Chapter

Salt and Water Stress Responses in Plants

Mirela Irina Cordea and Orsolya Borsai

Abstract

Climate change-driven ecological disturbances have a great impact on freshwater availability which hampers agricultural production. Currently, drought and salinity are the two major abiotic stress factors responsible for the reduction of crop yields worldwide. Increasing soil salt concentration decreases plant water uptake leading to an apparent water limitation and later to the accumulation of toxic ions in various plant organs which negatively affect plant growth. Plants are autotrophic organisms that function with simple inorganic molecules, but the underlying pathways of defense mechanisms are much more complex and harder to unravel. However, the most promising strategy to achieve sustainable agriculture and to meet the future global food demand, is the enhancement of crop stress tolerance through traditional breeding techniques and genetic engineering. Therefore, it is very important to better understand the tolerance mechanisms of the plants, including signaling pathways, biochemical and physiological responses. Although, these mechanisms are based on a well-defined set of basic responses, they can vary among different plant species.

Keywords: abiotic stress, salinity, drought, response mechanisms, tolerance

1. Introduction

Salinity and drought are the two major constraints that affect plant growth and crop production alongside other stress conditions such as extreme temperature, heavy metals, flooding etc. thus reducing agricultural productivity worldwide. Both the cellular and molecular responses of plants to these environmental stresses have already been investigated, however understanding these mechanisms by which plants can perceive stress signals and transmit them to cellular machinery to activate adaptive responses is a very important chain-link of plant physiology. Besides, extending knowledge about stress signal transduction becomes vital for breeding programs and genetic engineering to improve stress tolerance in crops.

Due to climate change, it is predicted that drought and salinity will became more severe in the upcoming years which could lead to a significant reduction of plant growth and yield of several economically important species. It has been estimated that worldwide food demand will increase by 70% until the end of 2050 [1] due to a population growth of 2.3 billion people. In this context, developing crop plants with high yield and better tolerance to harsh environmental conditions becomes an urgent need to meet future food demand for next generations.

In general, plant responses to salinity and drought may vary in morphological, physiological and biochemical aspects and processes. Most of the effects induced by salinity and drought are negative, however to some extent they can have positive effects as well [2]. It has been reported that salinity at certain concentrations enhanced plant fecundity due to an increase in reproduction, but it has also been observed that this enhancement was highly dependent on genotype and plant developmental stage [3]. Soil water salinity can also have a positive effect on fine particles helping them to bind together into aggregates, thus improving soil aeration, root penetration and root growth [4]. Nevertheless, salinity cannot be increased in favor of soil structure without considering the potential impacts on plant health.

Salt-stress resistance represents the ability of a plant to prevent, reduce or overcome the possible damaging effects caused directly or indirectly by the presence of excessive soluble salts (accumulation of toxic ions) in its root zone. A 50% reduction in yield can be considered a measure of salt stress.

Drought stress occurs after a relatively long period with no rains, inducing moisture stress in the soil detrimental to crop growth, especially in rainfed agriculture. The severity of drought is strongly related to the timing (growth stage of the plants) and intensity (duration of no rain period). Other factors such as soil characteristics and agricultural practices can interfere with crop yields.

Previous reports suggest that a positive transgenerational impact on seedling vigor of *Brassica napus* has been observed due to drought stress [5]. This phenomenon was explained as a result of the heterotic effects, altered reservoir of seed storage metabolites, and inter-generational stress memory formed by stress-induced changes in the epigenome of the seedling. Compared to salt stress, drought stress has more severe effects on plants and economy [6] but plant responses are closely related and their defense mechanisms even overlap.

The ability of a crop variety to perform better over other varieties under drought conditions is known as drought resistance which is linked to achieved yields and potential yields achievable in a given environment in the absence of drought conditions. Drought resistance is highly environment specific and yield stability might be influenced by crop management practices, and/or physiological mechanisms and might not necessarily be associated with the drought resistance ability of a genotype. In a drought resistant variety, plant growth and development are well-matched to specific drought environment(s) [7].

When sensing salinity or drought stresses, plants have the capability to combine a range of responses in order to avoid stress injuries and complete their life cycle. By the activation of various defense mechanisms plants can store reserves in their organs and use them later for yield production or, they can tolerate stress conditions without tissue dehydration [8]. Plant-associated organisms play an important role in improving the adaptation strategies of plants to environmental stresses. In this context, microorganisms, for example, can rescue plants from the deleterious effects of drought and salinity through their activity, such as nutrient solubilization, IST and production of phytohormones (IAA, Cytokinin, ABA or GA), EPS and ACC deaminase. The inoculation of plants with arbuscular mycorrhizal fungus can also increase plants' tolerance to short term salinity exposures [9, 10].

With all these fundamentals being provided to understand the underlying defense mechanisms of plants against stress conditions, further studies are still needed to reveal key mechanisms which govern salinity and drought tolerance responses in plants and which can lead us towards better direction in crop improvement, in order to obtain potential candidates for future saline agriculture.

2. Mechanism of salt stress and plant response

Stress factors, such as osmotic, ion toxicity, nutrient imbalance or soil pH alter the expression of several morphological, physiological and biochemical characteristics of plants. As the stress increases, plant growth is further restricted. Under severe stress conditions plants may die prematurely after germination or transplanting or can survive longer shriveling [11, 12].

Seed germination is often hindered and/or delayed when environmental stresses occur. Seedlings often fail to survive since in this stage of growth plants are the most vulnerable [13]. Plant growth is stunted affecting most of the vegetative characters, such as leaf number, size, shoot number, plant height etc. [14, 15]. Regarding the reproductive traits of the plants, salt stress can often induce an early flowering and abortion of flower buds [16, 17]. Furthermore, a significant overall reduction in yield can be observed in most of the plant species subjected to salt stress. Achieved yields are usually much lower than potential yields under normal growing conditions [18–20].

Plant growth in saline soils is usually affected because of the osmotic effect in the soil solution. High salt concentration increases the potential forces that hold water in the soil and makes it more difficult for plant roots to extract soil moisture. During dry periods, salt in soil solutions may be so concentrated as to kill plants by sucking water from them (exosmosis) [21]. Moreover, salt in the soil solution forces a plant to exert more energy to absorb water and to exclude salt from metabolically active sites. As salinity increases, plant growth is further restricted. A saline soil should be kept wet to dilute the salt concentration so as to cause the least salt hindrance to the growing plants. Also, plant growth in sodic/alkaline soils is affected due to high ESP throughout the profile, very low infiltration and hydraulic conductivity rates [22]. The exchangeable complex of alkaline soils is largely occupied by sodium ions which cause dispersion of soil due to the breakdown of aggregates forming a dense surface crust which greatly hinders seedling emergence due to low permeability of the soil to water and air. Poor drainage in such soils is due to a high water table which further restricts plant's ability to absorb water and nutrients in required amounts [23]. High pH results in reduced availability of some essential plant nutrients [24]. Accumulation of certain elements in plant parts at toxic levels may result in plant injury or reduced growth and even death in extreme cases. The most common toxic elements are sodium, molybdenum and boron. Selenium may also occur in toxic concentrations. Plant growth in degraded alkaline or solodic soils is largely due to poor drainage.

Crop species and varieties greatly vary regarding their response to salt stress (**Figures 1** and **2**). Many naturally occurring plants in salt-affected soils (halophytes) have certain specific structures and adaptation strategies, for example salt glands and salt hairs on their leaves [25, 26]. Detailed studies on salt glands in salt-tolerant plants, such as the halophyte kallar grass, *Leptochloa fusca*, showed the presence of enlarged cells protruding above the epidermis of both abaxial and adaxial surfaces of leaves and also on the exposed side of the leaf sheath [27]. These glands are associated with salt deposition (Na > K > Ca > Mg) on leaf surfaces. *Acanthus ilicifolius* and other crop species have salt glands on the adaxial leaf surface and studies have shown each gland to be surrounded by six collecting cells (salt-collecting cells) [28]. One of the most salt-tolerant plants, the halophytic wild rice, *Porteresia coarctata* has unicellular salt hairs on the adaxial surface of the leaves. Analysis of its leaf washing showed that Na and Cl were predominantly excreted, followed by K, Mg and Ca [29]. In other species such as *Puccinellia tenuifolia* the phenomenon of salt excretion has also been observed [30]. Moreover, some crop species have sunken stomata associated with the

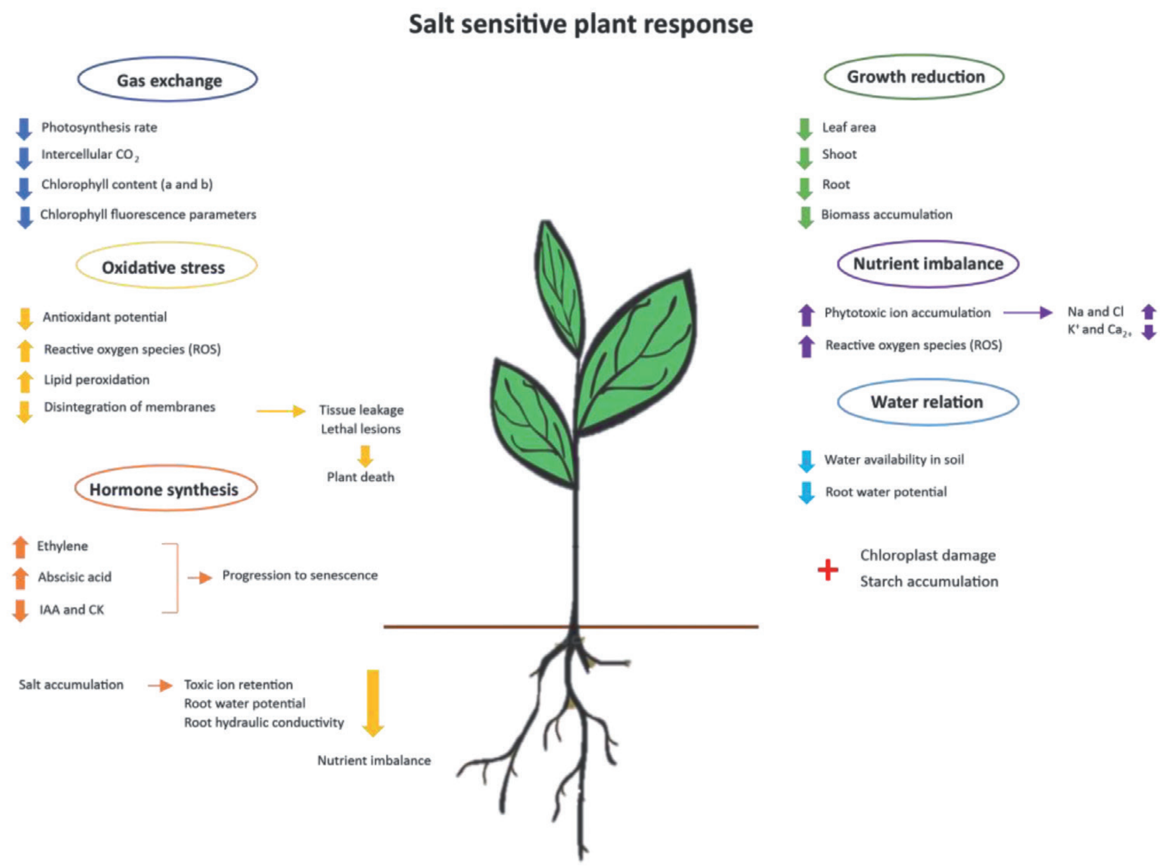

Figure 1.
The effect of salinity on salt-sensitive plants.

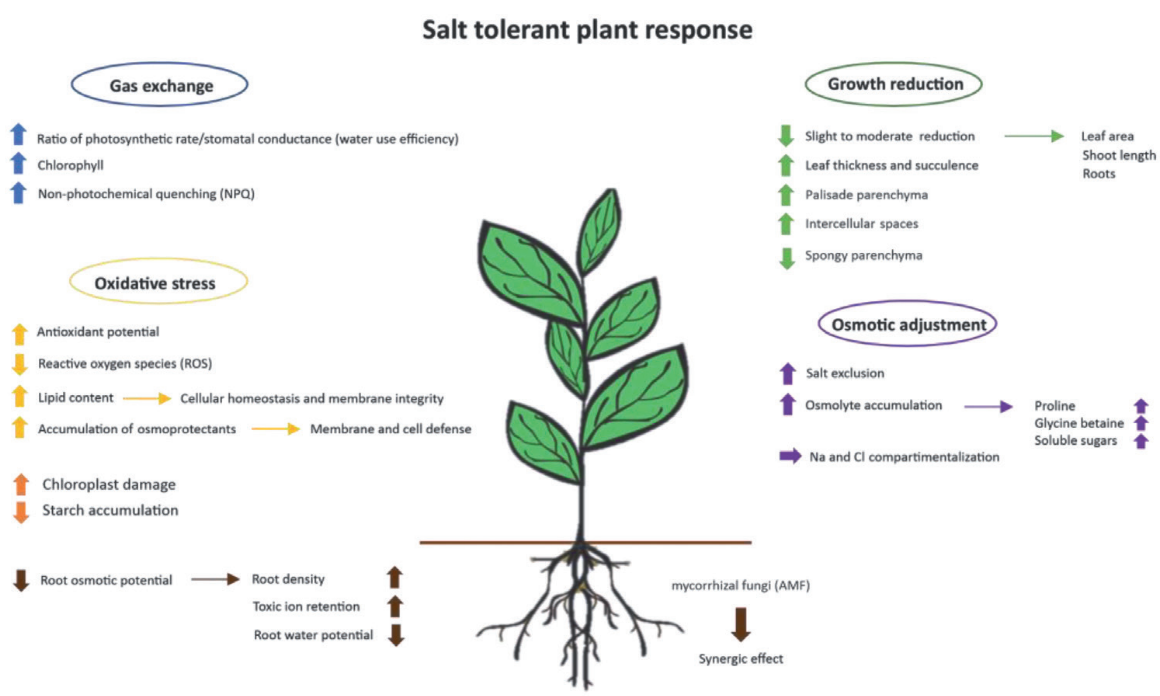

Figure 2.
The effect of salinity on salt-tolerant plants.

occurrence of high density of trichomes arising from the epidermis, as an adaptive mechanism to minimize water loss under stressful habitats [31].

Plants subjected to salt stress face the problem of reduced availability of water and response to changes in the processes related to maintenance of a favorable water balance [32, 33]. According to previous reports, the increase in salinity resulted in a decrease in transpiration in mustard [34], quinoa [35], wheat and pearl millet [36, 37], whereas leaf diffusive resistance (LDR) and leaf temperature increased. Higher LDR coupled with low transpiration might contribute to moisture conservation in plants under salt stress conditions [38].

Excessive salt in the root zone not only reduces the availability of water to plants, but their excessive absorption of salt increases the risk of ion toxicity and interference in the uptake of other essential nutrients [39]. Several reports indicate that increasing salinity and sodicity (Na content) decreases K ion concentration [40–42]. The antagonistic effect of both cations is well established. Tolerant varieties show a tendency to take up less Na while maintaining their K status.

Furthermore, plants growing at sublethal levels of salt stress may often appear greener due to increase in chlorophyll [43, 44]. Accumulation of certain amino acids, sugars and other osmotically active organic substances in response to salt stress are indications of altered nitrogen and carbohydrate metabolism. In this regard, it has been observed, for example, that two-week-old wheat plants doubled their amino acid content after 24 hours when subjected to electrolyte concentration (EC) of 22. Amino acids are very important components of plants, exhibiting various roles. Under abiotic stress conditions they can act as osmolytes, regulate the ion transport in the plant or regulate the stomatal opening and closure [45]. Besides, they can contribute to diverse enzyme synthesis improving plant abiotic stress tolerance through gene expression [46]. Among amino acids, glutamine (Glu), phenylalanine (Phe) and proline (Pro) proved to have significant roles in response to salt stress condition such as signaling precursors (Glu), building blocks of plant structure (Phe) and beneficial solutes (Pro). In this regard, previous research results show a considerable increase in glutamine, phenylamine and especially in proline content as a response to salt stress improving plant tolerance or indicating its sensitivity [39]. In general, the highest proline accumulation occurs in lamina followed by leaf sheath, stems or shoots and roots as observed in several plant species such as *Phaseolus sp*., *Portulaca sp.*, *Triticum sp.*, *Solanum lycopersicum* etc. **(Table 1)** [57–61]. Moderately tolerant barley varieties accumulated more proline than sensitive ones [62].

In wheat, water-soluble proteins increased in leaves in response to salinity [63]. Another example, such as rhodes grass, *Chloris gayana*, could be given for the increase of trichloroacetic acid and NaOH soluble proteins in response to salinity [64]. Enzymes are also influenced by change in plant water status as well as ionic imbalance [65, 66]. Decrease in (a) amylase activity with increase in salinity was observed in wheat and chickpea leaves after short term exposure to salt stress while activity of invertase and other enzymes of carbohydrate metabolism significantly increased [67, 68]. Nitrate reductase activity may also decrease with increase in stress level in many species [69, 70]. Tolerant varieties of pearl millet showed a tendency to maintain their nitrate-reductase activity [71]. Polyphenol oxidase activity has been reported to be higher in sensitive varieties of wheat, barley and rice [72–74].

Due to their occasional or constants exposure to harsh, unfavorable environmental conditions, plants developed a series of detoxification mechanisms to be able to

Plant species	Amino acids	Increase of amino acids	Salt concentration (NaCl)	References
Triticum aestivum	Glutamine	1.33-fold 2.02-fold	150 mM 300 mM	[47]
Anacardium occidentale	Glutamine	1.37-fold	100 mM	[48]
Oryza sativa L. cv. Kinuhikari	Glutamine	1.5-fold	150 mM	[49]
Helianthus annuus L. cv. SH222	Glutamine	6.2-fold	126 mM	[50]
Jatropha curcas L.	Phenylalanine	1.12-fold	150 mM	[51]
Salvia sp.	Phenylalanine	12–18-fold	100 mM	[52]
Solanum nigrum	Phenylalanine	23-fold	150 mM	[53]
Zea mays L.	Phenylalanine	2.26-fold	150 mM	[54]
T. aestivum	Proline	2.26-fold 19.29-fold	150 mM 300 mM	[62]
Solanum tuberosum L.	Proline	3.4-fold	250 mM	[54]
Hordeum vulgare	Proline	20–31-fold	300 mM	[55]
A. occidentale	Proline	22-fold	100 mM	[48]
Solanum lycopersicum L.	Proline	3-fold	60 mM	[61]
Portulaca halimoides	Proline	5.66-fold	400 mM	[59]
Phaseolus vulgaris L.	Proline	2.6-fold	150 mM	[56]

Table 1.
Prominent amino acids and their changes in responses to salt stress.

maintain their growth and alleviate potential damages caused by 'reactive oxygen species' (ROS) - at cellular level [75].

Oxidative damage in plants often occurs as a secondary effect of different harmful environmental conditions such as drought, salinity, cold, heat, or heavy metals in the soil. Under these conditions, the level of ROS can largely increase overwhelming plant defense systems, and thus inducing multiple deleterious effects at the cellular level. These effects are the result of the oxidation of membrane lipids, amino acid residues in proteins and the bases in DNA. In general, plants respond to an increase in ROS by activating enzymatic or non-enzymatic antioxidant processes to overcome ROS accumulation. Among them, malondialdehyde (MDA), a lipid peroxidation product is considered a reliable oxidative stress marker not only in plants but in animals also, which is generated by the oxidation of membrane lipids [76]. Several scientific reports show an increase of MDA levels in response to abiotic stresses in various plant species: rice, *Calendula*, *Miscanthus*, basil, *Solanum* and many others [77–81].

Moreover, phenolic compounds are known to have multiple roles in plants; some of them being part of the structural component of cell walls, while others are involved in growth regulation and developmental processes or the activation of defense mechanisms against biotic and abiotic stresses. Several reports also describe the mediatizing effects of antioxidant properties of many phenolic compounds on plant responses to salinity and drought showing an increase in their content under high salinity and water deficit conditions [82, 83].

Flavonoids, the most complex subclass of phenolic compounds are also involved in a wide-range of environmental interactions. The biosynthesis of flavonoids in plants is upregulated not only by UV-radiation but also in response to diverse biotic and abiotic stresses, from the depletion of mineral nutrients to salinity, cold or drought [84]. Previous studies suggest that flavonoid contents increase in plants when subjected to abiotic stress conditions and the accumulation of these compounds is tightly coupled with the intensity of the applied stress [85–87].

Ascorbic acid (Vitamin C) is one of the most powerful, water-soluble antioxidants as a scavenger ROS produced by most eukaryotic organisms. It occurs in all plant tissues, but mostly in the chloroplast, in mature leaves where these are fully developed and the chlorophyll levels are also the highest. It is considered the most important ROS detoxifying compound due to its ability to donate electrons in a number of enzymatic and non-enzymatic reactions [88].

Beside the above-mentioned compounds, α-tocopherols (vitamin E) are another family of antioxidants that can be found in all parts of the plants. They are the most biologically active and predominant antioxidants in the chloroplast membranes, and are mainly responsible for its protection against oxidative damages [89].

Antioxidant enzymes such as superoxide dismutase (SOD), several peroxidases (POD), catalase (CAT) and glutathione reductase (GR) play a crucial role as ROS scavengers in defense mechanisms against abiotic stresses. They are responsible for the maintenance of the proper redox equilibrium in plant cells [90]. Enzymatic activities have been studied in different plant species including both crop species and ornamental plants [91–93]. The results revealed that water stress, in general, led to a continuous increase of several antioxidant enzyme activities. In maize, for example, significant enhancements in the activities of several antioxidant enzymes (superoxide dismutase-SOD, catalase-CAT, ascorbate peroxidase-APX, and glutathione reductase-GR) occurred after 12 h of treatment showing an increase of 21%, 52% and 33% and 38% as compared to the control. It was also noticed that after 24 h of water stress treatment, the activities of the antioxidant enzymes showed a tendency to decrease when compared to the 12 h treatment [94].

3. Mechanism of drought resistance

Over the centuries plants have been exposed to different environmental conditions and applied diverse adaptation strategies to be able to cope with these challenges. Water deficit in plants occurs when the transpiration rate exceeds water uptake. Such water deficit is usual in most plants as a component of some developmental processes [95], but cellular water deficit can cause harmful changes in cell volume and membrane shape, disruption of water potential, decreased turgor pressure, or disruption of membranes. A total loss of free water will result in dehydration and plant loss. Plant responses to water deficit (**Figure 3**) primarily depend on the species and genotype, but also on the length and quantity of water loss, and the age and developmental stage of the plants. Among the complex plant mechanisms and regulatory networks for drought, osmotic adjustment plays an important role in water deficit avoidance, by lowering the water potential of the cells to support water uptake and maintain turgor. At molecular level, the accumulation of mRNA during water deficit may indicate gene induction, but in order to obtain a fully functional gene product, other additional mechanisms such as translational regulation and posttranslational modification may be required. In general, plants respond to water deficit by employing some basic mechanisms to avoid water loss, protect the cellular machinery and repair damage [96, 97].

Susceptibility to drought can occur during the early vegetative seedling stage, during the period of panicle development prior to flowering, or/and during the post flowering stage of grain development [97]. Susceptibility during post-flowering

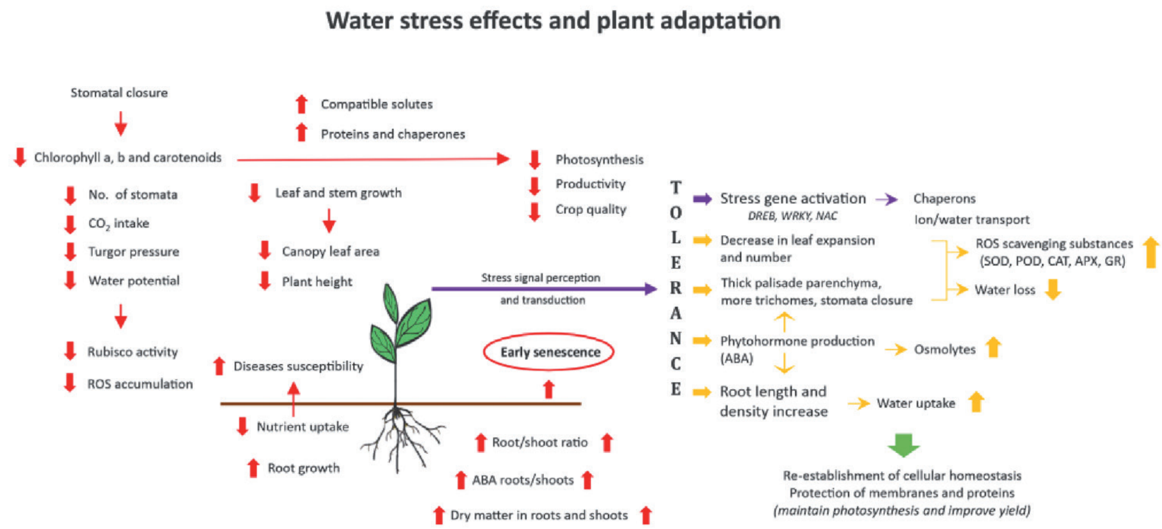

Figure 3.
Schematic representation of water stress effects and plant adaptation.

stage is characterized by reduced seed size and grain yield, pre-mature plant and leaf senescence and increased stalk lodging [98]. Terminal post flowering drought results in an abbreviated period of grain development and therefore reduces seed size [97, 99]. Genotypes with a high rate and reduced duration of grain filling may be more tolerant under terminal post flowering conditions [100].

Identification of critical stages of crop growth, those at which a crop is more severely affected by drought and more particularly its response to stress, if any, is important to be known to be able to understand the mechanism of drought resistance. This knowledge could further help to develop appropriate methodology for developing drought-resistant varieties. The usual mechanisms are as follows:

1. *Drought escape*: is a strategy applied by plants in early maturing crops/crop varieties to complete the critical stages of crop growth before severe deficit occurs, focusing more on flowering and reproduction instead of developing new shoots and increasing leaf area [101]. Early growth vigor may enable a variety to establish a good plant stand rather quickly while the moisture supply is suitable. Thus, crops or crop varieties applying this strategy can escape the adverse effects of drought and perform relatively better. Many indeterminate crops respond to reirrigation by resuming their growth and still perform better [102].

2. *Avoidance*: Drought avoidance is an alternate mechanism by which plants can maintain positive tissue water relations even under limited soil moisture conditions. Mechanisms of drought avoidance typically involve water conservation at the whole plant level. Avoidance is accomplished by decreasing water loss from the shoot or by more efficiently extracting moisture from the soil [103]. Many crop varieties/crops with deep as well as dense root system may be able to maintain minimal water uptake from soil to avoid internal stress, at least during the initial stages [104]. High varietal resistance to water loss has also been observed in a few cases, for example, in wheat, rice the amount of epicuticular wax deposition is reportedly associated with water loss [105, 106]. Previous findings suggest that different species such as *Catharanthus roseus, Sorghum sp.* and *Oryza sativa* reduced transpiration rate by as much as 44 to 82% due to water stress [107–109].

3. *Tolerance:* Drought tolerance is defined in a number of ways, namely, the performance per se, the stability of performance under drought and last but not least specific physiological or morphological traits that are believed to be associated with the expression of drought tolerance. The mechanisms responsible for drought tolerance are functioning at tissue or cellular level [99]. When the tissue desiccates, these mechanisms are activated to stabilize and protect the cellular and metabolic integrity of the plant. Crop varieties may differ in their ability to thrive under drought conditions. This has been demonstrated through various test regarding physio-morphological and biochemical traits including desiccation survival, heat tolerance, osmolytes, ion homeostasis etc. [110–115].

4. *Recovery*: Drought stress conditions may vary in duration, but when rainfall does commence the ability of a genotype (or crop variety) to recover quickly and resume active growth is an important character. In rice, recovery capacity from drought is strongly related with characters such as vegetative growth vigor, high tillering ability, shallow root system and rather long growth duration [116]. Similar characters have been observed in different annual and perennial species, in wheat, sugarcane etc. [117–119]

3.1 Assessment of drought resistance and plant traits associated with drought resistance

Drought resistance of an annual crop plant can at present be assessed for agronomic purposes only on the basis of yield [120]. Few of the many screening tests proposed have been adopted by breeders.

Several plant traits, such as dehydration avoidance and dehydration tolerance have been found to be positively associated with yield under stress across genotypes of wheat and barley [121]. Leaf rolling, root system, pubescence of aerial organs, reflectance of incoming solar radiation, increased heat dissipation through decreased boundary layer resistance at the organ level (narrow leaves, awns), etc., are the main traits that contribute to dehydration avoidance. In nature, a better balance is associated with a higher proportion of energy dissipated as latent heat and hence a lower canopy temperature. Dehydration tolerance related to cellular and subcellular processes can be readily assessed by measurements of membrane stability with the electrolyte leakage test [122]. It is difficult, however, to relate this type of test to plant production. Nevertheless, visual scores on morphological traits, such as leaf rolling, root habit, etc., and/or observations recorded through other methods, if any, in relation to the above-mentioned characters should invariably be used as an indirect measurement of drought resistance for practicing selection in a breeding programme.

In sorghum, the 'stay-green' character is reportedly associated with post-flowering drought tolerance. Stay-green is characterized as resistance to premature leaf and stalk death induced by post-flowering drought. Resistance to premature leaf and stalk death is thought to increase the potential period of grain development and thereby stabilizing the expression of seed weight [123]. Sorghum lines with high levels of stay-green have been identified and are being used in some breeding programs [124–126].

3.2 Genetics of plant traits associated with drought resistance

A variety of adaptive plant characteristics related to environmental stress have been investigated and were shown to exhibit genetic variation. The variability of traits extends to the physiological, morphological and chemical characteristics of the plants. These three groups of traits are the most representative and useful markers for stress tolerance identification. Drought stress can cause many changes in the physiological traits, affecting the capability of plants to maintain high level of leaf-water potential under water deficit conditions, the osmotic adjustment and last but not least the capability of plants to recover after short or long-term rehydration. The regulation of photosynthesis, by stomatal closure and the stability of cellular membranes and its maintenance are crucial for plants to tolerate stress conditions. Osmolytes, such as Pro, glycine betaine and soluble sugars also play an important role in osmotic adjustment under various stress conditions, where accumulation may greatly vary among species. Morphological or phenotypic characters are considered important in the adaptation of plant to stress conditions, their responses being reflected and becoming quantifiable through root growth and density, leaf number size and canopy area, leaf orientation, stem or shoot length and number, flower development (number and fertility, seedling survival or any other trait specific for every species (leaf succulence, pubescence etc.) [127–133].

'Stay-green' or the capacity of green color retaining for longer time of the leaves after flowering is a desirable attribute for crop production. Sorghum genetic studies of 'stay-green' have generally indicated a complex pattern of inheritance. It has been reported that both dominant and recessive expression were strongly influenced by the environment. Previous reports reveled the inheritance of stay-green in a set of recombinant inbred lines of sorghum [134]. Due to a quantitative trait loci (QTL) mapping in sorghum for the extension of photosynthetic period 13 regions of the genome were identified and associated with the stay-green phenotype of post-flowering drought adaptation [135]. Two QTLs were successfully identified as the ones influencing yield and 'stay-green' capacity under post-flowering drought conditions. The same loci were also linked to yield under successful irrigation conditions indicating the pleiotropic nature of these tolerance loci on yield under favorable environmental conditions [136]. Similarly, the QTL mapping results suggested many other loci that were linked to the rate and duration of yield development [137]. The findings also revealed that high yield and short grain development were associated with instability of yield performance under water paucity [138].

It may be noted that associations between markers and QTL were somewhat variable across testing environments. This highlights the importance of multi-environment testing when evaluating drought tolerance.

Similar studies have been carried out in maze, where 15 green-leaf-area related QTLs were detected thus identifying the most important genomic region responsible for maintaining green leaf area at the final developmental stage of maize [139].

However, the current screening and breeding techniques allow to explore the genetic basis for various plants and identify diverse traits which help the plants to perform under stress conditions, high yield performance, good quality and stress resistance remains the eternal flame for crop breeders. These desirable crop production traits and their transmission from one genotype to another will remain attractive and unexplored [140].

In this regard, selection for drought and salt resistance will therefore continue to be primarily based on yield assessment under stress conditions [141].

4. Selection and breeding for salt and drought resistant varieties

Salt tolerance thresholds are usually set based on the relative crop yield at defined stress levels of salt stress. Besides, the biological traits of the plant are also of a great importance in the selection process since, these characters are the summary of genetic and environmental effects upon plant growth as a result of physiological processes, effects which confer salinity tolerance. Therefore, two primary selection criteria can be established for plant selections follow:

1. Seed germination capacity and seedling survival: Seed germination and seedling development, are the very early stages of plant development which are critical. Therefore, plants that can cope with salt stress conditions in these stages of their life cycle should be the prime requisite in the selection process for salt tolerance. Various crops and genotypes that even fail to establish themselves under defined stress conditions cannot be expected to do any better at a later stage of their growth.

2. Yield: Varieties highly tolerant to salinity are those that exhibit minimum reduction in relative economic yield with per unit increase in stress. The slope of regression of yield against stress gives a fairly reliable estimate of salt tolerance of a crop/genotype. This is by far the best index for identification and screening of salt-tolerant genotypes.

A number of other plant attributes, namely Na and K content in shoots/leaves, Na/K ratio, pH of the cell sap, proline content and enzyme response may also have some potential use. The only limitation to their practical use so far however, is, that the differential genotypic response observed in various crops cannot always be explained on the basis of these data. For this reason, the use of physiological characters is highly recommended to obtain more reliable information and select potential candidates for future saline agriculture.

The first step that should be taken to develop drought and salt resistant varieties is to identify drought-resistance QTLs, which are essential to set valuable candidates for crop breeding. Regarding the selection criteria, there are several promising traits to be targeted in breeding programmes as follows:

1. Root architecture – which plays an important role in drought avoidance of crops. Transcriptomic differences between deep and shallow rooting systems strongly influences the ATP synthesis. Such traits can significantly improve abiotic stress resistance in crops by introducing or manipulating a single gene;

2. ABA-synthesis which can improve drought resistance even at seedling stage in different crops;

3. Direct-deep-seeding tolerance of different species which could significantly contribute to water saving and drought resistance, for example in rice production;

4. Yield capacity under stress conditions;

5. Exploitation or domestication of wild relatives (halophytes) of crop plants. Interspecific hybridization has an important role in the improvement of crop plant performance under abiotic stress conditions.

In the evaluation process for plant tolerance to salt and drought stress, it is important to take into consideration all the three groups of traits (physiological, morphological and chemical characters) and evaluate plant responses as a whole. Due to great genetic variation of the plants, in some cases it is not enough to solely analyze the physiological, chemical or morphological profile since they are interconnected.

5. Conclusions

Recently, several research have been carried out to depict the complex underlying mechanisms (physiological, morphological and chemical) that control abiotic stress responses in crop plants. However, the exact genes, and their activation, which control plant defense mechanisms are still unclear. Tolerance against abiotic stresses in different crop plants has been improved by the application of transgenic technology of reactive oxygen species components, but future research studies are still needed to determine and increase yield performance and quality under harsh environmental conditions. Genetic improvement of crops needs to identify further genetic variations that allow plants to increase their tolerance against the upcoming abiotic stress levels than the ones we are facing today. It has to employ new tools to analyze the genetic, physiological and molecular basis of stress tolerance and to identify genes associated with improved resistance and integrate them into practical breeding to develop "smart" crop varieties which require lower input and provide high yield.

Conflict of interest

The authors declare no conflict of interest.

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