varying effects on different organs and tissues within a plant, and as such, molecular, cellular and morphological responses to stress vary among tissues and throughout the developmental lifetime of a plant (after Aket and Islam, 2017).

Several lines of study indicate that exposure of plants to heat stress results in the disintegration of ultrastructural characteristics, mainly attributed to a lower stomatal density, larger stomatal chamber with a larger stomatal opening area, thinner leaves, loose arrangement of mesophyll cells, a partially developed vascular bundle and unstable organelle structure. Dan Wang et al. (2016) examined the effects of heat stress on leaf area index (LAI) in two species (a C3 and a C4, *Andropogon gerardii* and *Solidago canadensis*, respectively). They found that LAI was significantly lower at the plots heat-stressed than the control plots. Johkan et al. (2011) observed that the number of tillers in wheat plants decreased in response to heat stress, especially high night-time temperatures, however shoot elongation was promoted.

References

Agarwal M., Katiyar-Agarwal S., Grover A. (2002) Plant Hsp100 proteins: structure, function and regulation. Plant Science, 163: 397–405.

Ahamed K.U., Nahar K., Fujita M., Hasanuzzaman M. (2010) Variation in plant growth, tiller dynamics and yield components of wheat (*Triticum aestivum* L.) due to high temperature stress. Advances in Agriculture and Botanics, 2: 213-224.

Akter N., Islam R.M. (2017) Heat stress effects and management in wheat, a review, Agronomy for Sustainable Development, 37(5): DOI: 10.1007/s13593-017-0443-9

Al-busaidi A., Ahmed M., Chikara J. (2012) The impact of heat and water stress conditions on the growth of the biofuel plant *Jatropha curcas*. International Journal of Environmental Studies, 69: 273-288. (Al-busaidi et al., 2012)

Alvim F.C., Carolin S.M., Cascarado J.C., et al., (2001) The Arabidopsis embryo mutant schlepperless has a defect in the chaperonin-60alpha gene. Plant Physiology, 126: 717–730.

Alvim F.C., Carolin S.M., Cascarado J. C., Nunes C C., Martinez C.A., Otoni W.C., Fontes E. P. (2001) Enhanced accumulation of BiP in transgenic plants confers tolerance to water stress. Plant Physiology, 126: 1042–1054.

Asadulghani S.Y., Nakamoto H. (2003) Light plays a key role in the modulation of heat shock response in the cyanobacterium Synechocystis sp PCC 6803. Biochemical and Biophysical Research Communications, 306: 872–879.

Ashraf M., Hafeez M. (2004) Thermotolerance of pearl millet and maize at early growth stages: growth and nutrient relations, Biol. Plant 48: 81–86.

Baker N.R., E. Rosenqvist, (2004) Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities, J. Exp. Bot. 55:1607–1621

Bannon S., Fernandez J.A., Franco J.A, Torrecillas A, Alarćon JJ, Sanchez-Blanco M.J. (2004) Effects of water stress and night temperature preconditioning on water relations and morphological and anatomical changes of Lotus creticus plants. Sci. Hortic., 101:333–342

Berry J.A., Bjorkman O. (1980) Photosynthetic response and adaptation to temperature in higher plants, Annu. Rev. Plant Physiol., 31: 491–543.

Bukhov N., Carpentier R. (2004) Alternative photosystemI-driven electron transport routes: mechanisms and functions, Photosynth. Res. 82: 17–33.

Bukhov N.G., Samson R. (2000) Carpentier, Nonphotosynthetic reduction of the intersystem electron transport chain of chloroplasts following heat stress. Photochem. Photobiol., 72: 351–357.

Chaves M.M., Maroco J.P., Pereira J.S. (2003) Understanding plant responses to drought-from genes to the whole plant. Funct. Plant Biol., 30: 239.

Chen J., Wang P., Mi H.L., Chen G.Y., Xu D.Q. (2010) Reversible association of ribulose-1,5-
bisphosphate carboxylase/oxygenase activase with the thylakoid membrane depends upon the
ATP level and pH in rice without heat stress. J. Exp. Bot. 61: 2939–2950

Djanaguiraman M., Prasad P.V.V., Al-Khatib K. (2011) Ethylene perception inhibitor 1-MCP decreases oxidative damage of leaves through enhanced antioxidant defense mechanisms in soybean plants grown under high temperature stress. Environ. Exp. Bot., 71: 215–223.

Driedonks N., Rieu I., Vriezen W.H (2016) Breeding for plant heat tolerance at vegetative and reproductive stages. Plant Reprod. 29: 67–79

Dutta S., S. Mohanty, B.C. Tripathy, (2009) Role of temperature stress on chloroplast biogenesis and protein import in pea, Plant Physiol. 150: 1050–1061.

Efeoglu B., Terzioglu S. (2009) Photosynthetic responses of two wheat varieties to high temperature, Eur. Asia J. BioSci., 3: 97–106.

Fitter A.H., Hay R.K.M. Environmental physiology of plants, 3rd edn. London: Academic Press; 2002.

Garruna-Hernandez R., Orellana R., Larque-Saavedra A., Canto A. (2014) Understanding the physiological responses of a tropical crop (*Capsicum chinense* Jacq.) at high temperature. PLOS One 9: (11):e111402. Doi: 10.1371/journal.pone.0111402

Greer D.H., Weedon M.M. (2012) Modelling photosynthetic responses to temperature of grapevine (*Vitis vinifera* cv. Semillon) leaves on vines grown in a hot climate, Plant Cell Environ., 35: 1050–1064.

Hamilton E.W. III, Heckathorn S.A. (2001) Mitochondrial adaptations to NaCl. Complex I is protected by antioxidants and small heat shock proteins, whereas complex is protected by proline and betaine. Plant Physiol., 126:1266.

Hasanuzzaman M., K. Nahar, Md.M. Alam, R. Roychowdhury, M. Fujita, (2013) Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants, Int. J. Mol. Sci., 14: 9643–9684.

Hasanuzzaman M., Nahar K., Fujita M. (2013) Extreme Temperature Responses, Oxidative Stress and Antioxidant Defense in Plants, DOI: 10.5772/54833.

Havaux M., Greppin H., Strasser R.J.(1991) Functioning of photosystems I and II in pea leaves exposed to heat stress in the presence or absence of light, Planta, 186: 88–98.

Havaux M.S. (1996) Short-term responses of photosystem I to heat stress – induction of a PS II-independent electron transport through PSI fed by stromal components, Photosynth. Res. 47: 85-97.

Hong S.W., Vierling E. (2001) Hsp101 is necessary for heat tolerance but dispensable for development and germination in the absence of stress. Plant Journal, 27: 25–35.

Howarth C. (1991) Molecular responses of plants to an increased incidence of heat shock. Plant Cell Environ, 14: 831.

Ishikawa A., Tanaka H., Nakai M., Asahi T. (2003) Deletion of a chaperonin 60 beta gene leads to cell death in the Arabidopsis lesion initiation 1 mutant. Plant and Cell Physiology, 44(3): 255-61)

Janka E., O. Korner, E. Rosenqvist, C.O. Ottosen, (2013) High temperature stress monitoring and detection using chlorophyll a fluorescence and infrared thermography in chrysanthemum (Dendranthema grandiflora), Plant Physiol. Biochem., 67: 87-94.

Johkan M., Oda M., Maruo T., Shinohara Y. (2011). Crop production and global warming. In: Casalegno S (ed) Global warming impacts-Case studies on the economy, human health, and on urban and natural environments. Rijeka: In Tech; , 139-152.

Joly D., Carpentier R. (2007) Regulation of energy dissipation in photosystem I by the redox state of the plastoquinone pool, Biochemistry 46: 5534–5541.

Khan A.L., Kang S., Dhakal K.H., Hussain J., Adnan M., Kim J., Lee I. (2013) Flavonoids and amino acid regulation in *Capsicum annuum* L. by endophytic fungi under different heat stress regimes. Sci. Horti. 155:1–7

Khanna-Chopra R. (2012) Leaf senescence and abiotic stresses share reactive oxygen species-mediated chloroplast degradation. Protoplasma, 249: 469–481. Doi: 10.100/s0009-011-0308-z

Krishna P., Gloor G. (2001) The Hsp90 family of proteins in Arabidopsis thaliana. Cell Stress & Chaperones 6: 238–246.

Lee J.H., Schoffl F. (1996) An Hsp70 antisense gene affects the expression of HSP70/HSC70, the regulation of HSF, and the acquisition of thermotolerance in transgenic Arabidopsis thaliana. Molecular and General Genetics, 252(1–2): 11–19.

Li J., Yang P., Kang J. et al, (2016) Transcriptome analysis of pepper (Capsicum annuum) revealed a role of 24-epibrassinolide in response to chilling. Front. Plant Sci., 7:1281

Lin B.L., Wang J.S., Liu H.C., Chen R.W., Meyer Y., Bakarat A., Delseny M. (2001) Genomic analysis of the Hsp70 superfamily in Arabidopsis thaliana. Cell Stress & Chaperones, 6: 201-208.

Lupas A.N., Martin J. (2002) AAA proteins. Current Opinion in Structural Biology, 12: 746–753.

Mathur S., A. Jajoo, P. Mehta, S. Bharti, (2011) Analysis of elevated temperatureinduced inhibition of photosystem II by using chlorophyll a fluorescence induction kinetics in wheat leaves (*Triticum aestivum*), Plant Biol. 13:1–6.

Mayer M.P., Brehmer D., Gassler C.S., Bukau B. (2002) Heat schock protein 70 (Hsp70) chaperone machines. Advances in Protein Chemistry, 59: 1–44.

Mazorra L.M., Nunez M., Echerarria E., Coll F., Sanchez-Blanco M.J. (2002) Influence of brassinosteriods and antioxidant enzymes activity in tomato under different temperatures. Plant Biol 45:593–596

Mogk A., Schlieker C., Friedrich K.L., Schoffeld H.J., Vierling E., Bukau B. (2003b) Refolding of substrates bound to small HSPs relies on a disaggregation reaction mediated most efficiently by ClpB/DnaK. Journal of Biological Chemistry, 278: 31033–31042.

Morales D., Rodriguez P., Dell'amico J., Nicolas E., Torrecillas A., Sanchez-Blanco M.J (2003) High temperature pre-conditioning and thermal shock imposition affects water relations, gas exchange and root hydraulic conductivity in tomato. Biol. Plant, 47:203–208

Nahar K., Hasanuzzaman M., Ahamed K.U., Hakeem K.R., Ozturk M., Fujita M. (2015). Plant Responses and Tolerance to High Temperature Stress: Role of Exogenous Phytoprotectants, in Crop Production and Global Environmental Issues, Doi: 10.1007/978-3-319-23162-4_17.

Papageorgiou G.C., Govindjee (Eds.), Chlorophyll Fluorescence: A Signature of Photosynthesis Advances in Photosynthesis and Respiration, vol. 19, Springer, Dordrecht, The Netherlands, 2004, 47.

Pastenes C., Horton P. (1996) Effect of high temperature on photosynthesis in beans (II. CO2 assimilation and metabolite contents), Plant Physiol. 112: 1253–1260.

Porter J.R., Gawith M. (1999) Temperature and the growth and development of wheat: A review. European Journal of Agronomy, 10: 23-36.

Potters G., Pasternak T.P., Guisez Y., Jansen M.A.K. (2008) Different stresses, similar morphogenic responses: integrating plethora of pathways. Plant Cell Environ 32:158–169

Powles S.B. (1984) Photoinhibition of photosynthesis induced by visible-light, Ann. Rev. Plant Physiol. Plant Mol. Biol., 35: 15–44.

Prasad PVV, Staggenborg S.A., Ristic Z. (2008) Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. In: Ahuja L.H., Saseendran SA (Eds).

Response of crops to limited water: Understanding and modeling water stress effects on plant growth processes. Advances in Agricultural Systems Modeling Series 1. ASA-CSSA, Madison, Wisconsin; (2008), 301-355.

Prasad PVV, Boote K.J., Allen Jr L.H. (2006) Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. Agricultural and Forest Meteorology, 139: 237-251

Prasad T.K., Stewart C.R. (1992) cDNA clones encoding Arabidopsis thaliana and Zea mays mitochondrial chaperonin HSP60 and gene expression during seed germination and heat shock. Plant Molecular Biology: 873–885.

Sabehat A., Weiss D., Lurie S. (1998) Heat-shock proteins and cross-tolerance in plants. Phsiologia plantarum, 103: 437-441

Sangster T. A., Lindquist S., Queitsch C. (2004) Under cover: causes, effects and implications of Hsp90-mediated genetic capacitance. BioEssays, 26: 348–362.

Sangster T.A., Queitsch C. (2005) The HSP90 chaperone complex, an emerging force in plant development and phenotypic plasticity. Curr. Opin. Plant Biol. 8(1): 86-92.

Savicka M., Škute N. (2010) Effects of high temperature on malondialdehyde content, superoxide production and growth changes in wheat seedlings (*Triticum aestivum* L.). Ekologija, 56:26–33.

Sayed O.H., Emes M.J., Earnshaw M.J., Butler R.D. (1989) Photosynthetic responses of different varieties of wheat to high temperature, J. Exp. Bot. 40: 625–631.

Schroda M., Vallon O., Wollman F. A., Beck C. F. (1999) A chloroplast-targeted heat shock protein 70 (HSP70) contributes to the photoprotection and repair of photosystem II during and after photoinhibition. Plant Cell, 11(6): 1165–1178.

Schuster W.S., Monson R.K. (1990) An examination of the advantages of C3-C4 intermediate photosynthesis in warm environments. Plant, Cell and Environment, 13: 903-912.

Senthil-Kumar M., et al., (2003) Screening of inbred lines to develop a thermotolerant sunflower hybrid using the temperature induction response (TIR) technique: A novel approach by exploiting residual variability. J. Exp. Bot., 54: (392) 2569-78.

Shah N., Paulsen G. (2003) Interaction of drought and high temperature on photosynthesis and
grain-filling of wheat. Plant Soil, 257: 219–226

Sharkey T.D. (2005) Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene, Plant Cell Environ. 28 269–277.

Silva E.N., Ferreira-Silva S.L., de Vasconcelos Fontenelea A., et al., (2010) Photosynthetic changes and protective mechanisms against oxidative damage subjected to isolated and combined drought and heat stresses in *Jatropha curcas* plants. J. Plant Physiol. 167:1157–1164.

Srivastava A., B. Guissre, H. Greppin, R.J. Strasser, (1997) Regulation of antenna structure and electron transport in Photosystem II of Pisum sativum under elevated temperature probed by the fast polyphasic chlorophyll a fluorescence transient: OKJIP, Biochim. Biophys. Acta 1320: 95-106.

Stirbet A. Govindjee, Govindjee, (2011) On the relation between the Kautsky effect chlorophyll a fluorescence induction] and photosystem II: basics and applications of the OJIP fluorescence transient, J. Photochem. Photobiol. 104: 236–257.

Sun W., Montagu M.V., Verbruggen N. (2002) Small heat shock proteins and stress tolerance in plants. Biochim. Biophys. Acta. 1577: 1-9.

Sung D.Y., Kaplan F., Lee K.J., Guy C.L. (2003) Acquired tolerance to temperature extremes. Trends in Plant Science, 8(4): 179–187.

Sung D.Y., Vierling E., Guy C.L. (2001) Comprehensive expression profile analysis of the Arabidopsis HSP70 gene family. Plant Physiol., 126: 789–800.

Swindell W.R., Huuebner M., Weber A.P. (2007) Transcriptional profiling of Arabidopsis heat shock protein and transcription factor reveals extensive overlap between heat and non-heat stress response pathway. BMC Genomics 8:125.

Takahashi S., A. Tamashiro, Y. Sakihama, Y. Yamamoto, Y. Kawamitsu, H. Yamasaki, (2002) High-susceptibility of photosynthesis to photoinhibition in the tropical plant *Ficus microcarpa* L. f. cv. Golden Leaves, BMC. Plant Biol. 2. DOI: 10.1186/1471-2229-2-2.

Vertovec M., Sakcali S., Ozturk M., Salleo S., Giacomich P., Feoli E., Nardini A. (2001) Diagnosing plant water status as a tool for quantifying water stress on a regional basis in Mediterranean dry lands. Ann. For. Sci., 58:113–125

Vierling E. The roles of heat shock proteins in plants. Ann. Rev. Plant Physiol., 199: 42:579.

Wahid A. (2007) Physiological implications of metabolites biosynthesis in net assimilation and heat stress tolerance of sugarcane (*Saccharum officinarum*) sprouts. Journal of Plant Research, 120: 219-228.

Wahid A., Close T.J. (2007) Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. Biol. Plant, 51:104–109

Wahid A., Farooq M., Hussain I., Rasheed R., Galani S. (2012) Responses and management of heat stress in plants. In: Ahmad P, Prasad M.N.V. (Eds) Environmental adaptations and stress tolerance of plants in the era of climate change. Springer, New York, pp 135–157

Wahid A., Gelani S., Ashraf M., Foolad M.R. (2007) Heat tolerance in plants: an overview, Environ. Exp. Bot. 61: 199–223.

Wang D., Heckathorn S.A., Mainali K., Tripathee R (2016) Timing Effects of Heat-Stress on Plant Ecophysiological Characteristics and Growth. Front. Plant Sci. 7:1629. doi: 10.3389/fpls.2016.01629

Wang H., Niu H., Zhai Y., Lu M (2017) Characterization of BiP genes from pepper (*Capsicum annuum* L.) and the role of CaBip1 in response to endoplasmic reticulum and multiple abiotic stresses. Front Plant Sci. 8:1122

Wang W., Vincour B., Shoseyov O., Altman A. (2004) Role of plant heat shock proteins and molecular chaperones in the abiotic stress response. Trends in Plant Science, 9: 244–252.

Wang W.X., Vinocur B., Altman A. (2003) Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. Planta, 218:1.

Wardlaw L.F., Wrigley C.W. (1994) Heat tolerance in temperate cereals: an overview. Aust. J. Plant Physiol. 21: 695–703

Wells D.R., Tanguay R.L., Le H., Gallie D.R. (1998) HSP101 functions as a specific translational regulatory protein whose activity is regulated by nutrient status. Genes and Development, 12: 3236–3245.

Xiong Z.T., Wang H. (2005) Copper toxicity and bioaccumulation in Chinese cabbage. Environ. Toxic., 20:188.

Yamane Y., Shikanai T., Kashino Y., Koike H., Satoh K., (2000) Reduction of Q(a) in the dark: another cause of fluorescence F-o increases by high temperatures in higher plants, Photosynth. Res. 63: 23–34.

Yang Z., Sinclair T.R., Zhu M., Messina C.D., Cooper M., Hammerd G.L. (2012) Temperature effect on transpiration response of maize plants to vapour pressure deficit, Environ. Exp. Bot. 78: 157–162.

Zróbek-sokolnik A. Temperature stress and responses of plants. In: Ahmad P, Prasad MNV (eds) Environmental adaptations and stress tolerance of plants in the era of climate change. New York: Springer (2012) 113-134.