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Chapter

Abiotic Stress Responses in Plants: Current Knowledge and Future Prospects

Deeksha Marothia, Navdeep Kaur and Pratap Kumar Pati

Abstract

Exposure to abiotic stresses has become a major threatening factor that hurdles the sustainable growth in agriculture for fulfilling the growing food demand worldwide. A significant decrease in the production of major food crops including wheat, rice, and maize is predicted in the near future due to the combined effect of abiotic stresses and climate change that will hamper global food security. Thus, desperate efforts are necessary to develop abiotic stress-resilient crops with improved agronomic traits. For this, detailed knowledge of the underlying mechanisms responsible for abiotic stress adaptation in plants is must required. Plants being sessile organisms respond to different stresses through complex and diverse responses that are integrated on various whole plants, cellular, and molecular levels. The advanced genetic and molecular tools have uncovered these complex stress adaptive processes and have provided critical inputs on their regulation. The present chapter focuses on understanding the different responses of the plants involved in abiotic stress adaptation and strategies employed to date for achieving stress resistance in plants.

Keywords: plants, abiotic stress, photosynthesis, reactive oxygen species, ion transport, osmoregulation

1. Introduction

Plants often experience unfavorable environmental conditions such as high salinity, drought, cold, heat, depletion of soil nutrients, and excess of toxic ions, etc. that hamper the plant growth and development [1–3]. These stresses not only play a major role in determining the crop yield and productivity but they also contribute to the differential distribution of plant species across different parts of the earth [4]. About 90% of the arable lands around the globe are susceptible to one or more of the above stresses causing up to 70% annual yield loss of major food crops [5]. The changing climate is further aggravating the impact of abiotic stress factors on the overall growth and development of various crops [6]. It is believed that exposure to salt stress in irrigated lands has been increased by 37% during the last 20 years [7]. Moreover, the occurrence of drought is increased due to alteration in the evapotranspiration and pattern of precipitation caused by global warming [8]. As per a recent meta-analysis study, a further increase of 2.0 to 4.9°C in the average earth temperature by 2100 is speculated which will further impose a huge challenge for sustainable agriculture in the future [9].

Plants respond to different environmental constraints through complex intricate mechanisms [1]. The ability of plants to adjust to different environmental conditions is directly or indirectly related to two major plant strategies - plant stress avoidance and plant stress tolerance. Plant's stress avoidance is a physiologically non- active phase like mature seeds, while stress tolerance is an active reversible adjustment which is generally referred to as acclimation [10]. Acclimation to stress is particularly mediated through profound changes at the level of gene expression which results in changes or modifications in the composition of plant transcriptome, proteome as well as metabolome [11]. During the last few decades, researchers have focused on recognizing and elucidating the different components and molecular partners underlying abiotic stress responses in plants [12]. Several attempts have been made to produce crops/species with improved abiotic stress adaptive traits including drought and salinity. However, one of the massive challenges in modern sustainable agriculture is the development of abiotic stress-resilient crops with new and desired agronomical traits using different approaches. For this purpose, understanding the mechanisms by which plants perceive stress signals and further transmit them to cellular machinery for activating adaptive responses is of huge importance [13–16]. In this context, marrying the various physiological, biochemical, and gene regulatory network knowledge is essential that will aid up in the development of stress-tolerant high-yielding food crop cultivars [17, 18]. Therefore, a holistic understanding of the different responses associated with abiotic stress adaptation by taking advantage of various available high throughput tools like proteomics, metabolomics, and transcriptomics is critical. Hence, the present chapter deals with the various responses associated with abiotic stress stimuli in plants and the current status, and future prospects of different approaches used to date for developing stress-resilient crops.

2. Plant's responses to abiotic stresses

Plants face several types of variations in their physical environment that hampers their growth and development. They respond to these oscillating environmental conditions through a series of external and internal changes [19, 20]. These stress-specific responses are associated with an array of molecular players that modulates the morphology, anatomy, and physiology of plants [12, 13].

2.1 Responses at the level of cellular membranes

Plant cells can sense changing environmental signals leading to significant changes in their physiology, metabolism, and gene expression [12, 13]. The stress stimuli are first perceived at the level of cellular membranes that initiates a cascade of events to transmit the signal to various organelles thus activating the appropriate molecular network [21]. In plants, the primary cell wall is composed of cellulose fibrils connected by hemicellulose tethers embedded in a pectin gel providing mechanical strength for load-bearing. It also contains several structural proteins, phenolics, and calcium [22]. These components are often modified when plants are exposed to abiotic stresses. The overall architecture of the cell wall is affected by exposure to abiotic stress depending upon the species, the stress intensity, plant phenotype, plant genotype as well as the age of plant. It appears to result in both loosening and tightening of the cell wall [23].

The viscoelastic properties of the primary cell wall are improved by elevating the levels of cell wall remodeling and biosynthetic enzymes, and by modulating the other cell wall loosening agents such as pectin, thus contributing to higher hydration

status of the plant which aids up in maintaining turgor pressure necessary for growth [23]. The viscoelastic properties are also modulated by reinforcement of the secondary wall with the accumulation of cellulose and non-cellulosic components. In response to abiotic stress stimuli, the biosynthesis of xyloglucan (the most abundant non-cellulosic components of type I primary walls), and cellulose is induced [24, 25]. It is associated with an up-regulation of EXP (expansin), XTH (xyloglucan endo-β-transglucosylases/hydrolases) and Ces A (Cellulose Synthase) encoding genes [25] Moreover, the comparative analysis of changes in the cell wall of two- different drought-resistant varieties of wheat under stress showed an increase in pectin polymers RGI and RGII (rhamnogalacturonan I and II) side chains that probably leads to hydrogel formation of pectin, limiting the damage to the cells [26]. Also, methyl esterification of homo-galacturonan (HG) levels regulated by PME (pectin methylesterase) reduces upon exposure to stress stimuli [27]. Such modifications in the cell wall architecture lead to relative maintenance of cell wall extensibility required to cope up with particular abiotic stress. Moreover, the genes encoding for cell wall proteins including arabino-galactan protein (AGP), glycine-rich protein (GRP), and proline-rich protein (PRP) are also induced in response to abiotic stress that could contribute to the cell wall strengthening [23].

One of the alternative responses against abiotic stress stimuli is to decrease the cell wall expansion and cell extensibility that can thus limit the water loss and prevent cell collapse due to dehydration stress [23, 28]. A decrease in cell wall extensibility or turgor pressure is often associated with the rigidification of the secondary cell wall by lignin deposition. As monolignols are the building blocks of lignin, they are synthesized from phenylalanine through the general phenylpropanoid and monolignol-specific pathways in the cytosol. The monolignols are then transported to the cell wall where they are polymerized by apoplastic peroxidase (PRX) and laccases into lignin [23].

A large number of integral plasma membrane proteins are also known to participate in stress perceptions which are the members of different receptor-like kinases RLKs (receptor-like kinases) [29]. Abiotic stresses are often responsible for alterations in wall-associated kinases (WAK) that are required for cell elongation and development [22]. In plants exposed to abiotic stresses, the expression of genes encoding for WAK proteins is up-regulated hinting towards the perception of stress at the cell wall or plasma membrane interface through the detection of released plant cell wall fragments [24, 30]. Thus, it can be concluded that modulation of the cell wall architecture is often a direct response that plays a vital role in the sensitization of the plant against abiotic stress stimuli. However, critical information on understanding this response comes from transcriptomics rather than biochemical analysis [26]. Therefore, a multidisciplinary approach is required for gaining an in-depth knowledge of this complex mechanism in the future.

2.2 Modulation of photosynthetic apparatus and gaseous parameters

Plants suffer numerous physiological reactions on exposure to environmental stress. These responses include alterations in photosynthetic rates, assimilate translocation, nutrient uptake and translocation, changes in water uptake, and evapotranspiration [31]. Among these, photosynthesis is one of the most critical plant processes affected by various abiotic stresses [31, 32]. These stresses negatively influence the photosystems (PS I and PS II) thus reducing the photosynthetic activity along with reduced chlorophyll biosynthesis, and photosynthetic electron transport. They also lead to impaired RuBp (ribulose 1,5-bisphosphate) regeneration that substantially affects the Rubisco activity. Generally, the stress-derived inhibitory effects on photosynthesis in plants may occur due to limitations in CO_2

diffusion factors and/or metabolic factors. Some reports provide evidence that stomatal closure is the key event under stress conditions resulting in a decrease in the sub-stomatal as well as chloroplast CO_2 concentration (Ci and Cc, respectively) thus producing a decline in CO_2 assimilation [32–36].

Under moderate drought stress, decreased stomatal conductance (g_s) is considered as the primary cause of photosynthetic inhibition from reduced supply of CO_2 to the intercellular space. In general, atmospheric CO_2 diffuses to the intercellular space (i.e. stomatal limitation) through stomata and then across the mesophyll (mesophyll limitations) at the carboxylation site [31]. Thus, mesophyll conductance (g_m) and biochemical limitation (b_L) (often termed as non-stomatal limitations to photosynthesis mainly under high water stress) have gained importance in the recent years, however, their relative importance to photosynthesis limitation has been a subject of debate [31, 36, 37]. Although, the function of non-stomatal limitations to photosynthesis is evident, however, controversies still exist because of the error and assumptions in the estimation of g_m and b_L under stress conditions [38].

2.3 Ion stress signaling and homeostasis

Abiotic stresses particularly salt and heavy metal stress are majorly responsible for an imbalance in ionic composition inside the plant cells [10]. For a normal metabolic function of plants, cells need to maintain high K^+ and low Na^+ levels. Thus, systematic exclusion of excess Na^+ ions from the cytoplasm or their accumulation within the vacuoles are the main adaptive mechanisms against ionic stress in plants [21]. This occurs through a highly sophisticated mechanism of ion homeostasis which involves the interplay of different molecular players. Ion homeostasis is maintained by ion pumps like symporters, antiporters, and carrier proteins located on the cell membranes [39]. At the plasma membrane of the cell, the stress signal is perceived by a sensor or a receptor which is generally regulated by the coordination of various ion pumps [40]. Exclusion of ions is typically carried out by transmembrane transport proteins excluding Na^+ from the cytosol, however, compartmentalization is carried out by H^+- pyrophosphatase proteins and vacuolar membrane H^+-ATPase [12].

Salt Overly Sensitive also known as SOS pathway is an excellent example of intracellular ion management or homeostasis which is turned 'on' after the activation of the receptor in response to stress and transcriptional induction of genes by signaling intermediate compounds along with certain downstream interacting partners which result in the efflux of excess ions [41]. *SOS1*, *SOS2*, and *SOS3* are the three genes encoding for SOS proteins, which work in a synchronized manner and aids in the transportation of Na^+ ions from the cytoplasm by effluxing excess of Na^+ ions using a plasma membrane Na^+/H^+ antiporter. This pathway is triggered by the high concentrations of Na^+ ions perceived by the intracellular calcium (Ca^{2+}) ion signals. The high concentration of sodium chloride (NaCl) disturbs the intracellular levels of Ca^{2+} via hypothetical plasma membrane sensors. This Ca^{2+} signal is then recognized and interpreted by the SOS3 protein which belongs to the calcineurin B-like protein (CBLs) family which in association with SOS2 activates the SOS1 [42]. SOS1 encodes for a Na^+/H^+ antiporter and various studies have confirmed the functional role of SOS1 in maintaining the homeostatic balance of ions during salt stress adaptation [43]. The vacuolar Na^+/H^+ and H^+/Ca^{2+} antiporters are also known to be differentially regulated by SOS2, thus contributing to enhanced Na^+ ions sequestration in vacuole imparting salinity tolerance. Furthermore, the SOS2/SOS3 kinase complex is responsible for the down-regulation of the activity of Na^+ ion transporters, mediating the entry of these ions into the cells of root tissue during salinity. Apart from the well-established function of ion homeostasis, SOS

proteins have also been known to play novel functions during stress acclimatization including regulation of cell cytoskeleton dynamics, development of lateral roots via modulation of auxin gradients as well as maxima in roots under moderate salt stress [43].

In plants, potassium (K^+) is one of the most abundant inorganic cations involved in various aspects of plant growth and development including abiotic stress management [44]. Thus, the maintenance of K^+ homeostasis through K^+ ion transporters and channels across the plasma membrane is necessary for the survival of plants, especially during stress conditions [45]. Plants have developed a unique transport system for K^+ acquisition and release using the high-affinity K^+ uptake transporters (HKTs) [46]. There are two sub-groups of these transporters (class I and class II) which have been identified to play a critical role in selective Na^+ ion transport and cationic co-transport of Na^+/K^+, respectively [12]. They also play a significant role in the maintenance and distribution of Na^+ ions between plant shoots and roots [47]. In *Arabidopsis thaliana* (Arabidopsis) knockout mutations in the *AtHKT1* gene along with *AtSOS1* gene {induced either by T-DNA insertion or ethyl methane sulphonate (EMS) treatment} lead to over-deposition of Na^+ ions in leaves due to the decreased amount of Na^+ ions in roots under salt stress [48].

Cl^- is a plant micronutrient which regulates turgor pressure, leaf osmotic potential, and stimulates growth in plants by acting as a critical messenger in plant developmental processes [49]. Cl^- ion signaling and transporters also regulate different pathways conferring abiotic stress tolerance in plants [50]. For instance, as an early salt stress response, the Cl^- ion signal in the soil with elevated salt concentration has been connected to stomatal closure in an ABA dependent manner [21]. However, increased deposition of these ions during ionic stress is detrimental to plant growth and development [51]. Thus, plants tend to decrease the net levels of Cl^- ions during stress through reduced net Cl^- uptake by roots, decreased intracellular compartmentation, reduced net xylem loading of Cl^-, and phloem recirculation and translocation [52]. Also, inside the cytosol, threshold levels of Cl^- ions are maintained primarily through its sequestration with the help of ion transporters and voltage-gated ion channels inside the vacuole [53]. A voltage gradient is maintained between the vacuole and the cytoplasm because of a slightly positive charged vacuole and a negatively charged cytoplasm. Hence, a large number of the Cl^- ions are sequestered through voltage-gated anion channels of the CLC family which are present on the tonoplast. Different CLC proteins function as anion/H^+ exchangers or anion-selective channels. In reports, AtCLCa has been characterized as a two-anion/H^+ exchanger which drives the active uptake of anions inside the vacuoles of Arabidopsis guard cells and mesophyll with higher selectivity for NO_3^- ions over Cl^- ions [54]. Besides, CLCs play a vital role in loading anions in the vacuole of guard cells for stomatal opening in response to light and later releasing them during ABA-induced stomatal closure [55].

2.4 Intracellular osmotic adjustment and osmoprotectants

The intracellular water loss from the cell due to drought and salinity stress results in cellular dehydration thus imposing osmotic stress in plants [56]. To counteract the effects of osmotic stress, plants and bacteria accumulate certain organic solutes like quaternary ammonium compounds, polyamines, fructose, sucrose, sugar alcohols, trehalose, fructans, oxalate, malate, and many others. These metabolites are referred as osmoprotectants or compatible solutes and may accumulate in large quantities without disturbing the intracellular biochemistry [57]. Among these osmoprotectants, quaternary ammonium compounds including proline and glycine betaine (GB) abundantly accumulate in response to abiotic stresses. The imino acid

proline is known to be deposited in considerable amounts in plant cells under the influence of drought, salinity, and other stresses [58]. It is synthesized inside the cytoplasm and plastids while it is degraded to glutamate (Glu) in the mitochondria. In addition to its role in osmotic adjustment, proline contributes in the stabilization of the cellular membranes and vital proteins by making clusters with water molecules that later get attached to membranes and proteins, thus, inhibiting their denaturation [59, 60]. Proline also scavenges free radicals to maintain or buffer the redox potential inside the cell under stressful conditions. It alleviates the cytoplasmic acidosis and sustains $NADP^+$/NADPH ratios at required levels for cellular metabolism, hence, supporting redox cycling [60, 61]. Researchers have observed a positive correlation between proline deposition and tolerance against various abiotic stresses in plants [58]. Furthermore, the exogenous application of proline has been used as an effective approach to improve stress tolerance in plants [62].

GB is another critical compound that plays an important role in osmoprotection, stroma adjustment as well as protection of thylakoid membranes for maintaining the photosynthetic activity during stress conditions [63, 64]. It protects the photosystem II (PS-II) complex from the impact of abiotic stresses [65]. GB also possesses a protective role for Rubisco against heat-induced destabilization [65]. The increased accumulation of GB provides abiotic stress resistance in several agronomically important crops including tobacco, potato, tomato, barley, and maize [11, 66, 67]. Moreover, the *Arabidopsis thaliana, Nicotiana tabacum,* and *Brassica napus* plants transformed with bacterial *choline oxidase* cDNA were found to show 5 to 10% increased levels of GB than the naturally found levels of GB in them that moderately improved their tolerance against different abiotic stresses [68].

The content of soluble carbohydrates also varies in response to abiotic stresses in plants. Simple and complex carbohydrates such as sugars, starch, and sugar alcohols accumulate under stress conditions in plants [68]. The major roles of these biomolecules are osmotic adjustment, carbon storage, and free radical scavenging. Their pattern of accumulation in response to stress varies under short- and long-term reactions. In short-term water stress conditions, decreased content of sucrose and starch were observed in the case of *Setaria sphacelata*, which is a naturally adapted C4 grass whereas an increased amount of soluble sugars and decreased amount of starch were reported under long term stress imposition [69]. Trehalose is a rare non-reducing sugar that occurs in some desiccation-tolerant higher plants along with various bacterial and fungal species [70]. It shows significant accumulation in plants in response to various environmental stimuli and acts as an osmolyte thus protecting the plant cells. It also protects the protein functioning by reducing the aggregation of denatured proteins and safeguards the biological molecules from the changing environmental stresses through its reversible water-absorption capacity [68, 71]. The sugar alcohols also show considerable accumulation in response to abiotic stress in plants and help in osmotic adjustment [72]. Mannitol, a sugar alcohol, accumulates upon salt and water stress conditions in plants. Wheat transgenics, expressing the *mtlD* gene (*mannitol-1-phosphate dehydrogenase*) of *Escherichia coli* showed significantly more tolerance towards salt as well as water stress. Upon analysis, increased plant height, biomass, and the number of secondary stems were observed in transgenic wheat [72].

Polyamines are small organic molecules ubiquitously present in all living organisms which play a vital role in diverse cellular processes. They are positively charged at physiological pH and are regarded as growth substances [73, 74, 75]. Under stress conditions, different plant species respond differently to polyamines levels. Some of the plants might increase the content of polyamines under stress conditions whereas others decrease their levels of endogenous polyamines when exposed to severe environmental conditions [73]. Exogenous application of polyamine and/or inhibitors

of enzymes which are involved in polyamine biosynthesis also hints towards a possible role of such compounds in plant adaptation or defense process in response to environmental stresses [76]. Moreover, studies involving either transgenic overexpression or loss of function mutants support the protective, adaptive, or defensive role of polyamines in plant's response to various abiotic stresses [76, 77].

2.5 Reactive oxygen species (ROS) regulation during stress acclimation

Many evidences suggest that various environmental stresses lead to the generation of ROS in plants. Actually, in plants, each cellular compartment is equipped with its own ROS homeostasis control [78–80]. The ROS signaling is changed depending upon the cell type, developmental stage, and level of stress [81]. Under optimal growth conditions, ROS inside the cell is mainly produced at a low level in organelles like chloroplast, mitochondria, and peroxisomes [82]. It has been estimated that 1–2% of the O_2 consumed by plant tissues, leads to the ROS formation that mainly involves $^1O_2$, H_2O_2, $O^{\bullet-}_2$, and OH• [83, 84]. At this low concentration, ROS acts as a signaling molecule that triggers signal transduction pathways involved in growth and development [21, 85]. However, in response to various abiotic stresses, the generation of increased levels of ROS causes irreversible damage to cells through their strong oxidative properties [86]. They possess lethal properties and cause extensive damage to DNA, proteins, and lipids thereby affecting normal cellular functioning [82]. Plants have developed an elaborate and efficient network of ROS generating and scavenging mechanisms to overcome this ROS toxicity. The two systems interplay with each other for maintaining a steady state in plants during stress acclimation [87, 88]. The delicate balance between the generation of ROS and its scavenging is responsible for duality in its function in plants which is orchestrated by a giant network of genes known as 'ROS gene network' [84].

Plant NADPH oxidases also referred as respiratory burst oxidase homologs (RBOHs) are the most studied enzymatic source of ROS in plants [88]. These are superoxide-producing enzymes that are widely involved in various processes including abiotic stress responses in plants [89]. The superoxide radical is a short-lived ROS molecule that is characterized by moderate reactivity and can trigger a series of reactions to produce other ROS species. It is produced inside mitochondria, chloroplasts, endoplasmic reticulum, and peroxisomes as a result of their normal metabolism [90]. The activity of plant NADPH oxidase is regulated by some key regulatory components like Ca^{2+}, calcium-dependent protein kinases (CDPKs), Ca^{2+}/CaM-dependent protein kinase, some small GTPases, and others. The production of ROS through NADPH oxidase may result in regulating the acclimation to abiotic stresses in plants. For instance, in barley, NADPH oxidase-mediated apoplastic ROS generation (acting upstream of xylem Na^+ loading) that is linked to ROS-inducible Ca^{2+} uptake systems in the xylem parenchyma tissue is considered as a critical factor contributing to salt stress tolerance in plants [91]. In *Arabidopsis*, the double mutants of *AtRbohD* and *AtRbohF* genes with significantly inhibited ROS generation exhibited less growth and relatively higher cellular Na^+ to K^+ ratios than the wild-type (WT) as well as a single null mutant *ATrbohd* and *ATrbohf* plants under salt stress [92].

Superoxide ions generated by NADPH oxidase are converted to hydrogen peroxide (H_2O_2), catalyzed by the different isoforms of superoxide dismutase (SOD) enzyme [93]. H_2O_2 production in plant cells not only occurs under normal conditions but also by oxidative stress which is caused by different abiotic factors. The major sources of H_2O_2 production in plant cells comprises of the electron transport chain in the chloroplast, endoplasmic reticulum (ER), mitochondria, cell membrane, β-oxidation of fatty acid, and photorespiration along with various other sources

including reactions comprising photo-oxidation by NADPH oxidase. The rates of H_2O_2 accumulation in peroxisomes, as well as chloroplasts, may be 30–100 times higher as compared with H_2O_2 generated in the mitochondria. It acts as a systemic signal that alerts various plant tissues to respond and adapt in response to the upcoming stress stimuli [94, 95]. H_2O_2 confer acclamatory stress tolerance by regulating osmotic adjustment, photosynthesis, ROS detoxification, and phytohormones signaling [95]. Studies have suggested that seeds pre-treated with H_2O_2, or together with the application of H_2O_2 and abiotic stress, induce an inductive pulse which aids up in protecting plants under abiotic stresses by the restoration of redox-homeostasis and mitigation of oxidative damage to membranes, lipids, and proteins by modulating the stress signaling pathways [95].

The stress-induced ROS activating responses occur rapidly with the appearance of the stress and it should decay immediately to protect the plants against their toxic effects. For this, plants are equipped with an array of ROS detoxifying proteins that mitigate the toxic effects of ROS generated as a result of different types of stresses [96]. In plants, the redox homeostasis during stressful conditions is maintained by the two arms of the antioxidant machinery—the enzymatic components consisting of the superoxide dismutase (SOD), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), catalase (CAT), glutathione-S-transferase (GST), and the non-enzymatic molecular compounds like reduced glutathione (GSH), ascorbic acid (AA), α-tocopherol, phenolics, carotenoids, flavonoids, and proline. These antioxidant enzymes are situated in different sites of the plant cells and work together to detoxify ROS. The omnipresent behavior of both arms of the antioxidant machinery explains the basic necessity of detoxification of ROS for cell survival [97].

3. Strategies to combat abiotic stresses in plants

Various strategies have been undertaken by the researchers from time to time to improve the abiotic stress tolerance in plants, particularly crop plants [98]. Plant breeding is the most traditional and widely used method for achieving the desired trait in given plants including stress adaptation [99]. However, the success of crop-breeding programs greatly depends on the availability of natural genetic variations among the germplasm resources and tedious selection procedures that are too slow and equally expensive [100]. Moreover, the various environmental factors such as plant developmental stage along with the logistical constraints of physiological screening of large breeding populations on a field-scale can affect the differential selection of a particular stress tolerant plant. Thus, plant breeding is almost always limited by the genetic complexity of the underpinning mechanisms along with the potential interaction among genetic determinants [101]. In this regard, the identification and recognition of discrete chromosomal regions having a major effect on the specific tolerance trait via quantitative trait loci (QTL) mapping and marker-assisted selection remain a valuable option for the success of many breeding programs [102]. Although, QTL mapping holds great promise, but still it remains complicated as the introgression of QTL regions in elite lines is tedious due to linkage drag that may introduce non-target regions. As an alternative, the cellular-based mutant introduction and subsequent selection under controlled *in vitro* conditions offer a method to quickly screen large populations with homogeneous backgrounds for novel fortuitous changes related to tolerance. Subsequent field screening then ensures the adequate performance of the tolerance trait under the external potentially mitigating factors [103].

In the past few decades, the genetic engineering approach has attracted the interest of the research community for producing stress-tolerant elite crops [104].

Genetic transformation with stress-inducible genes has been employed by the researchers to gain an understanding of their functional role in stress tolerance and ultimately to improve the traits in the target genotype [105]. The genetic manipulation techniques including insertional mutagenesis have largely contributed to deciphering the function of genes and thereby identifying the suitable candidates for crop improvement [106]. However, though success has been achieved in introducing desired tolerance traits into various crop varieties from wild relatives like barley and tomato, a restricted success has been reported in achieving abiotic stress tolerance with elite germplasm [107]. Moreover, the integration of transgenes into the host genome is sometimes non-specific and unstable [108]. Recently, the use of targeted genome editing using clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated protein9 nuclease (Cas9) (CRISPR/Cas) has generated a lot of interest in various fields of plant biology including abiotic stress management [109]. CRISPR/Cas has been adopted in the field of plant developmental biology for characterizing genes as well as to underpin the molecular mechanisms behind various plant traits [110]. It has been used in the model plants such as Arabidopsis and tobacco earlier and likewise, now it is being utilized effectively for crop plants like sorghum, rice, wheat, maize, soybean as well as woody plants. Researchers have worked on the potential use of the CRISPR/Cas9 technique for the production of abiotic stress-tolerant crops by targeting the key sensitivity (*S* genes and *cis*-regulatory sequences) and tolerance (*T* genes) players. In general, *T* genes are deployed to achieve stress tolerance in plants; however, the *S* genes negatively regulates the biological function of the *T* genes. Therefore, the silencing of *S* genes to disturb their functioning can help plants to adjust their physiological and biochemical pathways for providing tolerance in response to abiotic stress [111]. Like *S* genes, various *cis*-regulatory sequences have also been identified that negatively regulates abiotic stress tolerance mechanisms. These sequences are highly conserved and help in the regulation of gene expression by interacting with specific transcription factors [111]. Thus, editing such *cis*-regulatory sequences can also serve as a potential strategy for improving stress tolerance in plants. However, one major limitation of genome editing is the off-target mutations that are caused by Cas9 in transgenic plants. This limitation has been overcome to a considerable extent by the advent of stress-inducible CRISPR/Cas9 technique which reduces the rate of off-target mutations to negligible levels [112]. Thus, we can consider stress-inducible CRISPR/Cas as a promising tool for precise and efficient genome editing in crop plants for numerous traits, including abiotic stress tolerance.

4. Conclusion

In the last few decades, significant progress has been made in our understanding of the complex mechanisms governing abiotic stress tolerance in plants. However, still we are far from pinning the exact battery of gene activation mechanisms responsible for providing tolerance to various abiotic stresses. Our struggle to understand the complex mechanisms is ongoing and recent development of new tools for high-throughput phenotyping and genotyping gives us a new ray of hope. A complete understanding of the physiological, biochemical and molecular mechanisms especially the signaling cascades in response to abiotic stresses in tolerant plants will help to manipulate susceptible crop plants and increase agricultural productivity in the near future. Moreover, advances in genomics strategies including genetic engineering and genome editing have provided new opportunities for crop improvement by employing precise genome engineering for targeted traits in crop plants. However, the selection of the key genes is critical for the success of these approaches.

Acknowledgements

Conflict of interest

The authors declare no conflict of interest.

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