We are IntechOpen, the world’s leading publisher of Open Access books
Built by scientists, for scientists

5,500
Open access books available

136,000
International authors and editors

170M
Downloads

154
Countries delivered to

TOP 1%
Our authors are among the most cited scientists

12.2%
Contributors from top 500 universities

WEB OF SCIENCE™
Selection of our books indexed in the Book Citation Index in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com
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 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) [47–51]. Moderately tolerant barley varieties accumulated more proline than sensitive ones [52].

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 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 mediating 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].

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

| Plant species | Amino acids | Increase of amino acids | Salt concentration (NaCl) | References |
|---------------|-------------|-------------------------|---------------------------|------------|
| *Triticum aestivum* | Glutamine | 1.33-fold | 150 mM | [53] |
| *Anacardium occidentale* | Glutamine | 1.37-fold | 100 mM | [54] |
| *Oryza sativa* L. cv. Kinuhikari | Glutamine | 1.5-fold | 150 mM | [55] |
| *Helianthus annuus* L. cv. SH222 | Glutamine | 6.2-fold | 126 mM | [56] |
| *Jatropha curcas* L. | Phenylalanine | 1.12-fold | 150 mM | [57] |
| *Salsola sp.* | Phenylalanine | 12–18-fold | 100 mM | [58] |
| *Solanum nigrum* | Phenylalanine | 23-fold | 150 mM | [59] |
| * Zea mays* L. | Phenylalanine | 2.26-fold | 150 mM | [60] |
| *T. aestivum* | Proline | 2.26-fold | 150 mM | [52] |
| *Solanum tuberosum* L. | Proline | 3.4-fold | 250 mM | [60] |
| *Hordeum vulgare* | Proline | 20–31-fold | 300 mM | [61] |
| *A. occidentale* | Proline | 22-fold | 100 mM | [54] |
| *Solanum lycopersicum* L. | Proline | 3-fold | 60 mM | [51] |
| *Portulaca halimoides* | Proline | 5.66-fold | 400 mM | [49] |
| *Phaseolus vulgaris* L. | Proline | 2.6-fold | 150 mM | [62] |
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...

![Figure 3](image.jpg)

**Figure 3.**
Schematic representation of water stress effects and plant adaptation.
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 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 vigour, 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 revealed 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.
References

[1] FAO statistical yearbook. Food and Agriculture Organization of the United Nations, Rome, 2013.

[2] Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, et al. Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plants. 2019;8:34. DOI:10.1046/j.1365-2745.2003.00806.

[3] Van Zandt PA, Tobler MA, Mouton E, Hasenstein KH, Mopper S. Positive and negative consequences of salinity stress for the growth and reproduction of the clonal plant, Iris hexagonal. Journal of Ecology. 2003;91:837–846. DOI: 10.1046/j.1365-2745.2003.00806.x

[4] Igboama WN, Ugwu NU. Laboratory Evaluation of the Impact of Contaminants on Soil Resistivity and the Consequent Effect on Plant’s Growth. Journal of Environmental Protection. 2016;7:12:1802.

[5] Hatzig SV, Nuppenau JN, Snowdon RJ, Schiessl S V. Drought stress has transgenerational effects on seeds and seedlings in winter oilseed rape (Brassica napus L.). BMC Plant Biology. 2018;18:297. DOI: 10.1186/s12870-018-1531-y

[6] Ma Y, Dias MC, Freitas H. Drought and salinity stress responses and microbe-induced tolerance in plants. Frontiers in Plant Science. 2020;11:1750.

[7] Bacher H, Zhu F, Gao T, Liu K, Dhatt B K, Awada T, Walia H. Wild emmer introgression alters root-to-shoot growth dynamics in durum wheat in response to water stress. Plant Physiology. 2021. DOI:10.1093/plphys/kiab292

[8] Mantri N, Patade V, Penna S, Ford R, Pang E. Abiotic Stress Responses in Plants: Present and Future. In: Ahmad P, Prasad M, editors. Abiotic Stress Responses in Plants. New York Springer, 2021. DOI:10.1007/978-1-4614-0634-1_1

[9] Scagel Carolyn F, Jungmin Lee. Salinity sensitivity and mycorrhizal responsiveness of polyphenolics in ‘Siam Queen’ basil grown in soilless substrate. Scientia Horticulturae. 2020;269:10934.

[10] Pedranzani H, Rodríguezrivera M, Gutiérrez M, Porcel R, Hause B, Ruizlozano JM. Arbuscular mycorrhizal symbiosis regulates physiology and performance of Digitaria eriantha plants subjected to abiotic stresses by modulating antioxidant and jasmonate levels. Mycorrhiza. 2016;26:141–152. DOI:10.1007/s00572-015-0653-4.

[11] Yadav S, Modi P, Dave A, Vijapura A, Patel D, Patel M. Effect of abiotic stress on crops. Sustainable Crop Production. 2020.

[12] Lauer J. What happens within the corn plant when drought occurs. Corn Agronomis. 2003;10:22:153-155

[13] Uçarlı C. Effects of Salinity on Seed Germination and Early Seedling Stage. In Abiotic Stress in Plants. IntechOpen; 2020.

[14] Zahra N, Raza ZA, Mahmood S. Effect of salinity stress on various growth and physiological attributes of two contrasting maize genotypes. Brazilian Archives of Biology and Technology. 2020;63.

[15] Isayenkov SV, Maathuis FJ. Plant salinity stress: many unanswered questions remain. Frontiers in Plant Science. 2019;10:80.

[16] Yuan F, Guo J, Shabala S, Wang B. Reproductive Physiology of Halophytes:
Vadez V, Rashmi M, Sindhu K, Muralidharan M, Pushpavalli R, Turner NC, ... Colmer TD. Large number of flowers and tertiary branches, and higher reproductive success increase yields under salt stress in chickpea. European Journal of Agronomy. 2012;41:42-51.

Rao ES, Kadirvel P, Symonds RC, Ebert AW. Relationship between survival and yield related traits in Solanum pimpinellifolium under salt stress. Euphytica. 2013;190:2:215-228.

He Y, Chen Y, Yu CL, Lu KX, Jiang QS, Fu JL, Wang GM, Jiang DA. Photosynthesis and yield traits in different soybean lines in response to salt stress. Photosynthetica. 2016;54:4:630-5.

Di Caterina R, Giuliani MM, Rotunno T, De Caro A, Flagella Z. Influence of salt stress on seed yield and oil quality of two sunflower hybrids. Annals of Applied Biology. 2007;151:2:145-154.

Augie MA, Adegbite MA. Salinity and Sodicity Status of the Floodplain Soils of Kebbi State, North Western, Nigeria. Asian Journal of Soil Science and Plant Nutrition. 2021;23-31.

Crescimanno G, Iovino M, Provenzano G. Influence of salinity and sodicity on soil structural and hydraulic characteristics. Soil Science Society of America Journal. 1995;59:6:1701-1708.

Xu X, Huang G, Sun C, Pereira LS, Ramos TB, Huang Q, Hao Y. Assessing the effects of water table depth on water use, soil salinity and wheat yield: Searching for a target depth for irrigated areas in the upper Yellow River basin. Agricultural water management. 2013;125:46-60.
Salt and Water Stress Responses in Plants
DOI: http://dx.doi.org/10.5772/intechopen.101072

[33] Hussain S, Khalid MF, Hussain M, Ali MA, Nawaz A, Zakir I, Fatima Z, Ahmad S. Role of micronutrients in salt stress tolerance to plants. In Plant nutrients and abiotic stress tolerance. 2018; Springer: Singapore: 363-376 p.

[34] Silva JV, Lacerda CFD, Costa PHAD, Enéas Filho J, Gomes Filho E, Prisco JT. Physiological responses of NaCl stressed cowpea plants grown in nutrient solution supplemented with CaCl2. Brazilian Journal of Plant Physiology. 2003;15:99-105.

[35] Huang J, Redmann RE. Physiological responses of canola and weld mustard to salinity and contrasting calcium supply. Journal of Plant Nutrition. 1995;18:9: 1931-1949.

[36] Razzaghi F, Ahmadi SH, Adolf VI, Jensen CR, Jacobsen SE, Andersen MN. Water relations and transpiration of quinoa (Chenopodium quinoa Willd.) under salinity and soil drying. Journal of Agronomy and Crop Science. 2011;197:5:348-360.

[37] Nicolas ME, Munns R, Samarakoon AB, Gifford RM. Elevated CO2 improves the growth of wheat under salinity. Functional Plant Biology. 1993;20:3:349-360.

[38] Yadav T, Kumar A, Yadav RK, Yadav G, Kumar R, Kushwaha M. Salicylic acid and thiourea mitigate the salinity and drought stress on physiological traits governing yield in pearl millet-wheat. Saudi Journal of Biological Sciences. 2020;27:8:2010-2017.

[39] Agrawal RL. Fundamentals of plant breeding and hybrid seed production. Science Publishers, Inc. 1998.

[40] Silveira JAG, Araújo SAM, Lima JPMS, Viégas RA. Roots and leaves display contrasting osmotic adjustment mechanisms in response to NaCl-salinity in Atriplex nummularia.

Environmental and Experimental Botany. 2009;66:1-8.

[41] Mahmood K. Salinity tolerance in barley (Hordeum vulgare L.): effects of varying NaCl, K+/Na+ and NaHCO3 levels on cultivars differing in tolerance. Pakistan Journal of Botany. 2011;43:3: 1651-1654.

[42] QianYL, Engelke MC, Foster MJV. Salinity effects on zoysiagrass cultivars and experimental lines. Crop Science. 2000;40:2:488-492.

[43] Gulzar S, Khan MA, Ungar IA. Effects of salinity on growth, ionic content, and plant–water status of Aeluropus lagopoides. Communications in Soil Science and Plant Analysis. 2003;34:11-12:1657-1668.

[44] Jamil M, Rehman S, Rha ES. Response of growth, PSII photochemistry, and chlorophyll content to salt stress in four brassica species. Life Science Journal 2014;11:3:139-145.

[45] Zhen-hua ZHANG, Qiang LIU, Hai-xing SONG, Xiang-min RONG, Ismail AM. Responses of different rice (Oryza sativa L.) genotypes to salt stress and relation to carbohydrate metabolism and chlorophyll content. African Journal of Agricultural Research. 2012;7:1:19-27.

[46] Rai, V. Role of Amino Acids in Plant Responses to Stresses. Biologia Plantarum. 45: 481-487 (2002). DOI:10.1023/A:1022308229759

[47] Khan N, Ali S, Zandi P, Mehmood A, Ullah S, Ikram M, Ismail MA, Babar M. Role of sugars, amino acids and organic acids in improving plant abiotic stress tolerance. Pakistan Journal of Botany. 2020;52:2:355-63.

[48] Morosan M, Al Hassan M, Naranjo MA, López-Gresa MP, Boscau M, Vicente O. Comparative
analysis of drought responses in *Phaseolus vulgaris* (common bean) and *P. coccineus* (runner bean) cultivars. EuroBiotech Journal 2017;1:247-52.

[49] Borsai O, Hassan MA, Negrușier C, Raigón MD, Boscaiu M, Sestraș RE, Vicente O. Responses to salt stress in Portulaca: Insight into its tolerance mechanisms. Plants. 2020;9:12:1660.

[50] Poustini K, Siosemardeh A, Ranjbar M. Proline accumulation as a response to salt stress in 30 wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance. Genetic Resources and Crop Evolution. 2007 Aug;54:5:925-34.

[51] De la Torre-González A, Montesinos-Pereira D, Blasco B, Ruiz JM. Influence of the proline metabolism and glycine betaine on tolerance to salt stress in tomato (*Solanum lycopersicum* L.) commercial genotypes. Journal of Plant Physiology. 2018;231:329-36.

[52] Agami RA. Applications of ascorbic acid or proline increase resistance to salt stress in barley seedlings. Biologia Plantarum. 2014;58:2:341-7.

[53] Wang ZQ, Yuan YZ, Ou JQ, Lin QH, Zhang CF. Glutamine synthetase and glutamate dehydrogenase contribute differentially to proline accumulation in leaves of wheat (*Triticum aestivum*) seedlings exposed to different salinity. Journal of Plant Physiology. 2007;164:6:695-701.

[54] Silveira JA, de Almeida Viégas R, da Rocha IM, Moreira AC, de Azevedo Moreira R, Oliveira JT. Proline accumulation and glutamine synthetase activity are increased by salt-induced proteolysis in cashew leaves. Journal of Plant Physiology. 2003;160:2:115-23.

[55] Hoshida H, Tanaka Y, Hibino T, Hayashi Y, Tanaka A, Takabe T, Takabe T. Enhanced tolerance to salt stress in transgenic rice that overexpresses chloroplast glutamine synthetase. Plant Molecular Biology. 2000;43:1:103-11.

[56] Santos C, Pereira A, Pereira S, Teixeira J. Regulation of glutamine synthetase expression in sunflower cells exposed to salt and osmotic stress. Scientia Horticulturae. 2004;103:1:101-11.

[57] Gao S, Ouyang C, Wang S, Xu Y, Tang L, Chen F. Effects of salt stress on growth, antioxidant enzyme and phenylalanine ammonia-lyase activities in *Jatropha curcas* L. seedlings. Plant, Soil and Environment. 2008;54:9:374-81.

[58] Valifard M, Mohsenzadeh S, Niazi A, Moghadam A. Phenylalanine ammonia lyase isolation and functional analysis of phenylpropanoid pathway under salinity stress in 'Salvia' species. Australian Journal of Crop Science. 2015;9:7:656-65.

[59] Jaarsma R, de Vries RS, de Boer AH. Effect of salt stress on growth, Na+ accumulation and proline metabolism in potato (*Solanum tuberosum*) cultivars. PloS One. 2013;8:3:e60183.

[60] Gholizadeh A, Kohnehrouz BB. Activation of phenylalanine ammonia lyase as a key component of the antioxidative system of salt-challenged maize leaves. Brazilian Journal of Plant Physiology. 2010;22:217-23.

[61] Sanada Y, Ueda H, Kuribayashi K, Andoh T, Hayashi F, Tamai N, Wada K. Novel light-dark change of proline levels in halophyte (*Mesembryanthemum crystallinum*) and glycophytes (*Hordeum vulgare* L. and *Triticum aestivum* L.) leaves and roots under salt stress. Plant and Cell Physiology. 1995;36:6:965-70.

[62] Arteaga S, Yabor L, Díez MJ, Prohens J, Boscaiu M, Vicente O. The
use of proline in screening for tolerance to drought and salinity in common bean (*Phaseolus vulgaris* L.) genotypes. Agronomy. 2020;10:6:817.

[63] Kerepesi I, Galiba G. Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. Crop Science. 2000;40:2:482-487.

[64] Ortega L, Fry SC, Taleisnik E. Why are *Chloris gayana* leaves shorter in salt-affected plants? Analyses in the elongation zone. Journal of Experimental Botany. 2006;57:14:3945-3952.

[65] Nandakumar MP, Shen J, Raman B, Marten MR. Solubilization of trichloroacetic acid (TCA) precipitated microbial proteins via NaOH for two-dimensional electrophoresis. Journal of Proteome Research. 2003;2:1:89-93. DOI: 10.1021/pr025541x. PMID: 12643547.

[66] Zhang M, Fang Y, Ji Y, Jiang Z, Wang L. Effects of salt stress on ion content, antioxidant enzymes and protein profile in different tissues of *Broussonetia papyrifera*. South African Journal of Botany. 2013;85:1-9.

[67] Mandhania S, Madan S, Sawhney V. Antioxidant defense mechanism under salt stress in wheat seedlings. Biologia Plantarum. 2006;50:2:227-231.

[68] Kaur S, Gupta AK, Kaur N. Gibberellin A3 reverses the effect of salt stress in chickpea (*Cicer arietinum* L.) seedlings by enhancing amylase activity and mobilization of starch in cotyledons. Plant Growth Regulation. 1998;26:2:85-90.

[69] Rohilla P, Yadav JP. Acute salt stress differentially modulates nitrate reductase expression in contrasting salt responsive rice cultivars. Protoplasma. 2019;256:5:1267-1278.

[70] Khan MG. Effect of salt stress on nitrate reductase activity in some leguminous crops. Indian Journal of Plant Physiology. 1994;37:3:185-187.

[71] Sharma PC, Gill KS. Effect of salinity on yield and ion distribution in pearl millet genotypes. Arid Land Research and Management. 1992;6:3:253-260.

[72] Aly AAEH, Maraei RW, Aldrussi I. Changes in peroxidase and polyphenol oxidase activity and transcript levels of related genes in two Egyptian bread wheat cultivars (*Triticum aestivum* L.) affected by gamma irradiation and salinity stress. Bangladesh Journal of Botany. 2019;48:1:177-186.

[73] Özmen AD, Özdemir F, Türkan I. Effects of paclobutrazol on response of two barley cultivars to salt stress. Biologia Plantarum. 2003;4:2:263-268.

[74] Akhtar W, Mahmood T. Response of rice polyphenol oxidase promoter to drought and salt stress. Pakistan Journal of Botany. 2017;49:1:21-23.

[75] Plesa IM, González-Orenga S, Al Hassan M, Sestras AF, Vicente O, Prohens J, Sestras RE, Boscaiu M. Effects of drought and salinity on European Larch (*Larix decidua* Mill.) seedlings. Forests. 2018;9:6:320.

[76] Rasel M, Tahjib-Ul-Arif M, Hossain MA, Sayed MA, Hassan L. Discerning of rice landraces (*Oryza sativa* L.) for morpho-physiological, antioxidant enzyme activity, and molecular markers’ responses to induced salt stress at the seedling stage. Journal of Plant Growth Regulation. 2020;39:1:41-59.

[77] Baniasadi F, Saffari VR, Moud AA. Physiological and growth responses of *Calendula officinalis* L. plants to the interaction effects of polyamines and salt stress. Scientia Horticulturae. 2018;234:312-7.
Miscanthus NAC transcription factor MINAC12 positively mediates abiotic stress tolerance in transgenic Arabidopsis. Plant Science. 2018;277:229-41.

[80] Brenez M, Pérez J, González-Orenga S, Solana A, Boscaiu M, Prohens J, Plazas M, Fita A, Vicente O. Comparative studies on the physiological and biochemical responses to salt stress of eggplant (Solanum melongena) and its rootstock S. torvum. Agriculture. 2020;10:8:328.

[81] Caliskan O, Radusiene J, Temizel KE, Staunis Z, Cirak C, Kurt D, Odabas MS. The effects of salt and drought stress on phenolic accumulation in greenhouse-grown Hypericum pruinatum. Italian Journal of Agronomy. 2017;12:3.

[82] Rossi L, Borghi M, Francini A, Lin X, Xie DY, Sebastiani L. Salt stress induces differential regulation of the phenylpropanoid pathway in Olea europaea cultivars Frantoio (salt-tolerant) and Leccino (salt-sensitive). Journal of Plant Physiology. 2016;204:8-15.

[83] Attia H, Al-Yasi H, Alamer K, Esmat F, Hassan F, Elshazly S, Hessini K. Induced anti-oxidation efficiency and others by salt stress in Rosa damascena. Miller. Scientia Horticulturae. 2020;274:109681.

[84] Cetinkaya H, Kulak M, Karaman M, Karaman HS, Kocer F. Flavonoid accumulation behavior in response to the abiotic stress: can a uniform mechanism be illustrated for all plants.

Flavonoids-From Biosynthesis to Human Health. 2017;151-65.

[85] Shah A, Smith DL. Flavonoids in agriculture: Chemistry and roles in, biotic and abiotic stress responses, and microbial associations. Agronomy. 2020;10:8:1209.

[86] Di Ferdinando M, Brunetti C, Fini A, Tattini M. Flavonoids as antioxidants in plants under abiotic stresses. Abiotic stress responses in plants. 2012;159-79.

[87] Davies KM, Albert NW, Zhou Y, Schwinn KE. Functions of flavonoid and betalain pigments in abiotic stress tolerance in plants. Annual Plant Reviews Online. 2018;21-62.

[88] Pehlivan FE. Vitamin C: An antioxidant agent. Vitamin C. 2017;2:23-35.

[89] Muñoz P, Munné-Bosch S. Vitamin E in plants: biosynthesis, transport, and function. Trends in Plant Science. 2019;24:11:1040-51.

[90] Dietz KJ. Redox-dependent regulation, redox control and oxidative damage in plant cells subjected to abiotic stress. In Plant Stress Tolerance. Humana Press; 2010. 57-70 p.

[91] Kusvuran S, Kiran S, Ellialtioglu SS. Antioxidant enzyme activities and abiotic stress tolerance relationship in vegetable crops. Abiotic and biotic stress in plants-recent advances and future perspectives. 1st ed. Croatia: InTech; 2016. 481-503 p.

[92] You J, Chan Z. ROS regulation during abiotic stress responses in crop plants. Frontiers in Plant Science. 2015;6:1092.

[93] Hao Z, Wang X, Zong Y, Wen S, Cheng Y, Li H. Enzymatic activity and functional analysis under multiple abiotic stress conditions of a
dehydroascorbate reductase gene derived from *Liriodendron Chinense*. Environmental and Experimental Botany. 2019;167:103850.

[94] Jiang M, Zhang J. Water stress-induced abscisic acid accumulation triggers the increased generation of reactive oxygen species and up-regulates the activities of antioxidant enzymes in maize leaves. Journal of Experimental Botany. 2002;53:379:2401-10.

[95] Bray EA. Plant responses to water deficit. Trends in Plant Science. 1997;2:2:48-54.

[96] Wang W, Vinocur B, Altman A. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta. 2003;218:1:1-4.

[97] Metz J, Annighöfer P, Schall P, Zimmermann J, Kahl T, Schulze ED, Ammer C. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. Global Change Biology. 2016;22:2:903-20.

[98] Sanjari S, Shobbar ZS, Ghanati F, Afshari-Bebahanizadeh S, Farajpour M, Jokar M, Khazaei A, Shahbazi M. Molecular, chemical, and physiological analyses of sorghum leaf wax under post-flowering drought stress. Plant Physiology and Biochemistry. 2021;159:383-91.

[99] Tuinstra MR, Grote EM, Goldsborough PB, Ejeta G. Genetic analysis of post-flowering drought tolerance and components of grain development in *Sorghum bicolor* L. Moench. Molecular Breeding. 1997;36:439-48.

[100] Shavrukov Y, Kurishbayev A, Jatayev S, Shividenko V, Zotova L, Koekemoer F, de Groot S, Soole K, Langridge P. Early flowering as a drought escape mechanism in plants: How can it aid wheat production?. Frontiers in Plant Science. 2017;8:1950.

[101] Kooyers NJ. The evolution of drought escape and avoidance in natural herbaceous populations. Plant Science. 2015;234:155-62.

[102] Xu Z, Zhou G, Shimizu H. Plant responses to drought and rewatering. Plant signaling & behavior. 2010;5:6:649-54.

[103] Franks SJ. Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica rapa*. New Phytologist. 2011;190:1:249-57.

[104] Aroca R, Porcel R, Ruiz-Lozano JM. Regulation of root water uptake under abiotic stress conditions. Journal of Experimental Botany. 2012;63:1:43-57.

[105] Willick IR, Lahlali R, Vijayan P, Muir D, Karunakaran C, Tanino KK. Wheat flag leaf epicuticular wax morphology and composition in response to moderate drought stress are revealed by SEM, FTIR-ATR and synchrotron X-ray spectroscopy. Physiologia Plantarum. 2018;162:3:316-32.

[106] Zhu X, Xiong L. Putative megaenzyme DW A1 plays essential roles in drought resistance by regulating stress-induced wax deposition in rice. Proceedings of the National Academy of Sciences. 2013;110(44):17790-5.

[107] Jaleel CA, Gopi R, Sankar B, Gomathinayagam M, Panneerselvam R. Differential responses in water use efficiency in two varieties of *Catharanthus roseus* under drought stress. Comptes Rendus Biologies. 2008;331:1:42-7.

[108] Tsuji W, Ali ME, Inanaga S, Sugimoto Y. Growth and gas exchange of three sorghum cultivars under drought stress. Biologia Plantarum. 2003;46:4:583-7.

[109] Xiong J, Zhang L, Fu G, Yang Y, Zhu C, Tao L. Drought-induced proline
accumulation is uninvolved with increased nitric oxide, which alleviates drought stress by decreasing transpiration in rice. Journal of Plant Research. 2012;125:1:155-64.

[110] Gomez SM, Kumar SS, Jeyaprakash P, Suresh R, Biji KR, Boopathi NM, Price AH, Babu RC. Mapping QTLs linked to physio-morphological and plant production traits under drought stress in rice (Oryza sativa L.) in the target environment. American Journal of Biochemistry and Biotechnology. 2006;2:4:161-9.

[111] Khadka K, Earl HJ, Raizada MN, Navabi A. A physio-morphological trait-based approach for breeding drought tolerant wheat. Frontiers in Plant Science. 2020;11:715.

[112] Akman H, Zhang C, Ejeta G. Physio-morphological, biochemical, and anatomical traits of drought-tolerant and susceptible sorghum cultivars under pre- and post-anthesis drought. Physiologia Plantarum. 2021;172:2:912-21.

[113] Belay GA, Zhang Z, Xu P. Physio-Morphological and Biochemical Trait-Based Evaluation of Ethiopian and Chinese Wheat Germplasm for Drought Tolerance at the Seedling Stage. Sustainability. 2021;13:9:4605.

[114] Sdouga D, Amor FB, Ghribi S, Kabtni S, Tebini M, Branca F, Trifi-Farah N, Marghali S. An insight from tolerance to salinity stress in halophyte Portulaca oleracea L.: Physio-morphological, biochemical and molecular responses. Ecotoxicology and Environmental Safety. 2019;172:45-52.

[115] Borsai O, Hassan MA, Negruşier C, Raigón MD, Boscaiu M, Sestras RE, Vicente O. Responses to salt stress in Portulaca: Insight into its tolerance mechanisms. Plants. 2020;9:12:1660.

[116] Vetter VM, Kreyling J, Dengler J, Apostolova I, Arfin-Khan MA, Berauer BJ, Berwaers S, De Boeck HJ, Nijs I, Schuchardt MA, Sopotlieva D. Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought. Global Change Biology. 2020;26:6:3539-51.

[117] Abid M, Tian Z, Ata-Ul-Karim ST, Wang F, Liu Y, Zahoor R, Jiang D, Dai T. Adaptation to and recovery from drought stress at vegetative stages in wheat (Triticum aestivum) cultivars. Functional Plant Biology. 2016;43:12:1159-69.

[118] Jangpromma N, Thammasirirak S, Jaisil P, Songsri P. Effects of drought and recovery from drought stress on above ground and root growth, and water use efficiency in sugarcane (Saccharum officinarum L.). Australian Journal of Crop Science. 2012;6:8:1298-304.

[119] Vesk PA, Westoby M. Drought damage and recovery: A conceptual model. New Phytologist. 2003;7-14.

[120] Saba J, Moghadam M, Ghasemi K, Nishabouri MR. Genetic properties of drought resistance indices. Journal of Agricultural Science and Technology. 2001;3:1:43-49.

[121] Nevo E, Chen G. Drought and salt tolerances in wild relatives for wheat and barley improvement. Plant, Cell & Environment. 2010;33:4:670-85.

[122] Oliver MJ, Cushman JC, Koster KL. Dehydration tolerance in plants. In Plant stress tolerance: Humana Press; 2010. 3-24 p.

[123] Barnabás B, Jäger K, Fehér A. The effect of drought and heat stress on reproductive processes in cereals. Plant, Cell & Environment. 2008;31:1:11-38.

[124] Xu W, Rosenow DT, Nguyen HT. Stay green trait in grain sorghum:
relationship between visual rating and leaf chlorophyll concentration. Plant Breeding. 2006;119:4:365-7.

[125] Thomas H, Ougham H. The stay-green trait. Journal of Experimental Botany. 2014;65:14:3889-900.

[126] Hilli HJ. Genetics and Genomic basis of Stay-green Trait. International Journal of Agriculture, Environment and Biotechnology. 2021;14:2:119-22.

[127] Al-Yasi H, Atta H, Alamer K, Hassan F, Ali E, Elshazly S, Siddique KH, Hessini K. Impact of drought on growth, photosynthesis, osmotic adjustment, and cell wall elasticity in Damask rose. Plant Physiology and Biochemistry. 2020;150:133-9.

[128] Khalil F, Naiyan X, Tayyab M, Pinghua C. Screening of EMS-induced drought-tolerant sugarcane mutants employing physiological, molecular and enzymatic approaches. Agronomy. 2018;8:10:226.

[129] Devi K, Prathima PT, Gomathi R, Manimekalai R, Lakshmi K, Selvi A. Gene expression profiling in sugarcane genotypes during drought stress and rehydration. Sugar Tech. 2019;21:5:717-33.

[130] ElBasiny I, Saadalla M, Baenziger S, Bockelman H, Morsy S. Cell membrane stability and association mapping for drought and heat tolerance in a worldwide wheat collection. Sustainability. 2017;9:9:1606.

[131] Arteaga S, Yabor L, Díez MJ, Prohens J, Boscau M, Vicente O. The use of proline in screening for tolerance to drought and salinity in common bean (Phaseolus vulgaris L.) genotypes. Agronomy. 2020;10:6:817.

[132] Ahmed K, Shabbir G, Ahmed M, Shah KN. Phenotyping for drought resistance in bread wheat using physiological and biochemical traits. Science of the Total Environment. 2020;729:139082.

[133] Kumar A, Sharma A, Sharma R, Choudhary A, Srivastava P, Kaur H, Padhy AK. Morpho-physiological evaluation of Elymus semiocostatus (Nees ex Steud.) Melderis as potential donor for drought tolerance in Wheat (Triticum aestivum L.). Genetic Resources and Crop Evolution. 2021;10:1-20.

[134] Haussmann BI, Hess DE, Omanya GO, Folkertsma RT, Reddy BV, Kayentao M, Welz HG, Geiger HH. Genomic regions influencing resistance to the parasitic weed Striga hermonthica in two recombinant inbred populations of sorghum. Theoretical and Applied Genetics. 2004;109:5:1005-16.

[135] Ejeta G, Tuinstra MR, Grote EM, Goldsborough PB. Genetic analysis of pre-flowering and post-flowering drought tolerance in Sorghum. Production in Water-Limited Environments. 2000:137.

[136] Kebede H, Subudhi PK, Rosenow DT, Nguyen HT. Quantitative trait loci influencing drought tolerance in grain sorghum (Sorghum bicolor L. Moench). Theoretical and Applied Genetics. 2001;103:2-3:266-76.

[137] Alam MM, Mace ES, Van Oosterom EJ, Cruickshank A, Hunt CH, Hammer GL, Jordan DR. QTL analysis in multiple sorghum populations facilitates the dissection of the genetic and physiological control of tillering. Theoretical and Applied Genetics. 2014;127:10:2253-66.

[138] Bekele WA, Fiedler K, Shiringani A, Schnaubelt D, Windpassinger S, Upptomor R, Friedt W, Snowdon RJ. Unravelling the genetic complexity of sorghum seedling development under low-temperature conditions.
conditions. Plant, Cell & Environment. 2014;37:3:707-23.

[139] Wang AY, Li Y, Zhang CQ. QTL mapping for stay-green in maize (Zea mays). Canadian Journal of Plant Science. 2012;92:2:249-56.

[140] Sreeman SM, Vijayaraghavareddy P, Sreevathsa R, Rajendrareddy S, Arakesh S, Bharti P, Dharmappa P, Soolanayakanahally R. Introgression of physiological traits for a comprehensive improvement of drought adaptation in crop plants. Frontiers in Chemistry. 2018;6:92.

[141] Amelework B, Shimelis H, Tongoona P, Laing M. Physiological mechanisms of drought tolerance in sorghum, genetic basis and breeding methods: a review. African Journal of Agricultural Research. 2015;10:31:3029-40.