
Comparison Between the Water and Salt Stress Effects on Plant Growth and Development

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1. Introduction

Abiotic stress limits crop productivity [1], and plays a major role in determining the distribution of plant species across different types of environments. Abiotic stress and its effects on plants in both natural and agricultural settings is a topic that is receiving increasing attention because of the potential impacts of climate change on rainfall patterns and temperature extremes, salinization of agricultural lands by irrigation, and the overall need to maintain or increase agricultural productivity on marginal lands. In the field, a plant may experience several distinct abiotic stresses either concurrently or at different times through the growing season [2].

In reference [3] are showed some common examples of the abiotic stresses a plant may encounter which include a decreased availability of water, extremes of temperature including freezing, decreased availability of essential nutrients from the soil (or conversely the build-up of toxic ions during salt stress), excess light (especially when photosynthesis is restricted) or increased hardness of the soil that restricts root growth.

In the face of a global scarcity of water resources and the increased salinization of soil and water, abiotic stress is already a major limiting factor in plant growth and will soon become even more severe as desertification covers more and more of the world's terrestrial area. Plants are often subjected to periods of soil and atmospheric water deficits during their life cycle. Moreover, the faster-than-predicted change in global climate [4] and the different available scenarios for climate change suggest an increase in aridity for the semiarid regions of the globe. Together with overpopulation, this will lead to an overexploitation of water resources for agriculture purposes and increased constraints on plant growth and survival aid,

therefore, on realizing crop yield potential [5]. Thus, if a single abiotic stress is to be identified as the most common in limiting the growth of crops worldwide, it most probably is low water supply [1].

Like the water stress, salinity is one of the major severe abiotic factors affecting crop growth and productivity [6]. Salt's negative effects on plant growth have initially been associated with the osmotic stress component caused by decreases in soil water potential and, consequently, restriction of water uptake by roots.

The literature shows that drought and salinity are already widespread in many regions. Therefore, in reference [7] the authors have presented that in world where population growth exceeds food supply, agricultural and plant biotechnologies aimed at overcoming severe environmental stresses need to be fully implemented.

1.1. Plant stress definitions

The term stress is most often used subjectively and with various meanings. The physiological definition and appropriate term for stress are referenced as responses to different situations. The flexibility of normal metabolism allows the development of responses to environmental changes, which fluctuate regularly and predictably over daily and seasonal cycles [8]. Thus, stress plays a pivotal role in determining interaction outcomes because it strongly influences the strength of underlying positive and negative interactions.

Stress is defined as any external abiotic (heat, water, salinity) or biotic (herbivore) constraint that limits the rate of photosynthesis and reduces a plant's ability to convert energy to biomass [9]. The strength of positive interactions increases with increasing stress except at the most extreme levels. In contrast, the strength of negative interactions is either unrelated to stress and remains consistently high, or alternatively, decreases with increasing stress [10].

Environmental stress could be defined in plants as any change in growth condition(s), within the plant's natural habitat, that alters or disrupts its metabolic homeostasis. Such change(s) in growth condition requires an adjustment of metabolic pathways, aimed at achieving a new state of homeostasis, in a process that is usually referred to as acclimation [11]. However, the concept of plant stress is often used imprecisely, and stress terminology can be confusing, so it is useful to start our discussion with some definitions. Stress is usually defined as an external factor that exerts a disadvantageous influence on the plant. In most cases, stress is measured in relation to plant survival, crop yield, growth (biomass accumulation), or the primary assimilation processes (CO₂ and mineral uptake), which are related to overall growth. In addition, the concept of stress is intimately associated with that of stress tolerance, which is the plant's fitness to cope with an unfavourable environment. In the literature the term stress resistance is often used interchangeably with stress tolerance, although the latter term is preferred [12].

According with the literature [13], changes in strength of these underlying processes drive shifts between competition and facilitation. The stress gradient hypothesis (SGH) predicts that facilitation and competition vary inversely along stress gradients with facilitation more frequent and stronger when stress is high and competition more frequent and stronger

when stress is low. The SGH also predicts that the strongest facilitation should occur with competitive species at the upper limits of their stress tolerance while the strongest competition should occur with stress tolerant species located at their ecological optimum.

Shifts in the structure of interaction outcomes, i.e. a shift from competition to facilitation, along stress gradients are likely to have profound implications for community stability [14, 15]. Community compositional instability can be defined as changes in species abundances that drive directional changes in community composition. There is growing evidence that changes in the structure of species interactions can reduce such stability [16].

In both natural and agricultural conditions, plants are frequently exposed to environmental stresses. In [17] the work presents how some environmental factors, such as air temperature, can become stressful in just a few minutes; others, such as soil water content, may take days to weeks, and factors such as soil mineral deficiencies can take months to become stressful.

1.2. Concepts and consequences of water and salt stress on plants

Water-deficit stress can be defined as a situation in which plant water potential and turgor are reduced enough to interface with normal functions. Water stress is considered to be a moderate loss of water, which leads to stomatal closure and limitation of gas exchange. Desiccation is a much more extensive loss of water that can potentially lead to gross disruption of metabolism and cell structure and eventually to the cessation of enzyme catalyzing reactions. Water stress is characterized by reduction of water content, turgor, total water potential, wilting, closure of stomata, and decrease in cell enlargement and growth. Severe water stress may result in arrest of photosynthesis, disturbance of metabolism, and finally death [8, 18].

The term 'salinity' refers to the presence in soil and water of electrolytic mineral solutes in concentrations that are harmful to many agricultural crops. Except along seashores, saline soils seldom occur in humid regions, thanks to the net downward percolation of fresh water through the soil profile, brought about by the excess of rainfall compared with evapotranspiration. In arid regions, on the other hand, there may be periods of no net downward percolation and hence no effective leaching, so salts can accumulate in the soil. Hence the combined effect of meager rainfall, high evaporation, the presence of salt-bearing sediments, and – in many places, particularly river valleys and other low-lying areas – the occurrence of shallow, brackish groundwater which gives rise to saline soils [19].

Salinity in soil or water is one of the major stresses and, especially in arid and semi-arid regions, can severely limit crop production. The Figure 1 is showing that deleterious effects of salinity on plant growth are associated with low osmotic potential of soil solution (water stress), nutritional imbalance, specific ion effect (salt stress), or a combination of these factors [20].

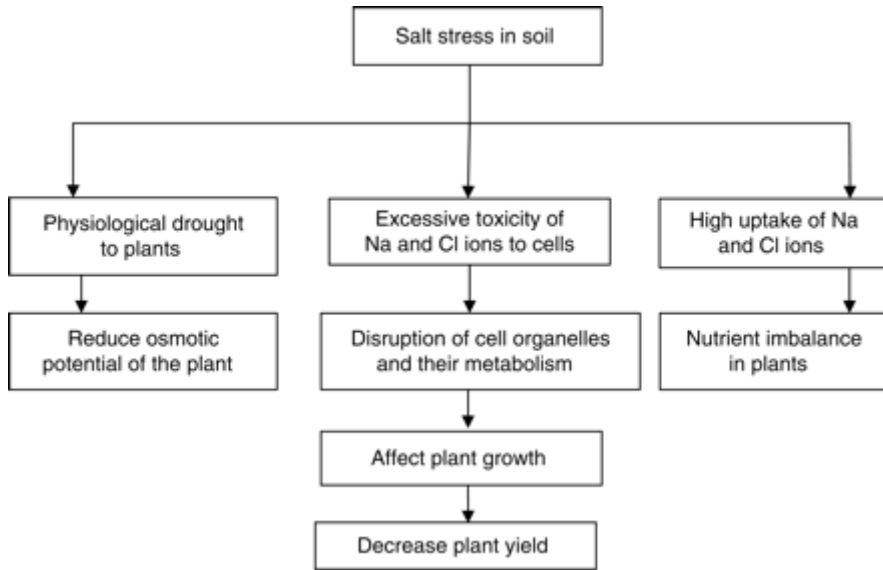


Figure 1. Effects of salt stress on plants (reproduced from [21]).

1.3. Mechanisms of acclimation or adaptation to water and salt stress

Drought and soil salinity are among the most damaging abiotic stresses affecting today's agriculture. It is understandable that plants are under periodic water stress because of the unpredictable nature of rainfall. Salt stress may also occur in areas where soils are naturally high in salts and/or where irrigation, hydraulic lifting of salty underground water, or invasion of seawater in coastal areas brings salt to the surface soil that plants inhabit. Plants have evolved mechanisms that allow them to perceive the incoming stresses and rapidly regulate their physiology and metabolism to cope with them. Very often such regulations and responses include feed-forward mechanisms for stress reduction that are in addition to the responses that are seen after stresses have caused irreversible damage to physiological functions. A good example of such a feed-forward mechanism is the ability of plants to regulate their water loss through partial closure of stomata and/or reduced leaf development, long before there is a substantial loss of their leaf turgor or some irreversible damage to inner membrane systems. [22-24].

In this way, talking specific about water deficit, the physiological responses of plants to water stress include leaf wilting, a reduction in leaf area, leaf abscission, and the stimulation of root growth by directing nutrients to the underground parts of the plants. Plants are more susceptible to drought during flowering and seed development (the reproductive stages), as plant's resources are deviated to support root growth. In addition, abscisic acid (ABA), a plant stress hormone, induces the closure of leaf stomata (microscopic pores involved in gas exchange), thereby reducing water loss through transpiration, and decreasing the rate of

photosynthesis. These responses improve the water-use efficiency of the plant on the short term [25]. The Figure 2 reveals physiological, biochemical and molecular responses to this abiotic stress in plants. It is very important highlight that most of these responses are similar in salt-stressed plants.

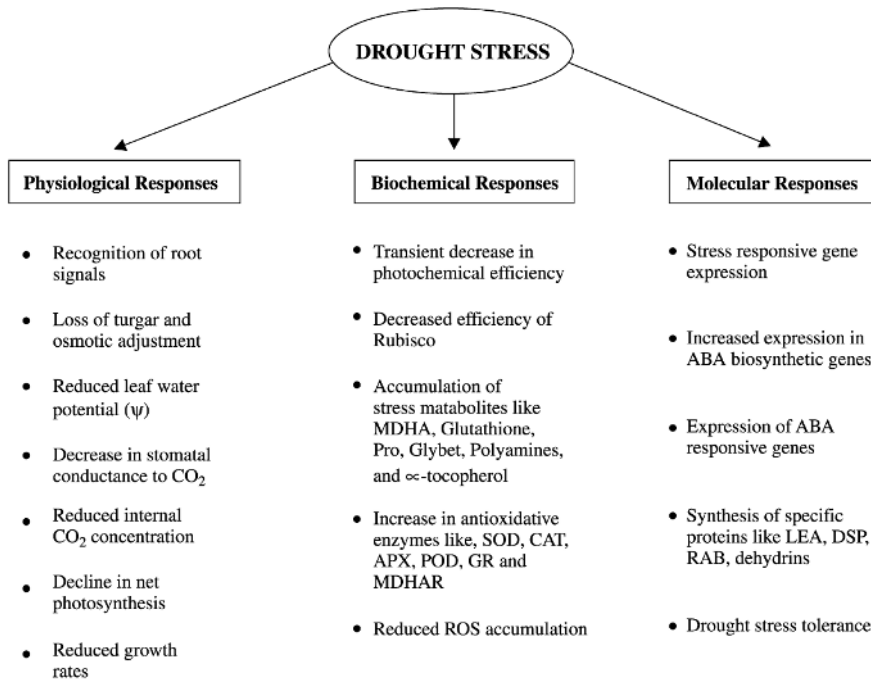


Figure 2. Physiological and molecular basis of drought stress tolerance (adapted from [8, 26]).

In salt-stressed plants, in addition to osmotic effects it is also affected by toxic damages as function of nutritional disequilibrium and high salt levels uptake for plants. Thus, salinity inhibition of plant growth is the result of osmotic and ionic effects and the different plant species have developed different mechanisms to cope with these effects [6]. The osmotic adjustment, i. e., reduction of cellular osmotic potential by net solute accumulation, has been considered an important mechanism to salt and drought tolerance in plants. This reduction in osmotic potential in salt stressed plants can be a result of inorganic ion (Na^+ , Cl^- , and K^+) and compatible organic solute (soluble carbohydrates, amino acids, proline, betaines, etc) accumulations [27]. However these changes are only any few initial responses of many others occurred from salt-stressed seedlings. For instance this behavior, in the Figure 3 has been showed a schematic summary of the stresses that plants suffer under high salinity growth condition and the corresponding responses that plants use in order to survive these detrimental effects.

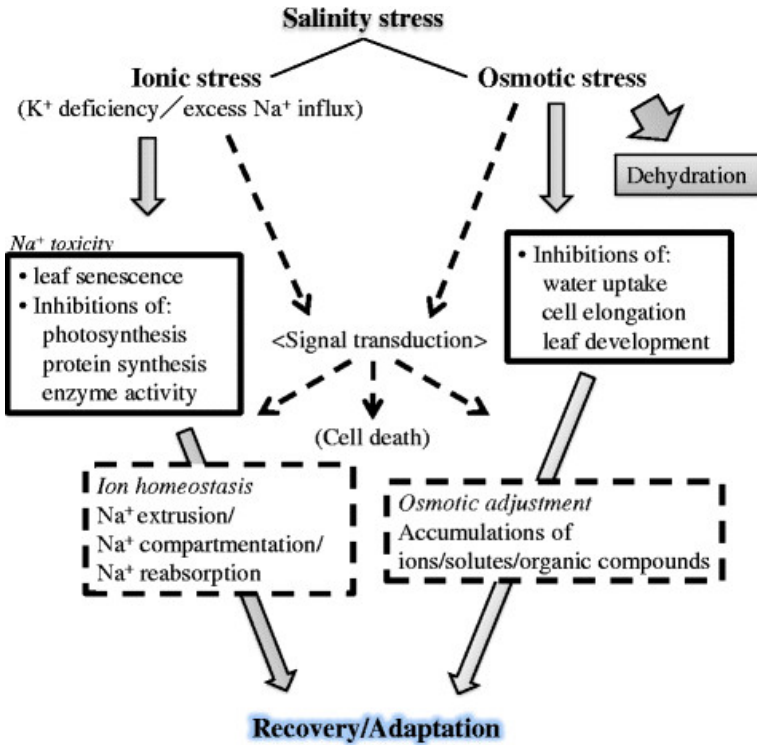


Figure 3. Adaptive responses of plants to salt stress (reproduced from [28]).

2. Water stress x salt stress effects on plant growth and development

Plant responses to drought and salinity are complexes and involve adaptive changes and/or deleterious effects. The decrease in the water potential occurred in both abiotic stresses results in reduced cell growth, root growth and shoot growth and also causes inhibition of cell expansion and reduction in cell wall synthesis [29]. According these authors, drought (likely to salinity) affects the regular metabolism of the cell such as carbon-reduction cycle, light reactions, energy charge and proton pumping and leads to the production of toxic molecules.

The literature has affirmed that plant responses to salt and water stress have much in common. For example, according reference [30], salinity reduces the ability of plants to take up water, and this quickly causes reductions in growth rate, along with a suite of metabolic changes identical to those caused by water stress. Therefore, most mechanisms were development by plants to tolerate abiotic stresses like water deficit and salinity, which are schematically showed in Figure 4.

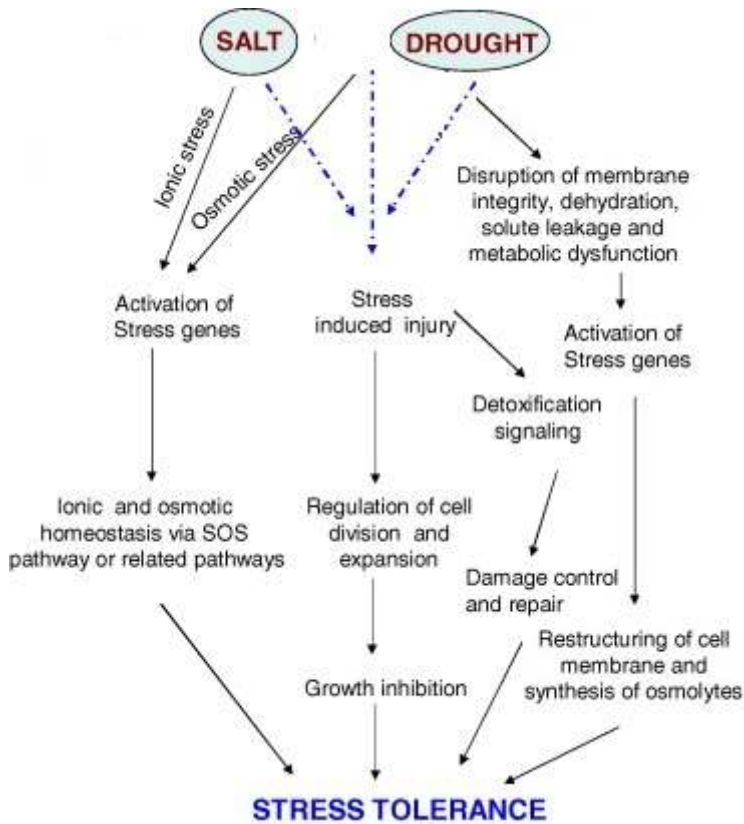


Figure 4. Water and salt stress tolerance mechanisms in plants (adapted from [31]).

2.1. Salinity and water deficit problem in arid and semi-arid regions

Arid and semiarid regions of the world such as Brazilian's Northeast, mostly faces with inadequate, irregular and erratic nature of rainfall. Moreover, according [3], in the field, drought can cause a number of plant stresses including temperature, light and nutrient stresses. However, the stress component that defines drought is a decrease in the availability of soil water. For [32], in addition with recurrent drought lack of efficient use of scarcely available water amplified the impact of water scarcity in agricultural production and productivity. These authors affirm the reduction of agricultural production results from a combination of many factors, such as crop management, crop genetics and biotic stress. Therefore, limited and irregular rainfall directly and indirectly leads to low production levels and consequently food insecurity in developing regions of the world such as Brazilian's semiarid. In addition, [33] have related it is widely recognized that land use–cover changes, such as desertification in arid and semiarid regions and deforestation in tropical zones, may

exert an influence on regional or even global environmental change by changing the hydrological cycle and surface energy balance.

Looking for avoid the water stress and to improve the productivity at arid and semiarid regions generally adopt the use of irrigation, principally the drip. In this way, drip irrigation has the potential to increase crop yields with less water and it can maintain relatively constant soil water content over time near the drip lines. However, [34] have related a disadvantage of drip irrigation is that salt accumulates near the periphery of the wetted area. According them, this salt accumulation can be a matter of concern if the emitter placement does not coincide reasonably well with the location of the plant row, particularly for crops that are sensitive or moderately sensitive to soil salinity.

2.2. Salinity in soil is increased by the water deficit and aridity conditions

In arid regions, there may be periods of no net downward percolation and hence no effective leaching, so salts can accumulate in the soil. In reference [19], the combined effect of meager rainfall, high evaporation, the presence of salt-bearing sediments, and – in many places, particularly river valleys and other low-lying areas – the occurrence of shallow, brackish groundwater which gives rise to saline soils. In addition, the irrigation has been one of the major practices that more contributes with the soil salinization, like showed in Figure 5.

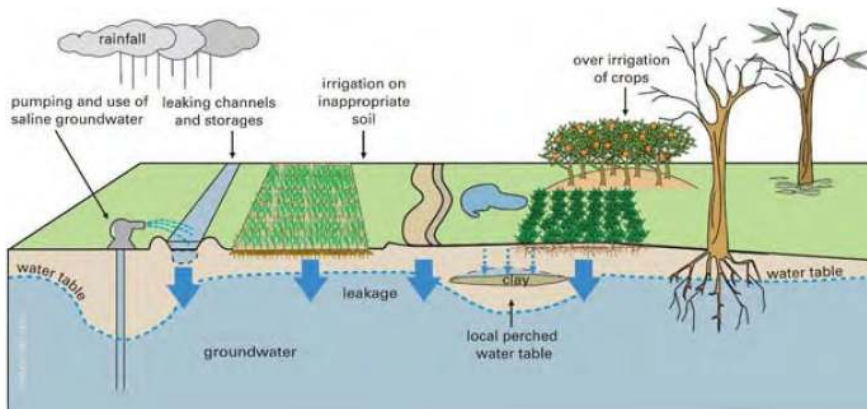


Figure 5. Causes of irrigation salinity (reproduced from [35]).

Less obvious than the appearance of naturally saline soils, but perhaps more insidious, is the inadvertent induced salinization of originally productive soils, caused by human intervention. Irrigation waters generally contain appreciable quantities of salts. (For example: even with relatively good-quality irrigation water containing no more than 0.3 kg salts m³, applying 10,000 mm water per season would add as much as 3 000 kg salts ha⁻¹ per year!) Crop plants normally extract water from the soil while leaving most of the salt be-

hind. Unless leached away (continuously or intermittently), such salts sooner or later begin to hinder crop growth [19].

These deleterious effects previously showed caused by salinization can be managed by changed farm management practices. In [30] has been indicated in irrigated agriculture, better irrigation practices, such as drip irrigation, to optimize use of water can be employed. In rain-fed agriculture, this researcher suggest practices such as rotation of annual crops with deep-rooted perennial species may restore the balance between rainfall and water use, thus preventing rising water tables bringing salts to the surface. All such practices will rely on a high degree of salt tolerance, not only of the perennial species used to lower a saline water table, but also of the crops to follow, as some salt will remain in the soil.

2.3. Salt stress and irrigation and bad water uses

Irrigation water quality can have a profound impact on crop production. In reference [36], the work affirms that all irrigation water contains dissolved mineral salts, but the levels and composition of the salts vary depending on the source of the irrigation water. Salinity from irrigation can occur over time wherever irrigation occurs, since almost all water (even natural rainfall) contains some dissolved salts. When the plants use the water, the salts are left behind in the soil and eventually begin to accumulate. Since soil salinity makes it more difficult for plants to absorb soil moisture, these salts must be leached out of the plant root zone by applying additional water. This water in excess of plant needs is called the leaching fraction [37].

Salination from irrigation water is also greatly increased by poor drainage and use of saline water for irrigating agricultural crops. Therefore, inefficient or bad irrigation water and drainage systems are a major cause of excess leakage and increase the risk of salinity and waterlogging in irrigation areas. Poor water distribution on paddocks results in some areas being under-irrigated, causing salts to accumulate (where watertables are high) and other areas being over-irrigated and waterlogged. Groundwater mounds can develop under irrigation areas as a result of leakage from inefficient systems and restrictive layers. This puts pressure on the regional groundwater system forcing saline groundwater into waterways. Irrigating with saline water adds salt to the soil and increases the need for applying more irrigation water to leach salts past the plant root zone [38].

From studies of FAO [39] we can affirm that prevention and reclamation of salt-affected soils require an integrated management approach, including consideration of socioeconomic aspects, monitoring & maintenance of irrigation schemes and reuse and/or safe disposal of drainage water. Implementation of efficient irrigation and drainage systems and good farming practices can prevent and, in some cases, reverse salinization. If appropriate management practices are not applied in time, it may be necessary to take the land out of production altogether. Moreover, actions to fight or mitigate salinization can be implemented by local institutions and research stations, while research and technology transfer can play a crucial role in providing tools, setting up management strategies or spreading water-saving techniques.

2.4. Growth and plant development affected by multiple stresses as water and salt stress

Plant growth can be limited by water deficit and by excess water. Water deficit occurs in most natural and agricultural habitats and is caused mainly by intermittent to continuous periods without precipitation. Excess water occurs as the result of flooding or soil compaction [12].

When plant cells experience water deficit, cellular dehydration occurs, this promotes reductions of cell turgor (Ψ_p) and cell volume. It is also associated with the water potential (Ψ_w) of the apoplast becoming more negative than that of the symplast. Cellular dehydration could causes ion concentration reaching cytotoxic levels [12].

Water deficit not only decreases turgor pressure, but also decreases wall extensibility and increase yield threshold. The water deficit effects on yield threshold are presumably involved in complex structural changes of the cell wall that may not be readily reversed after relief of water deficit [12].

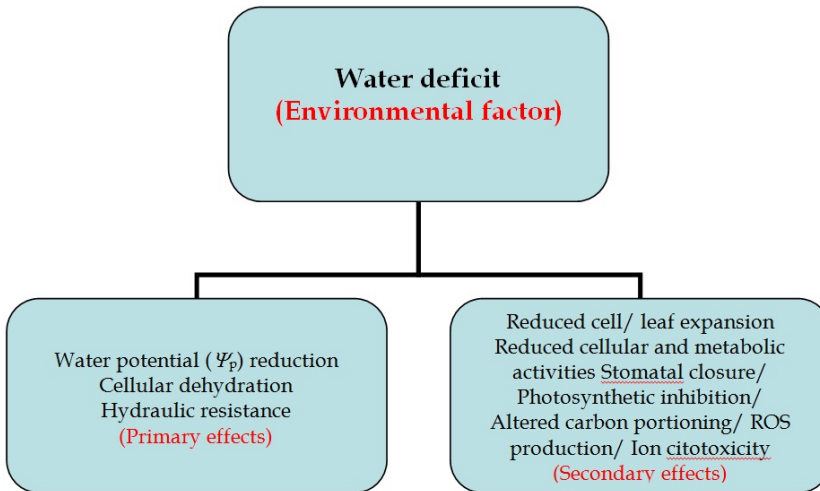


Figure 6. Some physiological and biochemical perturbations in plants caused by fluctuations in abiotic environments [12].

Salinity can have similar aspects to water stress in plant growth, except for the addition of ion cytotoxicity, which appears with salt excess in soil. [12].

The toxicity of high Na^+ and Cl^- in the cytosol is due to their specific ion effects. High salt concentrations, outside the cell, can result in osmotic stress. Once in the cytosol, however, certain ions act specifically, either singly or in combination, affecting whole plant because ions move to the shoot in the transpiration stream [6].

The increase of solutes on root medium, mainly the ions, can promote a reduction of water absorption by plant root system, contributing to reduction of root conductivity. As

consequence, the plant absorbs less water, and if the transpiration rate is higher than water absorption rate, and the result is a water deficit, which could result in photosynthetic rate reduction and growth rate reduction [40]. According to the figure below, salt stress effects in timescale alters initially, absorption of water and nutrients, and membranes permeability [41].

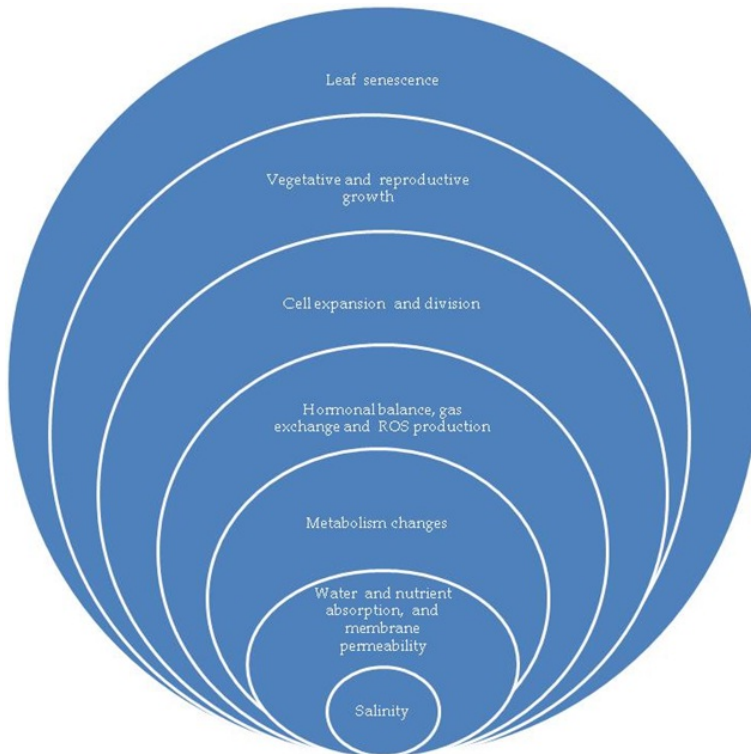


Figure 7. Change in plant physiology as consequence to salinity adapted from [40].

These previous changes reflect in nutritional and hydric balance of plants and promote changes in metabolism, in hormonal balance, gas exchange and ROS production. All these changes undertake cell expansion and division, vegetative and reproductive growth and acceleration of leaf senescence, which result in plant death [12].

An important strategy to avoid ion toxicity is the accumulation of ions during osmotic adjustment in vacuoles, where the ions are kept out of contact with cytosolic enzymes or organelles. Many halophytes utilize vacuolar compartmentalization of Na^+ and Cl^- to facilitate osmotic adjustment that sustain or enhances growth in saline environments. When ions are compartmentalized in vacuoles, at the same time other solutes must accumulate in the cytoplasm to maintain water potential equilibrium within the cell, as example of these compati-

ble solutes, can be cited the quaternary ammonium compounds, sugar alcohols, quaternary ammonium compounds (QACs) and tertiary sulfonium compounds (TSCs) [12].

According to [6], the growth responses to salinity stress occurs in two phases: a rapid and intense response to the increase in external osmotic pressure related to NaCl increase in the medium, which contribute to a stronger reduction in growth. Followed, it can be observed, a slower response due to toxic ion accumulation in tissues (Ionic phase), which is related to a severe toxicity in leaves, represented in most of times by chlorosis and can be originated necrosis in these tissues (See figure 8). Leaf injury and death is probably due to the high salt load in the leaf that exceeds the capacity of salt compartmentation in the vacuoles, causing salt to build up in the cytoplasm to toxic leaves [6,30]. These responses vary strongly between genotypes, salinity levels, soil and other abiotic factors [6].

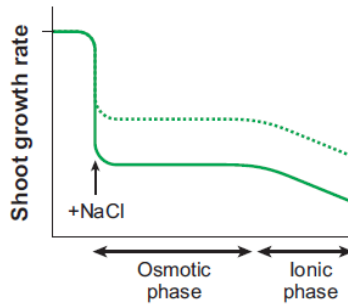


Figure 8. Growth responses to salt stress from [6].

Plants undergo characteristic changes from the time salinity stress is imposed until they reach maturity [30]. Salinity inhibition of plant growth is the result of osmotic and ionic effects and the different plant species have developed different mechanisms to cope with these effects [30]. The plant responses to salinity are different between the species, the salt levels and also depends of the time exposition. In the table below could be observed the plant response to salinity at different time scales [Table modified from 30].

| | Water stress effects (Observed effect on growth of a salt-tolerant plant) | Salt-specific effects (Additional effects on growth of a salt-sensitive plant) |
|---------|--|---|
| Minutes | Instant reduction in leaf and root elongation rate then rapid partial recovery | |
| Hours | Steady but reduced rate of leaf and root elongation | |
| Days | Leaf growth more affected than root growth; Reduced rate of leaf emergence | Injury visible in oldest leaf |
| Weeks | Reduced final leaf size and/or number of lateral shoots | Death of older leaves |
| Months | Altered flowering time, reduced seed production | Younger leaves dead, plant may die before seed matures |

Table 1. Water and salt-specific effects on plant growth

As can be observed in this table, in the first few seconds or minutes, it has been observed that cells lose water or shrink. When the hours are passing, cells regain the original volume but cell elongation is reduced, contributing to lower rates of leaf and root growth. After some days, cell elongation and cell division promote alterations in leaf size appearance [30]. In plants, with high salt absorption, the oldest plants become senescent, and some leaves can die. After months, differences between months, with high and low salt uptake become very pronounced, with a large amount of leaf injury and complete death in some cases if the salinity level is high enough [30].

The tolerance or plant response to salt can vary with cultivars, the plant age and growth stage, environmental conditions, cultural practices, irrigation management, soil fertility, and the intensity or other plant stress. Another stress factor is wind that can be injurious to plants as salt. When the two are combined near the ocean, plants suffer even greater damage. Some crassulaceae and succulent plants are highly salt and wind tolerant, in different way, moderate salt tolerant plants of soil salinity usually tolerate light salt spray but should not be used in exposed locations [42].

The comparative effect of salinity and water stress on growth was analyzed in *Jatropha curcas* seedlings. The plants subject to water stress, through the exposition to PEG, showed higher restrictions in leaf growth compared to the salt-stressed ones. Moreover, only the PEG treatment caused a pronounced effect on leaf membrane integrity. Since the plants subjected to mild water and salt stresses showed a rapid and almost complete recovery, these physiological alterations could represent a set of adaptive mechanisms employed by *J. curcas* to cope with these stressful conditions [43].

Pinus seed germination was evaluated in different conditions: water stress simulated by PEG agent experiments, salt stress using sodium chloride (NaCl) and diluted sea water, associated to different temperatures (heat stress). Seed germination and the activities of the main enzymes involved in Pinus seed reserve utilization (glyoxylate cycle enzymes) decreased with increasing PEG, NaCl and seawater concentrations. In addition, the seawater treatment was the less severe on seed germination. As regard to heat treatments, the maximum germination percentage (80%) was obtained at 80°C and short exposure time (3 min) [44].

Another study involving water and salt stress effects on plant growth was verified in Tamarisk (*Tamarix chinensis* Lour.) seedlings, where it was observed that the water supply and salt content had interactive effects on Tamarisk biomass, while interactive effects of the both stress had no influence in biomass allocation. This parameter was more affected by water supply, which implied that the balance between soil water availability and atmospheric evaporative demand defined the biomass allocation [45].

Salinity affects both vegetative and reproductive plant development, which promotes negative implications depending on the harvested organ, stem, leaf, root, shoot, fruit, fiber or grain [46]. Salinity generally reduces shoot growth more than root growth and can reduce the flowering and increase sterility. Considering the salt-tolerance importance from an agronomic or horticulturist perspective is based on the yield of the harvestable organ, relative to

that in non-stressed environments, understanding how salinity affects vegetative and reproductive development is important for developing management strategies that can minimize stress at critical times [46]. Salinity stress could delay germination, although most plants are tolerant and there may be no difference in the percentage of germinated seeds.

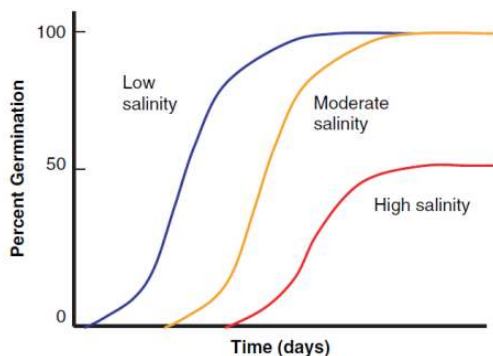


Figure 9. Salinity effects on relationship between percent germination and time after water addition at low, moderate and high salinity, modified from [46].

Helianthus annuus seed germination was evaluated using treatment to overcome salt and drought stress during germination. In this study, it was verified that seeds subjected to salinity and water stress showed reduced germination in both conditions [47]. Germination, root and shoot length were higher in NaCl than PEG conditions, but mean germination time and abnormal germination percentage were lower in these conditions [47]. The authors concluded that germination inhibition at the same water potential of NaCl and PEG resulted from osmotic effect rather than salt toxicity, in addition it was observed that hydropriming increased germination and seedling growth under salt and drought stresses [47]. Another study with germination approached salt and water stress on seed germination and early embryo growth in two cultivars of sweet sorghum. In this study, it was observed that salt stress prolonged the germination time. Shoot and root growth was adversely affected by water stress (PEG), whereas the effect of salt stress was less relevant [48].

2.5. Salt tolerant plants “Halophytes” and water stress tolerant plants

Halophytes are plants that can survive and reproduce in environments with high salt concentration (200 mM NaCl), these plants constitute about 1% of the world’s flora. Halophytes can be classified as “natural” and plants that tolerate salt but do not normally live in saline conditions [49]. Other classifications of halophytes are based on the characteristics of naturally saline habitats [49] or the chemical composition of the shoots (‘physiotypes’, [50] or the ability to secrete ions (recreto-halophytes, [51]).

The effect of salinity on growth varies amongst halophytes, which can be observed in figure bellow for different species [49]. According this figure, *Sueada maritima* was the specie that

could growth in the highest NaCl concentration, however the best condition was around 40 mM NaCl. The most affected species was *Thellungiella halophila*, which showed stronger growth reduction from 200 mM NaCl. In addition, it can be highlighted that dicotyledonous species showed higher tolerance to NaCl than monocotyledonous species, except for *T. halophila* [49].

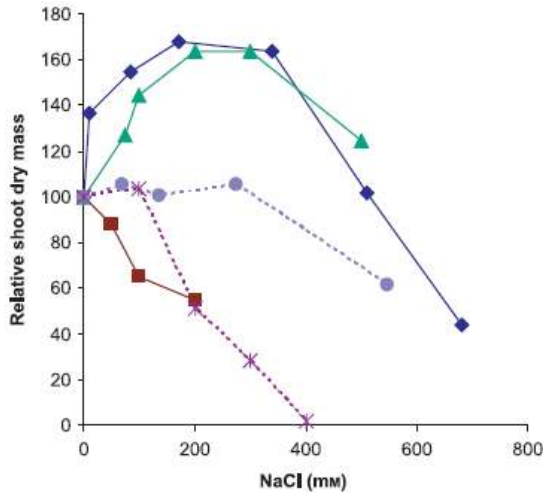


Figure 10. Effect of NaCl increasing on the growth on shoot dry mass in different halophytes. Solid lines represents dicotyledonous species; broken lines, monocotyledonous species. (◆) *Suaeda maritima* (35 d), (■) *Thellungiella halophila* (14 d); (▲) *Disphyme australe* (60 d); (*) *Puccinellia peisonis* (42 d); (●) *Distichlis spicata* (21 d). (Modified from 49)

The salt requirement by halophyte during their growth and development were evaluated in two halophytic species (*Inula crithmoides* L. and *Plantago crassifolia* Forssk.) and a maritime dune species (*Medicago marina* L.) [52]. In this study was observed that growth parameters results showed that all three species grew much better on the salt-free and nutrient-rich substrates, peat and garden soil, than on saline soil and dune sand. These results indicate that salts are not necessarily required for development of halophytic species, and suggest that limitation of water and nutrients, rather than soil salinity per se, are the most important restrictive factors for plant growth in saline habitat [52].

Studies involving extreme dicotyledonous halophytes show that optimal growth in the presence of low or moderate salt concentrations; on the other hand, this stimulatory effect is not commonly detected in monocotyledonous halophytes, nor in other salt-tolerant dicots, which grow best in the absence of salt [53]. The salt tolerance degree usually varies among halophytes and, for a specific species, also at different developmental stages [53], but inhibition of plant growth is always observed at sufficiently high salinity levels, in all investigated taxa [52, 53].

Tamarix chinensis that is used as a windbreak for preventing desertification and erosion in arid areas and potential bio-energy resources for marginal land utilization [54], was evaluated with relation to salt and water stress on biomass and photosynthetic characteristic. In this study was observed that soil salt increment had no significant effect on biomass allocation of *T. chinensis* seedlings [45], while water deficit significantly favoured root biomass accumulation [45].

In study about growth parameters and anatomical changes in the halophyte *Atriplex nummularia* Lindl, it was observed that the height, diameter and fresh and leaf dry biomass, stems and roots were sensitive to soil moisture. Moreover, anatomical changes in the vesicular trichomes of the leaves were detected with water soil variations and druse formed by deposition of sodium chloride within cells [Figure from 55]. A low water content in the oil is related to small average diameters and volumes of the epidermal vesicles [55].

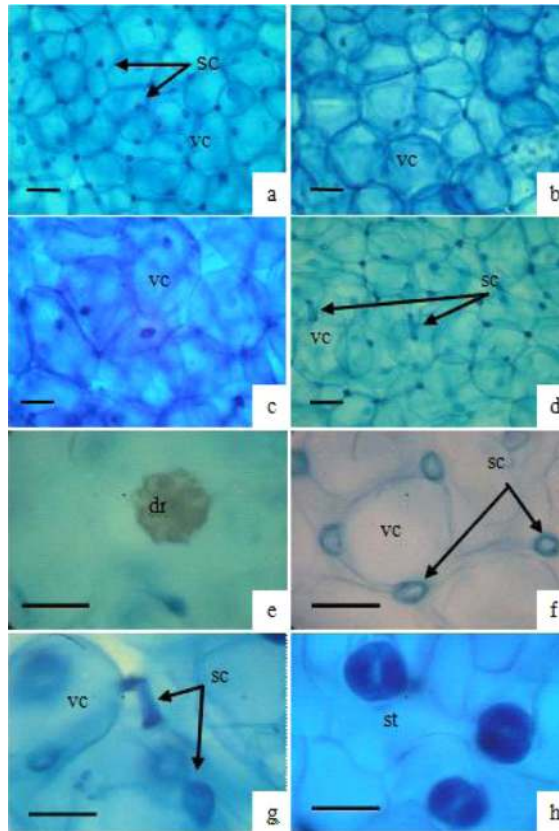


Figure 11. Epidermis front view of the leaves of *Atriplex nummularia* Lindl. grown in sodic saline soil under different water regimes: (a) 35%; (b) 55%; (c) 75; (d) 95% of FC. Vesicular trichome consisting of stalk cell surmounted by a vesicular cell (f–g) and stomata (h). sc: stalk cell; vc: vesicular cell; dr: drusa; st: stoma. Bar: 50 μ m (a–d), 25 μ m (e–h). Modified from [55]

In another study also with *A. nummularia* was observed that leaves display a most prominent osmotic adjustment than roots. In addition, it has been also concluded that Na^+ and Cl^- ions are the major components to the overall osmotic adjustment, in both salt-untreated and treated leaves but in untreated roots the K^+ is the major component [56]. For *Atriplex allimus*, the decrease in fresh weight might be attributed to the decrease in water content. Moreover, the decrease in photosynthesis could result from a decrease in stomatal conductance, which corresponds to a protective mechanism against water loss to improve water use efficiency [57]. The *A. allimus* could tolerate NaCl and drought through decreasing growth, reducing gas exchange parameters to improve water use efficiency. In another study with halophytes, it was verified the effect of salinity and soil drying on nutrient uptake and growth of *Spartina alterniflora* in a simulated tidal system [58]. This study demonstrated that high salinity associated with drought decreased survival to 71%. Furthermore, leaf chlorosis and browning occurred in plants subjected to increased salinity and drought conditions, which can demonstrated that drought may magnify the adverse effects of salinity on plant nutrient status [58]. Some plants can develop a lot of mechanisms to support water deficit, as example the development of internal water deficit, which can be important for some crops such as coffee and mango in order to trigger phenological events such as flower bud release. Additionally, it has been know that for a tropical environment the range of evaporative demand on average is higher than that of temperate zones. This implies that leaf water status changes much more diurnally in tropical trees than in many temperate trees or annuals, and leaf water deficits may occur under the high evaporative demand even without any soil water shortage, such as in banana, cocoa, coffee, papaya, and tea [59].

The development of thick cuticular membranes generally is interpreted as an adaptation to drought with regard to the formation of an efficient transpiration barrier. The capacity of *Teucrium chamaedrys* in maintaining a low but still measurable stomatal conductance under drought stress at maximum light intensity can be interpreted as a mechanism to adjust leaf temperature below the heat resistance limit by transpiration cooling [60].

Jatropha curcas L. is a biodiesel crop that is resistant to drought stress, and the tolerance of *Jatropha curcas* seedlings to NaCl was evaluated through some ecophysiological analyses. This study showed that the negative NaCl effects on *J. curcas* crop, are mainly due to Cl^- and/or Na^+ toxicity and to a nutritional imbalance caused by increase in Na^+/K^+ . Moreover, the osmotic effect on salinity in this species is very pronounced, probably due to strong control of leaf transpiration, which reduces water loss [61].

The NaCl differential tolerance of different maize genotypes were evaluated through some growth and physiological parameters and it was concluded that the SDM/RDM ratios, leaf Na^+ content or leaf soluble organic solute content had no relation with salt tolerance. On the other hand, Na^+ and soluble organic solute accumulation in roots due to salinity appeared to play an important role in the acclimation of maize genotypes, being that these characteristics could be used as physiological markers to salinity [62].

2.6. Studies involving adaptations or acclimations of tropical plants to water and salt stress

Plants under salt stress can occasionally tolerate alterations in the environmental conditions. Salt tolerance in plants is determined by multiple biological traits that will determine their water retentions and/or acquisition capacity in safeguarding photosynthetic functions and ion homeostasis. The plant ability of eliminating free radical under salinity and water stress using active osmolytes, usually demand a lot of energy. Many plant species that are salt tolerant to salt stress show the ability to produce and accumulate osmoprotectants [63].

Water deficit and saline soils of the Brazilian semi-arid northeastern region are limiting factors and most of the times negatively affect the plant development. *Mimosa tenuiflora* popular known as Jurema preta is a small, multiple use tree that is widely distributed in environments with severe water stress. In this study, it was verified that Jurema preta seeds germination showed more sensitive to NaCl than to water stress, and due to the stronger germination reduction in this condition, this species can be classified as a glycophyte [64].

Some studies evaluate the plant acclimation to abiotic stresses, and it is very common the pretreatment use for alleviates the negative effects on plants. The H₂O₂ pretreatment effect in maize seeds during germination and seedling acclimation to salinity, and it was observed that H₂O₂ pretreatment of seeds induced acclimation of the plants to salinity. It decreased the salinity deleterious effects on the maize growth. In addition, it was also verified differences in antioxidative enzyme activities, which may explain the increased tolerance to salt stress of plants originated from H₂O₂ pretreated seeds [65]. Another plant that is cited as water tolerant is *Jatropha curcas*, which was evaluated with relation to organic and inorganic solutes contribution of to osmotic adjustment under salinity. This plant showed an effective osmotic adjustment in leaves under salinity, maintaining their hydration status, mainly via Na⁺ and Cl⁻ accumulation, and in relation to organic solutes, glycinebetaine was more important to osmotic adjustment than proline in both salt-treated and untreated plants [66]. The salt tolerance was evaluated in cotton, sorghum and maize, which are considered very adapted to Brazilian semi-arid and show contrasting tolerance to salt [67]. In this study, it was observed that growth results confirmed the highest salt tolerance to cotton, whereas cowpea presented highest susceptibility to salinity, because it was verified stronger reduction in shoot and root dry mass from moderate salinity level. In addition, antioxidant enzyme activities changes suggest that cotton constitutive enzyme system seems to be more efficient than the others [67]. Cowpea is widely cultivated in arid and semi-arid regions of the world where salinity is a major environmental stress that limits crop productivity [68]. This author evaluated the relationship between salt tolerance with differences in ion accumulation, biomass allocation and photosynthesis in cowpea cultivars. Salt stress caused reduction in biomass accumulation and photosynthetic rates per unit leaf mass, mainly in 'TVu' cowpea cultivar. 'Pitiúba' showed the relative advantage over 'TVu' cultivar under salt stress, which was associated with reduced Na⁺ accumulation in leaves related to increase in Na⁺ concentration in roots at early stages of salt treatment. In general way, these responses would allow greater whole-plant carbon gain, thus contributing to a better agronomic performance of salt-tolerant cowpea cultivars in salinity-prone regions [68]. In another

er study, seven cowpea cultivars were analyzed in relation to growth and organic and inorganic contents in response to salinity. It was demonstrated that salinity reduced dry mass of all cultivars, and 'Pitiúba' and 'Vita 5' were the most tolerant and 'TVu' the most sensitive [69]. The growth parameters showed strong correlation with the salt tolerance degree but increased significantly with the salt increment concentration only in the most tolerant cultivars. Overall, Na^+ and Cl^- shoot content increased due to salinity but accumulated drastically only the more susceptible cultivars, particularly in 'TVu' cowpea cultivar. K^+ content in leaves was higher than Na^+ and Cl^- contents but none of the ions were significantly in this tissue. Consequently the Na^+/K^+ ratio was higher in the most sensible cultivars. This may represent an important factor for the growth reduction observed in the stressed plants. Considering the organic solutes (proline, soluble carbohydrate and N-amino solutes) were not correlated with NaCl degree tolerance in the cultivars [69]. Another species that is widely distributed in Brazilian semi-arid region is cashew nut (*Anacardium occidentale* L.) showing some adaptations and acclimations to water deficit, and it has been strongly used as a model to evaluate salt tolerance mechanisms. In relation to seed germination and seedling establishment of dwarf-cashew, salinity delayed emergence and establishment seedling, however, only the final percentage of established seedlings was reduced, accompanied by inhibition of reserves depletion and an embryonic axis dry mass decrease. [70]. The salinity effects on seed germination and seedling establishment could also be resulting of negative salt influence on metabolic processes, such as the mobilization of the stored reserves for the growing embryonic axis. In addition, salinity could inhibit seedling development through the inhibition of enzymes involved in the mobilization of lipid reserves of the seed [70, 71]. Also with relation to cashew nuts, it was evaluated the changes in physiological indicators in two contrasting cashew rootstocks. Among the physiological parameters evaluated, leaf membrane damage was closely associated with the differences in salt tolerance between the two cashew genotypes. In addition, under salinity the tolerant rootstock showed greater ability to accumulate compatible organic solutes (amino acids, proline and soluble sugars) in leaves in addition to maintaining the soluble sugar concentration in roots as compared with the sensitive rootstock [72]. Further, evaluating physiological and biochemical changes occurring in dwarf-cashew seedling under salinity showed that organic solutes was few affected by salt stress, except for proline that showed in increment. In addition, the most representative enzyme activity in roots was guaiacol and ascorbate peroxidase in removing reactive oxygen species, due to roots were considered more protected to salinity stress than leaves. In addition, changes in protein pattern were related mainly to salt stress rather than by alteration in developmental stage [73]. Another study with salt-stressed cashew nuts suggest that the ability of these seedlings to adapt to salt stress is, at least in part, correlated to maintenance of integrity and protection against oxidative plasma membrane damage, which could contribute to the activation of H^+ -ATPase plasma membrane, as a cellular mechanism to regulate ion exclusion from the shoot [74]. In another study, it was evaluated the gas exchange in leaves of sun and shade of cashew in different water regimes, where it was verified that light exposition influenced more stronger the physiological parameters than suppression of water. It occurred probably because the presented results were better related to the phenological stages than with the treatments, demonstrating a conspicuous physio-

logical effect of the strength of the drains and the irradiance in these plants [75]. Also studying adult plants of cashew, it was verified that the increase in electric conductivity did not contribute to alterations in plant growth and development, once it was not observed changes in evaluated parameters. Metabolic alterations was more related to plant developmental stage, showing higher values in fructification stage [76].

The water relations in six adult species of Caatinga, a typical vegetation from Brazilian semi-arid, in the middle of the dry season. Based on results, the trees were classified into four groups: (I) *Mimosa caesalpiniiifolia* had low leaf water potential (Ψ_w) at predawn and no significant decrease at midday; (II) *Caesalpinia pyramidalis* and *Auxemma oncocalyx* had low Ψ_w at predawn and significant decrease at midday. For these species the recuperation of water status at night may have been sufficient for maintaining stomata open during the day; (III) *Caesalpinia ferrea* and *Calliandra spinosa* had relatively high Ψ_w at predawn and a significant decrease at midday. They might also have deeper root systems; and (IV) *Tabebuia caraiba* with the highest Ψ_w at predawn and no significant decrease at midday, possibly indicating a combination of good stomatal control of water loss and a deeper root system [77].

In relation to common bean plants, mild water deficit affected the photochemical apparatus in these plants, probably due to by down-regulation since plants did not show photoinhibition. The photochemical apparatus of A222 and A320 genotypes was more sensitive to drought stress. On the other hand, even after 10 d of water withholding, the maximum efficiency of photosystem 2 was not affected, what suggest efficiency of the photoprotection mechanisms [78].

The seasonal variations of physiological aspects of caatinga species demonstrated the high levels of water potential, even in the dry period, a situation in which commonly occurs water stress due to absence of soil water. It is related to water potential decrease during the absence of water in soil. The fluorescence data showed that the photosynthetic states were good with no apparent deficiency of water. In addition, it was verified that the survival strategies of these species to water deficit are efficient and result from a highly complex evolution [79].

In a study with *Vigna unguiculata*, an important crop largely cultivated in warm and hot lands, it were evaluated some photosynthetic parameters and metabolic changes in cowpea under water stress and recovery treatments. In this study it was verified that decreased CO_2 assimilation rates during water stress were largely dependent on stomatal closure, which reduced available internal CO_2 and restricted water loss through transpiration [80]. Additionally, the alterations in carbohydrate metabolism showed an accumulation of soluble sugars in water-stressed leaves, which also persisted in rewatering plants for 1 day. The authors conclude that a transient end-product inhibition of photosynthesis, contributing to a minor non-stomatal limitation during stress and recovery initial phase [80].

In relation to *Phaseolus vulgaris*, the mild water stress effects on photosynthetic parameters and water potential were analyzed in five common bean. The stomatal conductance and net photosynthetic rate were significantly reduced in all genotypes due to the water deficit [81]. Mild water deficit affected the photochemical apparatus in bean genotypes probably by

down-regulation since plants did not show photoinhibition. It was also interesting in this study, that even after 10 d of water withholding, the maximum efficiency of photosystem 2 was not affected, what suggest efficiency of the photoprotection mechanisms [81].

In the figure below, it is resumed long-term or acclimations responses to drought stress and short-term responses that reach the plant perceive the water stress and develop the following responses against this condition [82]. The majority of traits related to plant drought adaptations, as example root size and depth, hydraulic conductivity and seed storage reserves are associated to plant development and structure and are constitutive rather than stress induced. In addition, a large part of drought plants resistance to drought and its ability to get rid of to excess radiation. The natural mechanisms responsible to leaf photoprotection, especially to related to thermal dissipation and oxidative stress. Plants can also endure water drought conditions by avoiding tissue dehydration, while maintaining tissue water potential as high as possible, or tolerating lower water potential. Dehydration avoidance is usually observed in annual and perennial plants, which has been associated to proper characteristics as example: capacity to minimize water loss and maximize water uptake [82]. The water loss could be done by stomata closer, reducing light absorbance by leaf or through reflectance increasing due to the development of a trichome layer, or by decresing of leaf surface with reduced growth or by shedding of young by old leaves. On the other hand, the maximizing water could be reaching by increasing in root system, which is resulting of alteration in allocation of plant sources [82].

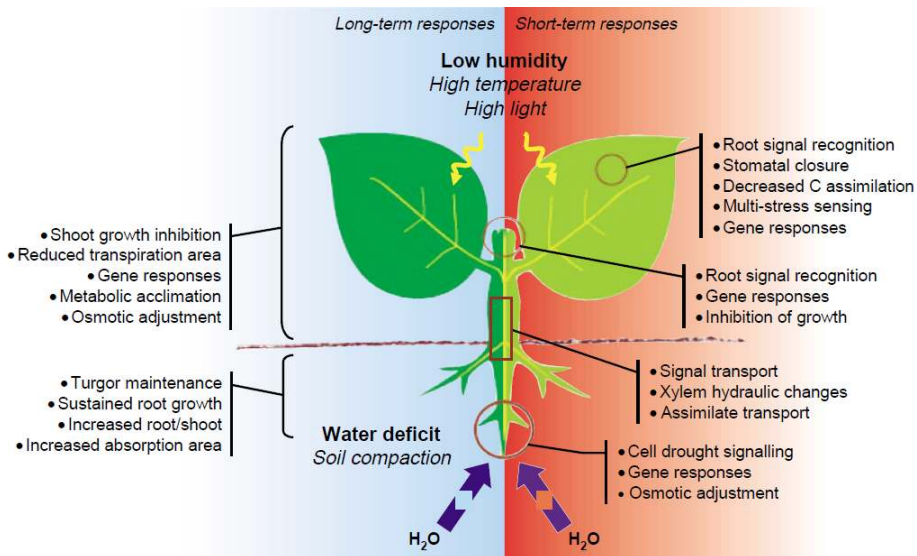


Figure 12. Plant responses to water stress from 82

3. Conclusion

Among the great number of abiotic stress affecting plants, drought and salinity are the most severe and stronger ones that limit plant growth and crop productivity in agriculture worldwide. These stress could have damages exceeding the sum of that attributed to all other natural disasters, and when they happen together promoted devastating changes in plants subjected to them. Plant responses to drought and salt stresses have much in common, the water limitations in water stress is very difficult to plant tolerate and maintain its normal growth and development. Salt stress occurs from both osmotic stress due to low water potentials and salt-specific effects, for this beyond the water restrictions, salt-stressed plants have to develop conditions to tolerate the toxic effects caused by ion accumulation, which could affect all aspects of plant metabolism. In the first view, we could speculate that salt stress in plants are more severe than water stress, by the fact that the first condition show two components, however, it is early to conclude this. This is because studies on the comparative physiology of plants to water and salt stress are few, and it is necessary perform more studies involving different plant species, as cultivate and as native, subjected at the same time to both stress to conclude what is the most severe for plant growth and development. Moreover, the development of new tools and strategies to evaluate the combination of water and salt stress on plant are also necessary, but the perspectives in relation to the better understanding of how some plants could tolerate, escape, acclimate and adaptate to these severe abiotic stresses. This knowledge could have the support of studies involving since molecular (genomics and proteomics tools) aspects as ecotype researches (isotopes, imaging) and this combination will allow the faster comprehension of plant performance in different environments, as well the bringing of genotype and phenotype gap.

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