



Review

Plant abiotic stress tolerance: Insights into resilience build-up

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Climate change and the consequential unpredictable environmental stress conditions negatively impact crop productivity. It has thus become a challenge to develop solutions for food security and sustainable agriculture in the backdrop of increasing population pressure and dwindling land and water resources. This further necessitates that focus of international research should be on curtailing yield losses through improved crop breeding practices and genetic manipulation for the development of resistant crop varieties. Plants being sessile, have developed a complex regulatory network of genetic machinery which includes transcription factors, small RNAs, signalling pathways, stress sensors and defense pathways. Needless to say, research efforts have exploited this genetic reservoir for manipulating crop plants for tolerance or resistance against different stresses. In the past few decades, significant achievement has been made for developing transgenic plants for a wide variety of single or multiple stress tolerance associated traits. Several regulatory mechanisms have been identified to fine tune and tailor the tolerance response in target sensitive crops. The advent of metabolic engineering has added new dimensions to manipulate stress tolerance pathways. Novel strategies are needed to develop stable, superior performing lines under challenging field environment without yield penalty and significant success has to be achieved to translate the research outcome from lab-to-land to reach farmer's fields.

Keywords. Abiotic stress; crop plants; crop resilience; genetic variation; stress determinants

1. Introduction

Globally, food security for rapidly increasing human population in a sustainable ecosystem is an ideal situation. However, the threat of climate change and unpredictable environmental extremities has become a challenge (Abberton *et al.* 2016). Climate-change-driven effects especially of erratic environmental fluctuations have resulted in unprecedented occurrence of abiotic (salinity, drought, etc.) and biotic (pests and pathogens) stresses in crop plants (Batley and Edwards 2016). In order to cope with such climate changes driven by abiotic stress factors, plants have developed highly

evolved mechanisms of resilience, including physiological, biochemical and molecular reprogramming (Ferguson 2019). Plant breeding has contributed to significant increases in genetic yield potential of crop plants with abiotic and biotic stress tolerance (Tester and Langridge 2010). Since conventional breeding methods are time consuming and intensive, biotechnological approaches have shown great promise in developing crop crops for tolerance to biotic and abiotic stresses (Varshney *et al.* 2011).

Plant abiotic stresses such as drought, salinity and heat affect plant growth and productivity through a plethora of morphological, physiological, biochemical and molecular alterations (Suprasanna *et al.* 2018). At the molecular level, stress impacts the structural, regulatory and other master regulators (Zhu 2016; Patel *et al.* 2019a). The stress-induced responses (figure 1) in signal

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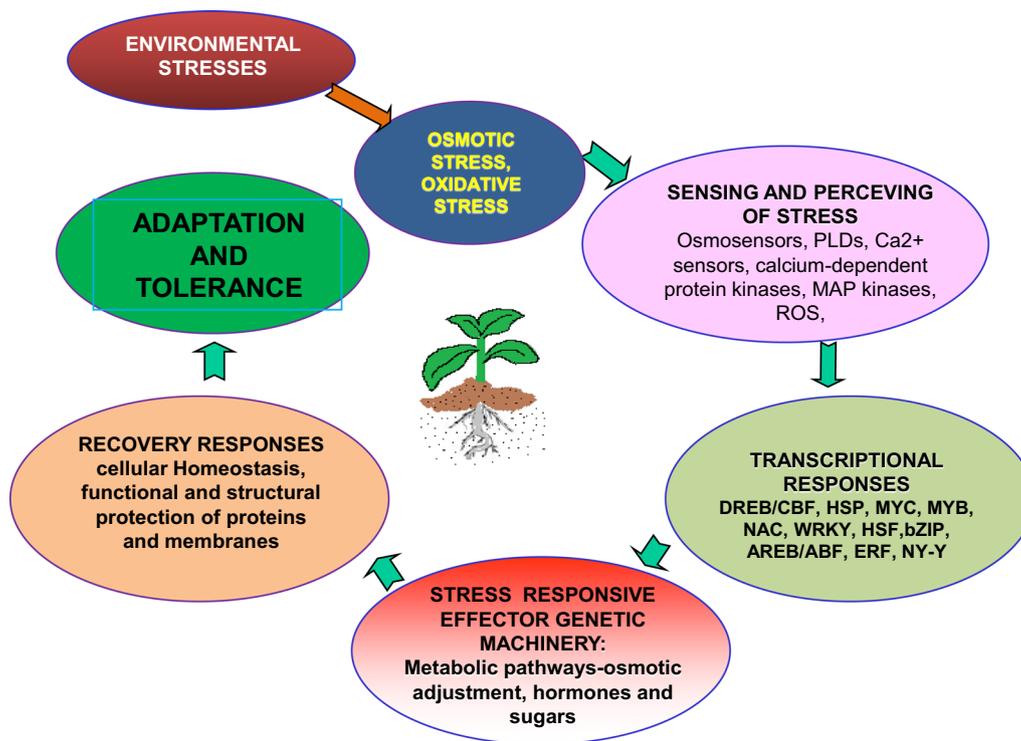


Figure 1. Diverse and coordinated plant responses to environmental stresses.

perception, osmotic and ionic homeostasis, hormone signalling, reactive oxygen species (ROS) scavenging system have been evidenced in different plant systems. In the past 2–3 decades, there has been a great interest in discovering candidate genes and quantitative trait loci for key traits that govern plant responses to abiotic stresses (Krasensky and Jonak 2012). Genomic, proteomic and metabolomic insights have shed light on how plants respond to heat, drought, salt, heavy metal and cold stresses (Haak *et al.* 2017). Besides these findings about responses unique to single stresses, responses to multiple stresses have also been studied and significant cross-talk has been shown under related and unrelated stress conditions. It is now very well understood that a number of genes are involved in stress perception and signalling, contributing to molecular, biochemical, cellular, physiological and morphological cues which culminate into whole plant tolerance (Munns and Tester 2008; Suprasanna and Ghag 2019). At the cellular level, manifestation of stress is perceived by different cellular compartments such as chloroplast, mitochondrion, nucleus, and cell membrane, and it is interesting to study and understand an integrated picture of all the signalling pathways and stress-induced gene expressions to restate and sustain all cellular activities (Zhu 2016). A crucial part of plant–environment interaction is also to comprehend how plants sense an external stress factor

like heat, drought or salinity. It will be interesting to explore for genic sensors of signalling pathways and how such local stress signals are processed and transmitted to different parts of the plant system. Research in the past few years has shed light on such sensing systems for example, photoreceptor phytochrome B as a sensor for heat stress, COLD1 for cold stress sensing, glycosylinositolphosphorylceramide sphingolipids for perceiving salt stress and calcium influx channel OSCA1 for drought induced osmotic sensing (Zhu 2016; Lamers *et al.* 2020).

2. Looking at genetic variation and stress determinants

Generation of novel genetic variability, screening of germplasm collections to characterize genetic variation for tolerant traits and genome-wide analyses are being prioritised in stress biology research (Suprasanna *et al.* 2018). Towards this end, there have been efforts to employ advanced genomics techniques to mine for trait-based alleles in crop germplasm and integrate phenomics tools for pre-breeding approaches (Pereira 2016; Varshney *et al.* 2018). The genome-wide association studies have also shown that variation in superior traits is associated with single base pair

changes (Yang *et al.* 2018). These interesting findings have now prompted researchers that it could become possible to edit such traits through point mutations.

Yet another dimension is to exploit natural genetic variation for gaining insights into stress-specific as well as shared stress adaptation mechanisms. Recent studies have shown that wild, untapped germplasm can be exploited as a source of evolutionarily stable alternative alleles which may show greater stress adaptability (Zhang *et al.* 2016; Isayenkov 2019). Observations from a comparative, haplotype study of GmSALT3 between salt-tolerant and -sensitive soybean accessions show that the tolerant ones had intense selection preference under saline condition than the sensitive ones favoured in lower saline regions (Guan *et al.* 2014), suggesting interesting stress associated, molecular evolutionary signatures in favour of stringent, strong selection for salt tolerance alleles while more relaxed selection is upon salt-sensitive alleles (Haak *et al.* 2017). Miller *et al.* (2015) has emphasized that stress-responsive gene expression in certain ecotypes (as parents) serves predictive of biomass heterosis in their hybrids. Other studies in Arabidopsis allotetraploids have also shown that higher vigour in tetraploids is associated with repression of stress-related gene expression in diploids, suggesting trade-off between growth and stress response (Kempel *et al.* 2011; VanWallendael *et al.* 2019). In addition, such a kind of stress-responsive tactic has its genetic base from adaptively divergent ecotypes, with more competitive species possessing decreased levels of constitutive expression of stress-responsive genes but superior inducible resistance. Plant biologists have shown that adaptive plant stress responses to a single stress factor are influenced by previous stress experience to same or different stress factor and studies have indicated the involvement of genetic, epigenetic and memory related mechanisms (Haak *et al.* 2017). Coolen *et al.* (2019) have reported genetic variation in Arabidopsis plants in their response to combinatorial stresses (herbivory or drought stress on resistance against *Botrytis cinerea*), and identified several candidate genes and some of which have been shown to be unknown key determinants which are crucial for plants adaptability to varying environmental cues.

Another area of increased interest is to find the role of transposons as key determinants of natural variation for stress tolerance (Negi *et al.* 2016). There have been ample evidences of such transposon insertion in stress tolerance genes, for example 'Ping' transposon insertion in the 5' regions of genes rendering them stress-responsive (Naito *et al.* 2009) and drought-tolerant

gene in maize (Mao *et al.* 2015). It is possible that the stress induced impetus in transposable element (TE) activation may induce propagation of SREs (stress-responsive elements) in host genomes to establish genome fluidity, phenotypic plasticity and stress adaptiveness (Negi *et al.* 2016). Such preponderance of TEs in plant genomes and possible regulatory functions in stress response could be useful to fine tune improvement in tolerance traits.

MicroRNAs (miRNAs) belonging to the small RNA world are known to regulate all the abiotic stress-related genetic and epigenetic pathways (Sunkar *et al.* 2012). With the advent of advanced sequencing tools and loads of data, species-specific miRNAs are being identified to have known or unknown targets. Stress-related expression has been shown to be associated with the miRNAs 156, 159, 160/161, 162, 164, 165/166, 167, 168, 169, 170/171, 172, 319, 390, 393, 395, 396, 397, 398, 399 and 400 (Patel *et al.* 2019a). In addition, stress-responsive elements such as CCAAT (heat shock-responsive element), MYB, MYC binding elements, ERD (early response to dehydration), CuREs (copper-responsive elements), ERE [ethylene (ET)-responsive elements] and GARE (gibberellic acid-responsive elements) have been shown to be present in the promoter region of some of these microRNA. Once the novel microRNAs are identified and their targets characterized, the next step is to employ them in genetic engineering for improving stress tolerance against salt, drought, heavy metal and temperature stress (Shriram *et al.* 2016). There have been successful reports of overall growth and yield improvement while maintaining stress tolerance (Zhang and Wang 2014).

3. Building crop resilience

There have been two main approaches that have played significant role in developing tolerant lines in crop plants (Suprasanna and Ghag 2019). The first approach utilizes natural genetic variability through quantitative trait loci (QTL) and marker-assisted selection. Salt tolerance-associated QTLs have been identified, for instance seedling-stage Saltol QTL for better Na⁺/K⁺ homeostasis under salt stress (Ren *et al.* 2005; Thomson *et al.* 2010) and SKC1 associated with shoot K⁺ concentration (Ren *et al.* 2005). In the second approach, gene resources from within and across plant families and also across other organisms are used to develop genetically engineered plants for better performance of their metabolic pathways, redox and ion homeostasis, antioxidant defense, osmotic adjustment, and stress

signalling pathways (Jha 2019). This requires thorough understanding and identification of key genes for functional and regulatory roles in abiotic stress tolerance. Both salinity and drought have very distinctive and common signals that often overlap. In case of drought stress, several candidates have been identified including transcriptional factors such as MYB and MYC, dehydration-responsive-element-binding (DREBs) (Lata and Prasad 2011), abscisic acid-responsive element binding proteins (AREBs)/abscisic acid-responsive element binding factors (ABFs), nuclear factor Y-B subunits (NF-YB), and tryptophan–arginine–lysine–tyrosine (WRKY) (Wang *et al.* 2016); osmolyte and molecular chaperones (Bhaskara *et al.* 2015).

Salinity causes adverse effects on plant productivity through various processes such as osmotic and ionic/hormonal homeostasis, besides other important metabolic pathways. A significant strategy is the compartmentation and the exclusion of deleterious sodium and chloride ions (Hasegawa 2013). Consequently, transgenic over-expression approach, by using HKTs which helps in lessening Na⁺ ion toxicity in shoots, has been successfully adopted to develop salt-tolerant plants. The involvement of salt overly sensitive (SOS) stress signalling pathway during ion homeostasis has shown great promise, however it is yet to be seen if we could develop tolerant lines. Enhancing salt tolerance through over-expressing the candidate genes for osmotic adjustment and sugar homeostasis is another approach which has shown great promise. Several genes for proline, glycine betaine, trehalose, polyols have been employed to achieve salt-specific expression and salt and drought tolerance (Paul and Roychoudhury 2018). Since some of the candidates can have pleiotropic effects on plant growth and development, it is often a good practice to use stress-inducible promoters (Checker *et al.* 2012), through the protein post-translational modifications such as ubiquitination (Lyzena and Stone 2012).

There is a great complexity in abiotic stress responses as there are several intricate, well coordinated genetic networks and regulatory pathways. Often these intersect, thus creating scope for cross-talk at biochemical and molecular levels. Despite such complexity, there have been several successes by utilizing single-gene based improvement in stress tolerance and their testing under single stress conditions (Mittler and Blumwald 2010; Varshney *et al.* 2011). On the other hand, there have been studies which have demonstrated that single or few functional genes for osmolyte or sugar accumulation could confer multiple stress tolerance. Often these reports have shown either growth or yield penalty which

is now managed through the use of stress-inducible and tissue-specific promoters. Exploitation of regulatory genes or master regulators like transcription factors and signalling proteins could be a successful strategy to develop abiotic stress-tolerant crops (VanWalleendael *et al.* 2019).

Advances in genomics and associated molecular technologies have made available some of the elite tools such as RNA interference (RNAi), microRNA, genome editing, and genome-wide association studies (figure 2) for improving plant abiotic stress tolerance (Mickelbart *et al.* 2015; Nongpiur *et al.* 2016; Mamta and Rajam 2018). Genome editing tools enable the introduction of targeted mutations or precise altering of gene sequences using zinc finger nucleases, transcriptional activator-like effector nucleases and clustered regularly interspaced short palindromic repeat-Cas9 (CRISPR-associated nuclease 9) (Puchta 2017). There have been few examples of altering plant stress-responsive traits (Wani *et al.* 2020). Recent reports suggest that miRNAs regulate expression of various genes under abiotic stresses and could be a sound target for genetic improvement of crops against abiotic stresses (Shriram *et al.* 2016; Patel *et al.* 2019a). For example, miR319 expression resulted in higher salt and drought tolerance in creeping bent grass (Zhou *et al.* 2013), miR408 was shown to improve tolerance to salinity, cold, and oxidative stress in *Arabidopsis* (Ma *et al.* 2015) and *Musa* miR397 enhanced plant biomass without compromising abiotic stress tolerance in banana (Patel *et al.* 2019b).

Another facet for developing salt tolerance in crop plants is through utilization of halophyte gene resources for the development of salt-tolerant glycophytes (Bose *et al.* 2014). The salt loving plants have an overall intrinsic efficiency of salt adaptation using reduced Na⁺ influx, vacuolar compartmentalization of Na⁺ or elimination of Na⁺ ions through transporters (Flowers and Colmer 2008, 2015). It is now established that their promoter regions and the *cis*-regulatory elements of various stress-inducible genes have stronger expression under saline environment besides efficient post-translational modifications (Bose *et al.* 2015, Nikalje *et al.* 2017). Several halophyte-derived candidates such as NHX, HKT, SOS, MYB, NAC, DREBs, BADH, APX and SOD have been incorporated into glycophytes (Wani *et al.* 2020). Despite considerable success in employing genes for improvement in ion homeostasis and salt tolerance in transgenic glycophytes under controlled conditions, field-level success is yet to be achieved.

Cellular redox homeostasis is the central player in the plant metabolic pathways and is considered a prime

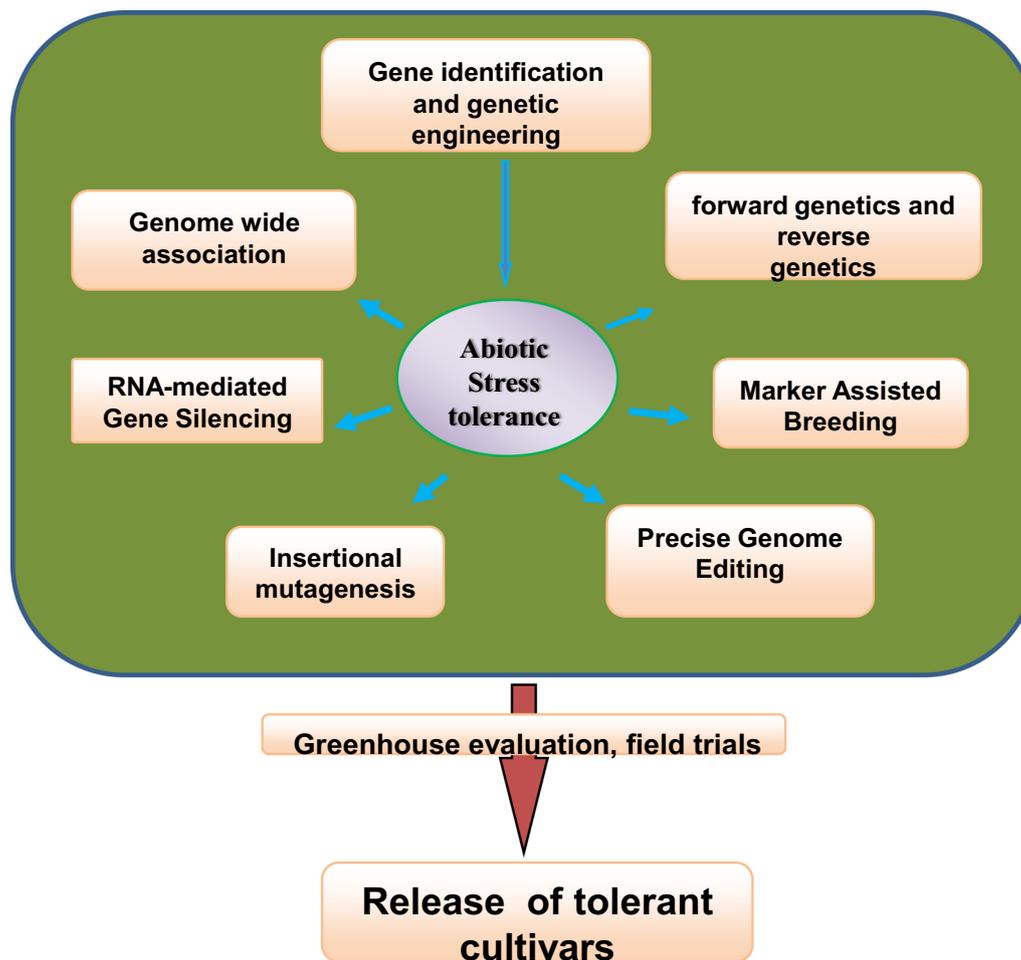


Figure 2. Genomic interventions for improving plant abiotic stress tolerance (modified after Suprasanna *et al.* 2018).

tool to regulate stress signalling. Chemical priming is an agronomic strategy to augment ability of a plant to tolerate abiotic stresses (Antoniou *et al.* 2016). The chemical priming agents are postulated to have unified mechanism of fine-tuning redox state homeostasis (Srivastava *et al.* 2016). In our studies, thiourea, which is a non-physiological thiol based ROS scavenger to confine stress induced redox imbalance and associated stress induced damages in plants, has been extensively tested under laboratory and field conditions, as well as to gain insights into its molecular mechanism of action. Thiourea improves source-to-sink relationship leading to increased crop yield (Pandey *et al.* 2013), improves cellular energetics, coordinates calcium and abscisic acid (ABA) signalling events (Srivastava *et al.* 2011, 2014), maintains plant-water homeostasis (Srivastava *et al.* 2010), and improved sulphur metabolism including stress mitigation through miRNA and hormone based regulation (Srivastava *et al.* 2017).

4. The way ahead

Excellent progress has been achieved in understanding plant abiotic stress tolerance using approaches of genomics, proteomics and metabolomics. Several options are now available for engineering tolerance traits in crop plants to a given stress condition. However, most of the studies have been limited to testing and assessment of plant's performance in green-house conditions demanding that experimental setup which can mimic natural field conditions is essential (Atkinson and Urwin 2012). Since genetic and metabolic signatures are prone to minor deviations in the environmental setup, it is also mandatory to keep minimum fluctuations in the experimental plant growth setup and other factors. Currently several phenomics platforms are available to set model environmental factors similar to realistic field conditions (Tardieu *et al.* 2017). Plant stress biology research is currently focussed on the identification of stress sensing and signalling

molecules. Majority of the studies have dealt with single stress regime for example salinity, drought and heat however, there has been a growing interest in investigating plant responses to multiple stresses, viz. high temperature, drought, high salt levels, flooding and biotic stresses. In future, omics research combining genomics, proteomics and metabolomics is expected to unravel the novel gene actions and interactions under multi-stress conditions. It is also equally critical to understand cross-talk between these stresses to identify common signatures, either in the form of sensing molecules or signalling genes, and apply them in improving stress tolerance in crop plants while maintaining plant productivity under field conditions.

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