



Potential Breeding Strategies for Improving Salt Tolerance in Crop Plants

Muhammad Afzal¹ · Salah El Sayed Hindawi¹ · Salem Safer Alghamdi¹ · Hussein H. Migdadi¹ · Muhammad Altaf Khan¹ · Muhammad Usama Hasnain² · Muhammad Arslan³ · Muhammad Habib ur Rahman^{3,5} · Muhammad Sohaib⁴

Received: 2 March 2022 / Accepted: 1 September 2022 / Published online: 3 October 2022
© The Author(s) 2022

Abstract

Salinity is one of the significant abiotic stresses that negatively affect plant production processes, growth, and development, which ultimately reduce yield. Plants adapt specific mechanisms to withstand saline conditions and activate diverse salt tolerance genes to counter osmotic and oxidative stresses induced by salinity. Genetic development in salinity tolerance is quite complex, while advancement has made less progress than expectation over the past few decades. Generating an explosion of genetics- and genomics-related information and technology in recent decades pledge to deliver innovative and advanced resources for the potential production of tolerant genotypes. Despite considerable progress in defining the primary salinity tolerance mechanisms, main obstacles are yet to be solved in the translation and incorporation of the resulting molecular knowledge into the plant breeding activities. Diverse approaches are proposed to enhance plant breeding efficacy to increase plant productivity in saline environments. Understanding the genetics of salt tolerance is a difficult task because multiple genes and pathways are involved. Important advances in tools and methods for updating and manipulating plant genomics knowledge provide detailed insights and dissect the salinity tolerance mechanism accomplished by the breeding goals. Genome-wide analyses (GWA) identify SNP variations and functional effects that appear to be the way of the future for developing salinity-tolerant plants. Gene discovery to manipulate the molecular mechanisms which underlie the complex phenotype of salinity tolerance methods, identification of genes, QTL, association mapping, linkage, and functional genomics, such as transcript identifying and proteins related to salinity, is necessary. The present analysis also discussed some of the opportunities and challenges, focusing on molecular breeding strategies used in conjunction with other crop development approaches to growing elite salt-tolerant lines.

Keywords Salinity · Plant · Abiotic stress · Omics approaches · Molecular · Tolerance mechanisms · New breeding technology

Abbreviations

EC Electrical conductivity
dS/m Desi Siemens/meter
NaCl Sodium chloride

mM Millimeter
gRNA Guides RNAs
CRISPR Clustered regularly interspaced short palindromic repeats
DNA Deoxyribonucleic acid
CO₂₊ Carbon dioxide

Handling Editor: Parvaiz Ahmad.

- ✉ Muhammad Afzal
mmushtaq@ksu.edu.sa
- ✉ Muhammad Arslan
m.arslan@uni-bonn.de
- ✉ Muhammad Habib ur Rahman
mhabibur@uni-bonn.de; habibagri@hotmail.com

¹ College of Food and Agriculture Sciences, Plant Production Department, King Saud University, Riyadh, Saudi Arabia

² Institute of Plant Breeding and Biotechnology, MNS University of Agriculture Multan, Multan, Pakistan

³ Institute of Crop Science and Resource Conservation (INRES), Crop Science, University of Bonn, Bonn, Germany

⁴ Department of Soil Science, College of Food and Agriculture Sciences, King Saud University, Riyadh 11451, Saudi Arabia

⁵ Department of Agronomy, MNS University of Agriculture, Multan, Pakistan

SC	Stomatal conductance
ROS	Reactive oxygen species
SOD	Superoxide dismutase
MDA	Malondialdehyde
Cl ⁻	Chloride
Na ⁺	Sodium
TFs	Transcription factors
sRNAs	Small RNAs
GMOs	Genetically modified organism
G x E	Genotype x environment
MAS	Marker-assisted selection
PGPR	Plant growth-promoting rhizobacteria
QTLs	Quantitative trait loci
GCA	General combining ability
SCA	Specific combining ability
SOS	Salt overly sensitive
cDNA	Complementary DNA
GR	Glucocorticoid receptor
APX	Ascorbate peroxidase
MABC	Marker-assisted backcrossing
RIL	Recombinant inbred line
SSR	Simple sequence repeats
STS	Sequence-tagged sites
GWAS	Genome-wide association study
SNP	Single-nucleotide polymorphism
DArT	Diversity arrays technology
LD	Linkage disequilibrium
TN	Tiller number
PH	Plant height
SPP	Spike per line
DWPP	Dry weight per plant
GY	Grain yield
RWC	Relative water content
SL	Shoot length
DAM	Days to maturity
RDW	Root dry weight
TDW	Total dry weight
TDWR	Total dry weight root
NGS	Next-generation sequencing
SSH	Subtractive hybridization
ESTs	Expressed sequence tags
RNA	Ribosomal Nucleic acid
tRNA	Transfer RNA
RRM	RNA recognition motif
HC	Hydraulic conductivity
AQP	Aquaporin
NHEJ	Non-homologous end joining
ZFNs	Zinc finger nuclease
TALENs	Transcription activator-like effector nucleases
DST	Dystonin
NGS	Next-generation sequencing

Introduction

Abiotic stresses, particularly salinity and drought, negatively impact plant growth and development, which ultimately incur significant losses in the production of essential food crops (Atkinson and Urwin 2012). Seed germination, root and shoot length, plant height, and fruit development are severely affected by salt stress (Liang et al. 2014; Sabagh et al. 2021). Salinity affects around 20% of the world's irrigated land (Munns and Tester 2008), and this is predicted to rise to 50% in future if current scenarios prevail (Mahajan et al. 2008). Soil with electrical conductivity (EC) of 4 dS m⁻¹ or higher (Horie et al. 2011) is saline, equating to 40-mM NaCl. Halophytes employ avoidance mechanisms, while glycophytes tolerate salinity by reducing ion imbalance and using secondary effects to withstand harsh conditions (Touchette et al. 2009). Osmotic stress and ion toxicity are the primary salt stress responses, and they cause oxidative stress followed by a series of secondary stresses and cannot maintain ion homeostasis (Munns and Tester 2008; Horie et al. 2011). As a result, plants adopted intracellular and extracellular osmoregulation processes to regulate osmotic stress and dehydration when soil environmental and salinity levels change (Rivera-Ingraham and Lignot 2017; Rahman et al. 2018). Fortunately, many naturally occurring plant events controlled different salt defense mechanisms by single or multiple genes. These defense mechanisms depend on many pathways and have been heavily investigated at the genetic, genomic, proteomic, and metabolomics levels (Gupta and Huang 2014).

A molecular understanding of the salt tolerance mechanism is essential for producing new salt-tolerant germplasm. Salt-tolerant genotypes are essential for enhancing stress tolerance in crop plants (Xu et al. 2016). Moreover, tolerance mechanisms require the coordinated actions of mechano-receptors, ion transport channels, and secondary signaling molecules to maintain ion homeostasis. Upon exposure to salt stress, plants activate a defense mechanism based on physiological and biochemical responses to coping with the abiotic stress (Pastori and Foyer 2002; Ul Hassan et al. 2021). Activation of gene cascades under saline conditions triggers hormone breakdown, signal transduction pathways, and stress perception and response genes (Silva and Gerós 2009). When stress signals are activated and transferred to cells, many other signals are activated instantly and trigger phosphorylation cascade reactions; as a result, signals are sent to specific proteins used for cell defense (transcription factors). These cell defense proteins control the expression of stress response genes, and as a result, the plant tolerates and adapts to specific mechanisms under a harsh environment (Ahanger et al. 2017).

Omics approaches like genomics, proteomics, metabolomics, and transcriptomics have been widely deployed to dissect mechanisms of salinity tolerance in plants (Cramer et al. 2011). The new genomic era includes nuclease systems with non-specific domains bonded with specific DNA sequence-binding domains help to find the genes easily and transfer them to new crop plants (Gaj et al. 2013). Applying new genome editing technologies to several crops has created opportunities for desirable traits (Jaganathan et al. 2018). However, CRISPR/Cas9 technology uses Cas9 and guides RNAs (gRNA) to target multiple sites within genomes. Genome-edited crops have advantages over transgenic plants because they contain edited DNA for specific traits (Malzahn et al. 2017). However, systematic research on the physio-chemical and biochemical variation in plant tolerance mechanisms under salt stress and genetic engineering approaches will further enhance our understanding of plant tolerance mechanisms. The techniques mentioned earlier discussed the effect of salinity on agro-morphological and physiological responses against salinity in the first section. Furthermore, the second part discussed the new breeding and omics technologies used to update the knowledge on complex pathways to overcome the salinity problems in crop plants. The implications of using these molecular processes in breeding to figure out genetic diversity gene pairs significant for salt tolerance and engineering these genes pairs in crop plants for salinity tolerance in connection to sustainable crop production in saline soils are also highlighted. The objective of the study is to conduct the systematic critical review of opportunities and challenges and further to develop potential breeding strategies for improving salt tolerance in crop plants.

Effects of Salinity on Plant Phenological Traits

Plant growth is affected by salt stress at different developmental stages: germination, seedling, growth, and development, vegetative, flowering, fruit set, and root structure. Excess salt in the soil slows down plant growth by affecting physiological and biochemical processes (Shahid et al. 2021). Further, it limits the amount of water in the root zone and upward movement to plant organs called osmotic stress. It is difficult to determine the effects of salinity by the physical or morphological characteristics of a plant, and these effects can instead be recognized using physiological and biochemical means (Munns 2002). Salinity affects plant water use, and many plants undergo osmotic regulation when exposed to salt stress by increasing the osmotic potential of the leaf sap (Gama et al. 2009). Salinity inhibits the water by imbibition seeds, as it lowers the osmotic potential of the germination media (Khan et al. 2002). Salinity also

causes toxicity, restricts enzyme activity and nucleic acid metabolism, and limits the nutrients stored in seeds (Othman et al. 2019).

Salinity has been shown to affect crop plants' germination process, i.e., in *Brassica spp.* (Akram and Jamil 2007), *Chenopodium quinoa* (Al-Barakah and Sohaib 2019), *Oryza sativa* (Xu et al. 2011), *Triticum aestivum* (Akbarimoghaddam et al. 2011; Sohaib et al. 2020), and *Zea mays* (Khodarahmpour et al. 2012). Khodarahmpour et al. (2012) reported that germination rate was reduced by about 32%, plumule length by 78%, seedling length by 78%, radicle length by 80%, and seed vigor by 95% in *Zea mays* L. when the plant was exposed to 240-mM NaCl stress. Salt stress affects plant growth in terms of plant height (ph), decreases with increased sodium chloride (NaCl) concentration (Memon et al. 2010), and the number of leaves in *Kyllingia peruviana* (Ha et al. 2008) was also decreased. The leaf blade is an essential parameter for Na⁺ toxicity in crop plants, as sodium ion is deposited in the transpiration stream rather than in the roots (Munns 2002). Salinity stress at the reproductive stage inhibits microsporogenesis and reduces the size of the stamen filaments, causing cell death, ovule abortion, and senescence of fertilized embryos (Ashraf and Harris 2004). These factors have direct physiological and biochemical effects on different growth phases during the plant life cycle (Shrivastava and Kumar 2015) and molecular level (Isah 2019). Moreover, the nutrient status of the soil is also disturbed by disrupting the osmotic and oxidative processes, which restricts water uptake from the soil. Available phosphorus is significantly reduced in saline soils because it precipitates with Ca²⁺ ions (Bano and Fatima 2009). Excessive accumulation of sodium ions in cell walls quickly causes osmotic stress and leads to cell death (Munns 2002). Similarly, a recent study on faba bean genotypes was evaluated to determine the salt stress effect on agronomical and physiological response. The results suggested that the salinity affects the agronomical and physiological traits under high (100 mM and 200 mM) salt stress relative to control (Afzal et al. 2022a).

Effect of Salinity on Photosynthetic Activity and Pigments

Physiological changes observed in plants experiencing salinity and ion toxicity include membrane disruption, reactive oxygenated species (ROS) production, limited photosynthetic rate, and antioxidant scavenging (James et al. 2011). (Patel et al. 2010) experimented to determine the effects of salinity (2, 4, 6, 8, and 10 dS m⁻¹) on seed germination and other growth parameters, i.e., root length (cm), plant height (cm), Na⁺ concentration, Cl⁻ concentration, proline concentration, and Na⁺:K⁺ ratio in cowpea. The

results demonstrated that all cultivars were less affected at low salt concentrations (2 dS m^{-1}), while reductions took place at 10-dS m^{-1} EC. Significant reductions in growth characteristics, i.e., plant height, root length, and leaf Ca^+ and K^+ contents were recorded at a higher salt concentration (10 dS m^{-1}). Moreover, Na^+ , Cl^- , and proline contents were also increased (Khosravinejad et al. 2008). Gong et al. (2018) conducted experiments to determine the effect of different salt concentrations on photosynthetic activity and chlorophyll pigments in *Kalidium foliatum*. Results showed that chlorophyll and carotenoid contents were higher in *Kalidium foliatum* when compared with the control. Salt stress also reduces leaf surface area and thus photosynthetic activity can be affected. A reduced leaf surface area leads to decreased stomata conductance and chlorophyll content and hence the efficiency of photosystem II is reduced (Netondo et al. 2004). Saravanavel et al. (2011) investigated the effect of NaCl (0–2.0%) on chlorophyll content and photosynthetic activity in *Avicennia officinalis* L. plants. The results suggested that maximum chlorophyll contents were accumulated at 0.75% NaCl relative to control; in addition, the photosynthetic activity were enhanced at 0.75% NaCl, while at higher concentration the photosynthetic activity was reduced.

Moreover, at high NaCl concentrations, the photosynthetic activity also increased (Munns and Tester 2008). Salinity affects a series of events in the form of oxidative and ionic stress. This reduced the water in the root zone area and limits the stomata opening and closing of stomata which in turn reduced intercellular CO_2 and hence reduced photosynthetic efficiency. It has also been reported that the artificial application of NaCl (200 mM) produces a 50% reduction in the photosynthetic rate of *Olea europaea*. The stomata conductance (SC) and photosynthetic efficiency were decreased and limit the carbon assimilation rate because of limited stomata opening in *Aegiceras corniculatum* at higher salt (50–500 mM) NaCl concentration (Ball and Farquhar 1984). In short, leaf expansion is reduced due to ionic stress and, as a result, the accumulation of unexploited photosynthates in growing tissues may produce signals to down regulate photosynthesis. Under salinity stress conditions, salts can build up in leaves to excessive levels. However, deposition of salts causes dehydration in apoplasts and salt accumulation in the cytoplasm, thus limiting the activities of enzymes involved in carbohydrate metabolism. Carbohydrates may then accumulate in the chloroplast and directly affect photosynthetic processes (Munns and Tester 2008). Moreover, chlorophyll contents and relative water content are also decreased in roots and shoots under saline conditions. (Vysotskaya et al. 2010) reported that chlorophyll (a & b) contents decreased and carotenoid contents increased when barley plants were subjected to salinity stress. High NaCl concentrations damaged chloroplast electrons and mitochondria and increased

reactive oxygen species (ROS). Under stress conditions, plants respond differently and produce certain antioxidant enzymes to maintain homeostasis for average plant growth. The enzymes, i.e., Superoxide dismutase (SOD) and Malondialdehyde (MDA), protect plants against ROS damage (Sen Raychaudhuri and Deng 2000). Malondialdehyde restores lipid peroxidation levels when plants suffer from salt stress. Oxidative stress occurs when plants are exposed to highly saline conditions, leading to increased MDA concentrations and significant adaptation by the plant (AbdElgawad et al. 2016). MDA level consider as biomarker for biological system in advanced oxidative states in plant: a low concentration of MDA reflects a high anti-oxidative ability and more excellent stress resistance (Hirt 2009). Rubisco activity is decreased at low NaCl concentrations (100 and 250 mM) and is increased at high NaCl concentrations (400 and 500 mM). Superoxide dismutase (SOD) levels were increased at high salt concentrations, while MDA levels were decreased at 250-mM sodium chloride salt concentration (Munns and Tester 2008). Sheldon et al. (2017) experimented to determine the effects of salt stress on water viability in wheat and chickpea cultivars. The results demonstrated that water absorption was highest under control conditions, however, somewhat reduced in wheat, and severely reduced in chickpea under salt stress treatment. From the results, it would be concluded that this may be due to Cl^- toxicity at lower concentrations rather than to the osmotic effects of salinity stress. Similar results were reported by (Rivelli et al. 2002) when four wheat genotypes were examined under different salt stress conditions to determine the elimination of Na^+ on water retention. The results suggested that stomata conductance was decreased under highly saline conditions but decreasing isotope discrimination ability in expanding leaves and more efficient transpiration were recorded when plants were exposed to saline conditions (Rivelli et al. 2002; Ali et al. 2022; Habib-ur-Rahman et al. 2022). Barley is considered more tolerant of salinity stress than other crops, based on its physiological behavior and water retention ability (Jamshidi and Javanmard 2018).

Mechanisms of Salt Tolerance in Plants

Salt tolerance mechanisms are processes that allow plants to resist stress, take up nutrients from the soil, and complete their life cycle under high salt concentrations in the soil. These types of plants can be obligate halophytes. Their relative growth is improved by around 50% in seawater, and they can be found in less saline habitats. Halophytes are also characterized by their physiological diversity, which permits them to adopt a variety of strategies under control and saline conditions (Parihar et al. 2015). The relative importance of the salt stress tolerance

processes depends on the type of species, salinity level, the growing environment, available air moisture, evapotranspiration, and leaf water potential (Wang et al. 2009; Rahman et al. 2020b). Moreover, the salt tolerance phenotypes of these plants are incredibly complex, and studies have not yet fully explained the mechanisms behind their salt tolerance. Future research alone can shed more light on salt stress and salt tolerance mechanisms (Liang et al. 2018). For this future research, we must understand crops at the genome, transcriptome, proteome, and metabolic levels to identify components at the genetic level involved in overcoming salt stress (Inan et al. 2004). Adaptation of plant salinity response, ion toxicity, homeostasis, and tolerance for improving salt tolerance mechanism is presented in Fig. 1. Biochemical alterations involved alteration in transcription changes in physiology, as a result, the growth and development processes were altered. Transcription factors (TFs) and small RNAs (sRNAs) are backbones that control core aspects of whole-plant transcriptional responses (Sunkar and Zhu 2007).

Strategies for Coping with Salinity Stress

As the global human population increases, the demand for food is also increasing, but agricultural production is not increasing quickly enough to meet this demand. Therefore, many attempts have been made to enhance crop salinity tolerance through conventional breeding and plant omics technologies. There are two general types of methods required to combat salinization of the soil. The first is salinity control using irrigation and drainage methods and activities to engineer the ecosystem and the other is an improvement in plant-based salinity tolerance

using conventional and advanced breeding and omics technologies. There are three mechanisms involved in inducing salinity tolerance in plants which are as follows: 1. Breeding, 2. Genetic Modifications (GMOs), and 3. Application of PGPR (Plant growth-promoting rhizobacteria). Breeding and GMOs are referred to as inherited salinity tolerance, while the use of PGPR to combat salinity tolerance is referred to as induced salinity tolerance (Bashan 1998; Bashan et al. 2014). An integrated plant breeding, molecular approaches, and biotechnological approaches can be used to enhance salt tolerance mechanisms in crop plants (Fig. 2). Each way of inducing salinity tolerance in plants has its own pros and cons. The response of plants to a constraint on salinity requires multiple processes which work coordinated to minimize hyperosmolarity and restore the ionic environments of homeostatic cells. A plant genotype's fitness to survive in saline environments, thus reducing yield loss, is called salinity tolerance. Salinity stress is a complex phenomenon that is controlled by many genes at the physiological and genetic levels. However, plant yield should be considered as the primary salinity tolerance criterion, which ultimately necessitates generating economically harvestable yield. Tolerance of salinity is a quantitatively inherited trait, highly regulated by multiple gene actions influenced by the genotypes, environment, and their interactions (G x E) (Arzani 2008). Despite its intrinsically dynamic existence of salinity tolerance in the genetic makeup, marker-assisted selection (MAS) has not done it, yet the anticipated improvement and procreation have depended primarily on the direct selection of the phenotypes. Genomic studies of tolerance to salinity in polyploid species including maize, alfalfa, cotton, and oat pose even more significant difficulties. Current crop physiology, genetics, and genomics techniques have given rise

Fig. 1 Salt stress affects the adaptation mechanism of plant salinity, response, and tolerance mechanism in crop plants

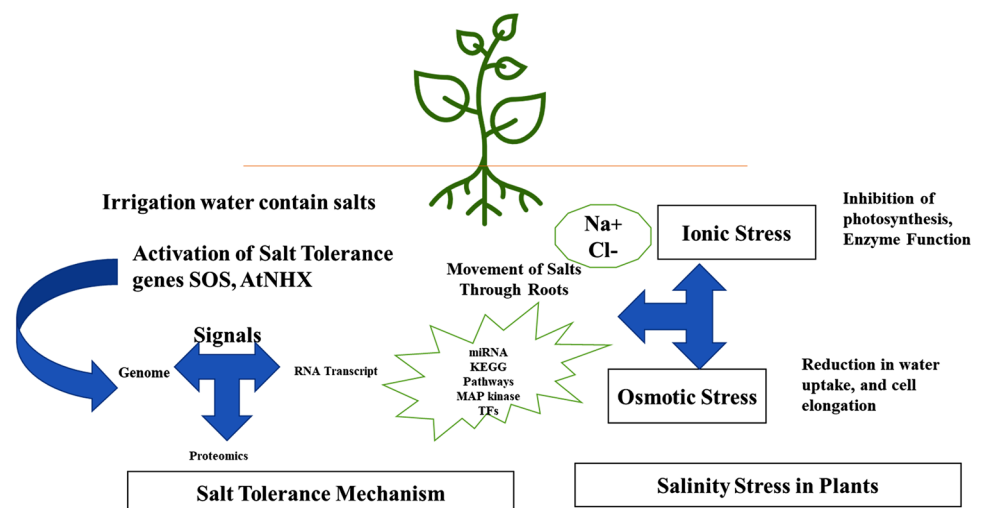
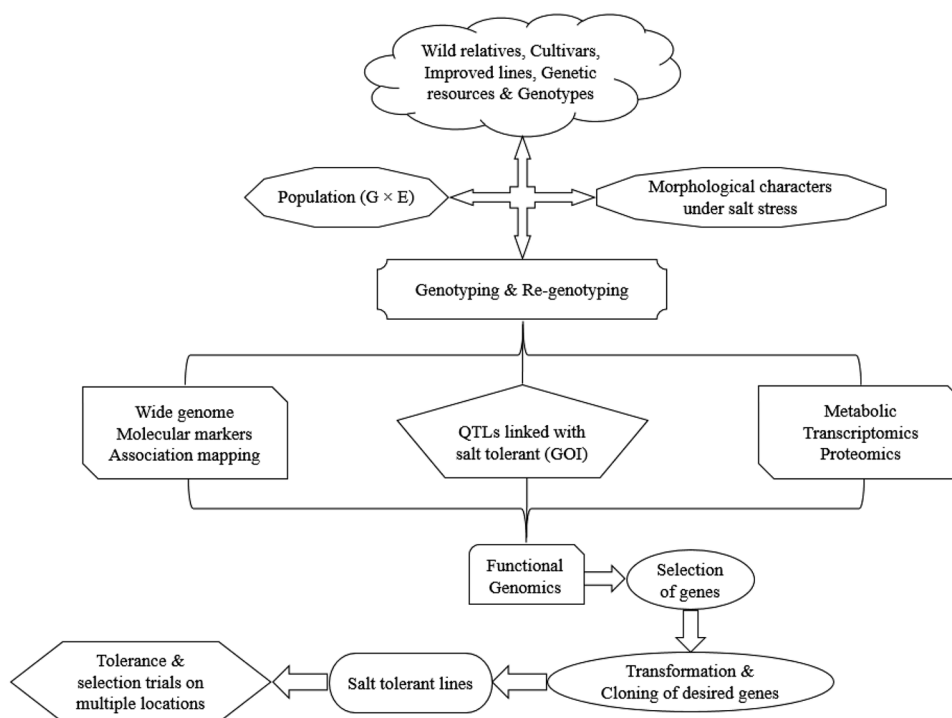


Fig. 2 Integrated plant breeding, molecular approaches, and biotechnological approaches to enhancing salt tolerance mechanisms



to new intuitions regarding tolerance in salinity, thereby providing a more profound knowledge of networks related to genes and new methods help to achieve the zero hunger goal (Lee et al. 2011; Rahman et al. 2019, 2020a). The biology of cellular plants strengthens our understanding of the diverse network of traits related to salinity tolerance and increases the structural genomics and functional methods suitable for use in the detection of the quantitative trait loci (QTLs) genes of interest linked with specific traits (Saradadevi et al. 2021). The genes are the key targets for transgenic generation and through molecular breeding, the QTLs can be used to improve crops. The QTLs thus help pave the path for MAS (Ashraf and Foolad 2013) and promote gene transformation (Negrão et al. 2011) and enabled researchers and scientists to make more resilient crops through genetic engineering and gene transformation technologies. Therefore, understanding salt tolerance mechanisms and analyzing salt stress-related genes and their functions will provide a theoretical basis for understanding the stress signal network and pathways for the improvement of the target crop (Zhang et al. 2018b).

Conventional Breeding Methods for Salinity Stress Tolerance

Conventional breeding methods are more powerful and efficient methods of enhancing salt tolerance. However, the success rate of conventional breeding approaches is less.

Plants' tolerance mechanism is a complex phenomenon and depends upon physiological and genetic responses. These processes involve phenotypic evaluation as well as the identification of QTLs closely related to molecular markers. Conventional plant breeding contributes to the screening genotypes to salt tolerance and involves improving crop plants through hybridization, selection, polyploidy, and introgression events. In addition, efficient biotechnology-aided modern breeding technologies are implemented for the development of salt-tolerant cultivars sustainably used in marginal and saline lands (Arzani and Ashraf 2016). A study by Thomson et al. (2010) identified the “*saltol*” QTL using a conventional breeding approach in rice. The “*saltol*” QTL controls the $\text{Na}^+:\text{K}^+$ ratio (shoot) at the seedling stage. Marker-assisted backcrossing is also an effective conventional breeding method used to transfer alleles at target loci (donor-recipient) (Hasan et al. 2022). However, conventional breeding mainly depends on genetic diversity (resources) and involves screening genotypes that confer salt tolerance. Conventional plant breeding can be replaced by genetic engineering. In many respects, plant genetic engineering is comparable to the backcross breeding method in which desirable genes are transferred (Singer et al. 2021). On the other hand, the backcross method can add one simple trait to a perfect variety/cultivar. The development of such a perfect cultivar act as a backbone to carry out conventional breeding processes. For example, for the development of a hybrid variety in the cross-pollinated crops several sequential procedures including recurrent selection, production of inbred

lines (gametic selection, hybridization), or screening of the superior inbred lines based on general combining ability (GCA) and eventually superior two inbred lines (best hybrid) based on the specific combining ability (SCA) value should be selected and used to develop a hybrid variety (Janaki Ramayya et al. 2021). To identify key genes and characterize salt tolerance genes, a collective approach is required to merge genomics, molecular markers, proteomics, metabolomics, transcriptomics, and transcription factors (TFs) to engineer new crops significant for salt tolerance. Integrated plant breeding, molecular approaches, biotechnological, and new breeding technology approaches to enhancing salt tolerance mechanisms are presented in Figure.

Modern Breeding Methods for Improvement of Abiotic Stresses Tools and Approaches for Crop Improvements Against Salinity Stress

Candidate Genes for Salinity Tolerance to the Characterization of Novel Genes for Salt Tolerance

The unraveling of genes responsible for salt tolerance and their molecular mechanisms that respond to the stress of salinity in cultivated crops should help breeders accelerate genetic improvement through genetic engineering and marker-assisted selection (MAS) (Hanin et al. 2016). Identification of new QTLs may lead to the development of new salt-tolerant lines. Some important QTLs that have been identified at different growth stages of crop plants exposed to salinity are presented in Table 1. The responses caused by salinity should be tested at molecular, environment, cell, and whole-plant levels. Plant respond to salinity stress in three different ways, such as “osmotic,” “ionic-specific,” and “oxidative stress” (Roy et al. 2013). Molecular biological and omics techniques are used to identify resistance genes, introduce these genes into crop varieties through genetic engineering, and could help to resolve the salinity problem. Some important QTLs and genes related to salt tolerance in crop plants at seedling, vegetative and reproductive stages are presented in Table 1. Zhu et al. (1998) identified salt overly sensitive (SOS) *Arabidopsis* mutants, which are hypersensitive to high external Na^+ , Li^+ , or K^+ concentrations. These mutants are mutated at three loci, namely *SOS1*, *SOS2*, and *SOS3* (Martínez-Atienza et al. 2007). Shi et al. (2002) reported that *SOS1* encodes a plasma membrane Na^+/H^+ antiporter, *SOS2* encodes a serine/threonine protein kinase that activates *SOS1* (Liu et al. 2000), and *SOS3* encodes an EF-hand-type calcium-binding protein (Mahajan et al. 2008). The *SOS3* protein regulates Na^+ and K^+ transport and increases the sensitivity of yeast to growth

inhibition by Na^+ and Li^+ stress (Mendoza et al. 1994). *SOS2* interacts with and activates *SOS3*, therefore these two mutant genes define a regulatory pathway for Na^+ and K^+ homeostasis and salt tolerance in plants (Halfter et al. 2000). In another study, He et al. (2005) reported that many genes responsible for salt stress responses can help to elucidate the tolerance mechanisms. The results of the study clarified that overexpression of a single gene could improve the salt tolerance of transgenic plants and that the *A. thaliana SOS1* gene (encoding a plasma membrane antiporter) and the vacuolar *AtNHX1* gene (encoding a *Nap/Hp* antiporter) can significantly enhance the salt tolerance of transgenic plants. Moreover, Liu et al. (2014) found that ABA-dependent regulatory pathways improved rice tolerance to high salt concentrations and extreme drought by introducing the *OsbZIP71* gene in transgenic plants. P-type and H^+ ATPases in the plasma membrane act as primary pumps that create a proton motive force for the active transport of solutes, such as Na^+ and K^+ (Sze et al. 1999). The Na^+ entering the cells is also transported into the vacuole through the action of antiporters (Na^+/H^+) (Apse et al. 1999). Overexpression of *SOS* genes in transgenic *Arabidopsis* plants improves salt tolerance by decreasing the amount of Na^+ and increasing the amount of K^+ within cells (Yang et al. 2009). In another study, a high abundance of *SOS* pathway-related transcripts was correlated with salinity tolerance in *Brassica* plants (Kumar et al. 2009). Moreover, rice salt tolerance has been linked to overexpression of the three *SOS loci* (*SOS1*, *SOS2*, and *SOS3*), which is linked to its ability to exclude Na^+ from the shoots to maintain a low cellular Na^+/K^+ ratio (Martínez-Atienza et al. 2007). Chakraborty et al. (2012) partially sequenced the cDNA of *Brassica juncea* genotypes and reported on the conserved nature of these genes and examined the intra- and intergenic diversity. The results showed that *SOS* pathway could be a factor that determines both plant salt stress tolerance and $\text{Na}^+:\text{K}^+$ ratio. Increasing the antioxidant activities of enzymes and increasing the metabolism level are other mechanisms by which plants can increase their tolerance to salt stress (Su et al. 2020). Genetic engineering can achieve a higher level of efficiency in transgenic plants and represents the best method of studying the function of antioxidant enzymes in terms of scavenging active oxygen. The activity of these enzyme has been confirmed in many transgenic plants, and the expression of the GAT, GR, SOD, and APX genes improves plant resistance to oxidative stress (Tanaka et al. 1999).

Marker-Assisted Backcross Breeding

Improving crop yield output, the primary goal of crop breeding for saline areas is under salinity stress as conventional breeding methods take the long haul for developing cultivar which tolerates salinity. Therefore, alternate approaches

Table 1 Identification of the QTLs of salt tolerance genes in crop plants at the seedling, vegetative, and reproductive stages

Crop	Trait	QTL	Chromosome	Position	Interval position	Source
Rice	K+ conc	qK1.386	1	38.63	38.79–39.04	De Leon et al. (2017)
	CHL	qCHL3.25	3	qCHL3.26	26.705–26.709	
	SHL	qSHL1.36	1	38.10	38.26–38.61	
	RTL	qRTL2.20	2	20.70	24.96–24.96	
	SRR	qSRR1.27	1	27.95	29.56–29.57	
Rice	SIS	qSIS2.1	2	99	–	Puram et al. (2018)
	Na+	qNa7.1	7	23	–	
	RTL	qRTL3.1	3	28	–	
	DWT	qDWT	8	16	–	
<i>Brassica napus</i> L	STR	qSTR1-a	1	12.61	–	Lang et al. (2017)
	SPAD	qSPAD1-b	1	36.35	–	
	EC	qEC1-b	1	15.3	–	
	RDW	qRDW1-c	1	5.27	–	
	SOD	qSOD1-b	1	19.7	–	
	SP	qSP8-b	8	12.91	–	
	BY	qBY2.1n	2	84.6	–	
Barley	RWC	qRWC1n	2	76.7	–	Barati et al. (2017)
	SPAD	qSPAD5n	5	150	–	
	PH	qPH2.1n	2	95.6	–	
	SL	qSL1n	1	144	–	
	DMA	qDMA1.1n	1	142.2	–	
	BY	qBY2.1n	2	84.6	–	
Barley	Tiller number	qT14s	4	–	bPb-1278-bPb-3512	Xue et al. (2009)
	Plant Height	qPH3s	3	–	bPb-0049-bPb-4564	
	Spike per line	qSPL4s	4	–	bPb-1278-bPb-3512	
	Spike per Plant	qSPP1s	1	–	bPb-6421-bPb-3921	
	DWPP	qDWP2s	2	–	bPb-6088-bPb-4377	
	Grain yield	qGY6s	6	–	bPb-7323-bPb-2751	
	Na+ concentration	qNA2s	2	–	bPb-3536-bPb-1103	
	Na+:K+ ratio	qNAKs	6	–	bPb-8889-bPb-7323	
Wheat	Chlorophyll content	Q. chl2D	2	–	gbm1209/wPt-0298	Genc et al. (2010)
		Q. chl5A	5	–	wPt1370/Vrn1A	
	Maturity	Q. mat5A	5	–	wPt-3114/wmc170	
	Na+ concentration	Q. Na2A	2	–	wmc272/barc349	
	Na+ concentration	Q. Na 2B1	2	–	wPt-4647/wmc147	
Wheat	RDW	qRDW.ST-4A	4A	–	<i>Xbarc170-Xbarc1136.2</i>	Genc et al. (2010)
	MRL	qMRL.ST-4D	4D	–	<i>Xbarc98-Xgwm55.2</i>	
	SDW	qSDW.ST-7A	7A	–	<i>Xbarc1136.4-Xgdm14.3</i>	
	TDW	qTDW.ST-3A	3A	–	<i>Xgwm156.2-Xbarc324</i>	
	TDWR	qTDW.ST-7A	7A	–	<i>Xbarc1136.4-Xgdm14.3</i>	

TN Tiller number, PH plant height, SPP spike per line, DWPP dry weight per plant, GY grain yield, RWC relative water content, SL shoot length, DAM days to maturity, RDW root dry weight, TDW total dry weight, TDWR total dry weight root

must be implemented effectively into the improvement program. The germplasm was genetically diverse and conventionally crossed to produce repetitive populations and selection was based on phenotypes and field data. The technique was now transformed either using MAS procedures that are connected to specific QTL or qualitative traits. Efficient application of MAS to tolerance to salinity depends mainly

on a marker being closely linked to either a resistant gene or a QTL related to tolerance. Therefore, with a detailed understanding of the genetic origin of the organisms underlying in combination with the functional genomics and salinity stress is important to decide whether the MAS process has a major impact on enhancing the tolerance to salinity. As

exemplified earlier, *SalTol* is a good QTL for ion absorption it was described in Rice (Ali et al. 2013).

A codominant-linked marker, *cslinkNax2*, was used successfully by a backcrossing technique in durum wheat for the *TmHKT1;5* gene MAS (Munns et al. 2012). They may be used to transfer (introgress) tolerance of salinity into the elite genotype from donor, resistance, and breeding lines without passing hostile genes from donor parents after validating the main QTLs in the required germplasm for salinity tolerance. Gupta et al. (2010) proposed a method called Marker-Assisted Backcrossing (MABC). MABC was modified to integrate appropriate QTLs into genotypes using set locus with markers and background markers in the genome (Frisch et al. 1999). Given the widespread use of MABC introgress to biotic stress resistance, there has been limited use of MABC in the development of cultivars tolerant to abiotic stress and salinity stress. However, in rice, MABC's successful application in improving abiotic tolerance was disclosed when a major QTL was used for submergence tolerance (Sub1) that was introduced to different cultivars (Singh et al. 2013). To date, there is only one known case in which a MABC strategy was used to introduce a QTL “*SalTol*” which was transformed into a rice cultivar (BR11) Bangladeshi and other genotype as well (Gregorio et al. 2013). Similarly, salinity-tolerant RILs line cross (Pokkali x IR29) was considered as “*SalTol*” parent donor for transition to *BR11* (parent recipient). The authors used polymorphic markers simple sequence repeats (SSR) and sequence tags sites (STS) to validate the plants with F1 and pick genome from the foreground, recombinant, and history. This method has been used for introversion for multiple QTLs in rice root traits, and the resulting PY 84 cultivar was printed in India, with increased root growth under stress from drought (Steele et al. 2013). Similarly, MABC was also used for maize with beneficial alleles found at five loci linked with flowering days and yield components (Ribaut and Ragot 2007).

QTLs Related to Salinity Stress: Utilization of QTLs Knowledge for Salinity Stress

Salinity tolerance has already been shown to be a complex function regulated by multiple genes (Fan et al. 2016b). The QTL study was used to evaluate the positions of genomes participating in salinity tolerance. To identify the QTLs, segregating population of progeny produced by selfing or biparental cross or duplicated contrasting haploidy with parents is used in salinity response. Nevertheless, this method is time consuming in a dynamic characteristic, such as tolerance to salinity to produce population mapping, and often includes multi-locational, phenotypic data that could be reproducible and accurate. In a different method to studies of the genome-wide association (GWA), a significant number of SNPs are examined in several plant genotypes,

for combination with the desired trait was employed to resolve this constraint on dissecting complex quantitative characteristics. The GWA analysis could be used to detect SNPs and the addition/deletion linked to the desired trait in germplasm collections (Mitchell-Olds 2010). In addition, the restricted availability of genomic data on minor crops makes this method more acceptable for them. Some association mapping reports exist to link different genes with salinity tolerance-associated phenotypic characteristics. Good association between *AtHKT11* gene was recorded for tolerance to salinity was discovered in Arabidopsis, the findings of a GWA analysis (Atwell et al. 2010). The GWA approach was implemented in rice and 20 SNPs were identified that were significantly linked to the Na^+/K^+ ratio (Kumar et al. 2015). This approach was extended to barley and a QTL tolerance for salinity was identified with *DArT* marker at chromosome 4 (Fan et al. 2016a).

An alternative approach called linkage disequilibrium (LD) mapping or association analysis is QTL finding to identify direct phenotypic and genotypic associations (Zhu et al. 2008). It has an advantage since it does not require the creation of population mapping and may be used in many populations. In addition, association mapping may lead to a greater likelihood of identification of QTLs because of the increased variation of the alleles in the working population compared to two binding parental alleles study (Buckler IV and Thornsberry 2002). Nonetheless, the method's limited statistical capacity, cannot detect rare alleles via linkage mapping (Lewis 2002). The association mapping method will validate the QTL-linked markers identified using classical methods (Thornsberry et al. 2001). The QTL analysis characteristics correlated with salinity tolerance performed at three growth and developmental stages in a variety of crop plants. Hence, QTL has been identified that influences directly or indirectly response differently to salinity stress, i.e., ionic status. The following information describing QTL analyzes are summarized for tolerance of salinity in the major crop species (Long et al. 2013).

Wheat, barley, and rice have been found to impart tolerance to salinity at the growth stage of seedlings (Ahmadi-Ochtapeh et al. 2015; Genc et al. 2010; Nguyen et al. 2013; Wang et al. 2012). The study results suggested that salinity tolerance is controlled by many additives and epistatic QTLs controlled different environmental activities in wheat and rice and help to enhance the salinity tolerance (Wang et al. 2012). The tolerance to salinity is also tested in rice by multiple QTLs during the reproductive stage, as *SalTol* QTL is closely correlated with tolerance to salinity (Ali et al. 2013; Merrium et al. 2022). The *SalTol* is considered best-characterized QTL responsible for both high K^+/Na^+ ratio and low Na^+ shooting under salinity stress. In barley, five QTLs responsible for salinity tolerance are present on H chromosomes at (1, 2, 5, 6, and

7 positions) affecting more than fifty percent variability at the seedling stage (Zhou et al. 2012). In addition, many genomic regions containing candidate genes responsible for tolerance have been recognized in barley using biparental population mapping (Nguyen et al. 2013) as well as other mapping techniques for linkage were studied (Long et al. 2013). In addition, Shavrukov et al. (2010) described a solitary H-derived QTL for Na⁺ elimination. Analysis of QTL for leaf Na⁺ exclusion showed that both large QTLs (Horie et al. 2005; Shavrukov et al. 2011) and small QTLs are present in wheat (Genc et al. 2010).

A QTL named *Kna1* significant for Na⁺ elimination, as well as involved in K⁺/Na⁺ discrimination enhancement (Dvořák et al., 1994), was linked to gene *TaHKTI;5* in bread wheat (*T. aestivum*) improved the Na⁺/K⁺ ratio (Byrt et al. 2014). Similarly, the *HvCBL4* gene encoded a protein identical to calcineurin B and *SOS3* homolog from Arabidopsis, mapped in rice (Rivandi et al. 2011) represents QTL for salinity tolerance genomic region. In rice, *OsHKTI;5* has been linked with *SKC1*, which involved the absorption of K⁺ on chromosome 1 in the shoot (Ren et al. 2005). The *SKC1* and *Saltol* are co-localized. *OsHKTI;5*, orthology of the gene *AtHKTI;1*, has been shown to regulate the xylem Na⁺ elimination (Hamamoto et al. 2015). Many other QTLs that control the homeostasis of the cellular ion have been found in rice. While considerable success in the identifying main QTL for tolerance salinity, in an empirical plant breeding, their position in MAS is not well known. However, it may also be possible to incorporate high adaptive features in the genomic era with only a relatively smaller QTL effect (Mirdar Mansuri et al. 2020). The application of next-generation sequencing (NGS) technologies allows for the rapid production of markers (indel) and SNP for specific traits, which end up and enable the pyramidization of different QTL tolerances to salinity from various sources within a single cultivar (Zhang et al. 2016). However, the integrative meta-analysis strategy led to the

discovery of several intriguing genes implicated in salinity tolerance, including some of the most important genes/gene families with sufficient evidence.

Transcriptomics: Application of Transcriptomics Knowledge for Salinity Stress

Recent advances in molecular plant science have improved our collective knowledge, and transcriptomics have emerged as a powerful method of understanding differential gene responses over a specific time series. Transcriptomics is a technique used to study the whole set of RNA transcripts (coding and non-coding) of a cell at a specific time and under specific conditions (Supplitt et al. 2021). Expression analysis of tissue under different growth conditions reveals the regulatory network of responsive genes for that specific stage or condition and helps to annotate genes that were previously unannotated due to lack of information (Lowe et al. 2017). Some important transcriptomics studies revealed total clustered transcript reads, upregulated genes, and downregulated genes in salt-stressed crop plants presented in Table 2. Gene identification methods were used based on expression analysis, including subtractive hybridization (SSH) (Putney et al. 1983), expressed sequence tags (ESTs) (Diatchenko et al. 1996), microarrays, serial analysis of gene expression (SAGE) (Velculescu et al. 1995), and massively parallel sequencing (MPSS). Among the modern transcriptomics approaches, microarrays and RNA-sequencing are the dominant methodologies. Microarrays were developed in the 1990s, with the first results being published in 1995 and representing a method of gene expression analysis. One single microarray chip can investigate thousands of genes simultaneously in a sample, such as the 22 k Barley1 gene chip (Close et al. 2004) and the Model Organism Barley Gene Expression Microarray, 4 × 4 k (Agilent tech. USA) was used the first time. Initially, only one sample could be run per chip multi-sample gene chips are now available with technological advancement. Microarrays for transcriptome

Table 2 Transcriptomics studies revealed total clustered transcript reads, upregulated genes, and downregulated genes in salt-stressed crop plants

Crop	Stage	Clustered transcripts (reads)	Upregulation genes	Downregulation Genes	Source
<i>S. maritima</i>	Seedling	72,588	647	735	Gharat et al. (2016)
<i>Gossypium hirsutum</i> L	Root, leaf (seedling)	25,929	9500	11,000	Zhang et al. (2018a)
<i>Arabidopsis thaliana</i>	Seedling	27,673,695	1024	264	Liu et al. (2017)
<i>Glehnia littoralis</i>	3 months growth	105,875	5,018	5317	Li et al. (2018)
Barley	Leaf	9277, 3861	–	–	Bahieldin et al. (2015)
Wheat	Germination	453,882	865	2171	Goyal et al. (2016)
Wheat	Early and late leaf stage	6,131,401	–	–	Luo et al. (2019)
Maize	15 days after germination		54	94	Zhang et al. (2015)
Soybean	Seedling stage	2374, 998	1746	630	Zeng et al. (2019)

analysis of plants under salinity stress have been completed in crop plants, such as wheat (Peng et al. 2009), rice (Zhou et al. 2007), maize (Zheng et al. 2006), barley (Atienza et al. 2004), *Arabidopsis thaliana* (Liu et al. 2013), potato (Legay et al. 2009), and sorghum (Buchanan et al. 2005). RNA-sequencing (RNA seq.) is a high-throughput sequencing technology in which whole transcripts can be sequenced. It has the potential to replace microarrays analysis (Mutz et al. 2013). It is considerably more efficient than microarrays as it can detect novel transcripts even at low abundance, non-coding RNA, allele-specific expression, and alternate splice junctions. RNA-seq does not require any prior knowledge of annotations or sequence assemblies. There is no bias involved in this method of sequencing like that which occurs in probe hybridization during a microarray experiment (Zhao et al. 2014). Mutz et al. (2013) crosschecked gene expression profiles of the same sample from Illumina and a microarray analysis and concluded that RNA-seq recorded more prominent results and could also detect transcripts with very low abundances, differentially expressed genes, and identify sequence variants and new transcripts relative to microarray analysis. Different transcriptome analyses of different crops have been reported under salinity stress, i.e., rice (Mutz et al. 2013), *Rosa chinensis* (Tian et al. 2018), *pearl millet* (Shinde et al. 2018), and wild barley (*H. spontaneum*) leaves under salt stress (Bahieldin et al. 2015).

Genome-Wide Analysis Studies (GWAS) for Salt Tolerance

GWAS investigations are increasingly being utilized to identify and explain the genetic basis of agronomic features, like germination, which are generally influenced by many small genes (Naveed et al. 2018; Yu et al. 2018). GWAS uses linkage disequilibrium (LD) to find the relationships between genetic variations and phenotypes across many genotypes

from natural populations. Hundreds of accessions covering thousands of gene loci can be genotyped using high-throughput markers to improve the effectiveness of present breeding procedures due to recent breakthroughs in genome-wide genotyping technology (Russell et al. 2011; Kilian and Graner 2012; Tondelli et al. 2013). To find the targeted gene, GWAS can precisely discover polymorphisms and the underlying genetic loci that are responsible for phenotypic variances under different abiotic stress conditions (Naveed et al. 2018; Xu et al. 2018; Yu et al. 2018) as well as biotic stress conditions (Afzal et al. 2022b). Aside from the high-density SNPs commonly used in GWAS, GWAS has another advantage, i.e., natural variety population selection has been done for genotyping based on phenotypic variation. The osmotic pressure in the soil is increased by high salt levels, creating a drought-like situation (Sayar et al. 2010), reducing water absorption by the seed from the soil surface, delayed seed imbibition, or even prevented for subsequent germination.

Furthermore, excess Na^+ and Cl^- ions create toxicity, which obstructs normal cellular functions (Hampson and Simpson 1990), resulting in a lower rate of seed germination (Luan et al. 2014). The interplay effects of ionic and osmotic stress eventually reduce the number of sprouted seeds and the germination rate (Kazemi and Eskandari 2011). Several distinct loci control salinity tolerance at this stage (Mano and Takeda, 1997). A similar study suggested by (Angessa et al. 2017) used a doubled haploid barley population developed by CM72 Gairdner cross controlled both traits by QTLs on chromosomes 2H and 3H position, respectively. Another study reported similar results and found 17 QTLs influencing ABA response on 1H, 2H, 3H, and 5H positions in the Steptoe Morex population at the germination stage (Mano and Takeda 1997). Salinity tolerance genes were tightly connected at the chromosome 5H position in both populations. A single QTL on chromosome 5H was shown to be responsible for 42% of the phenotypic variation responsive

Table 3 Important genes/TFs and protein families involved in salt tolerance in crop plants

Genes, TFs, Protein family	Crop	Function	References
<i>P. indica</i> -insensitive protein 2	<i>Arabidopsis</i>	Phytohormones development	Xu et al. (2018)
Protein Kinase superfamily	Barley	Abiotic stress tolerance	Yang et al. (2017)
Protein Kinase superfamily	Wheatgrass	Salinity tolerance	Shen et al. (2001)
Kinase family (TFs, miRNA)	Cotton	Regulated ROS	Shehzad et al. (2019)
Lipase Expression	Cotton	Enhanced salinity tolerance	Naranjo et al. (2006)
Heat shock protein (HSPs)	Alfalfa	Salinity tolerance; heat tolerance	Song and Ahn (2010) and Mu et al. (2013)
HSPs	Transgenic Barley	Salinity tolerance	Chaudhary et al. (2019)
Kinase, lipase, HSPs	Barely	Enhanced the germination under salt stress	Mwando et al. (2020)
Na^+/H^+ exchanger and a potassium transporter	Wheat	Improved salt tolerance	Quamruzzaman et al. (2021)
CaLG05; CaLG07	Chickpea	Osmoregulation under salt stress	Ahmed et al. (2021)

at three salt concentrations (Cattivelli et al. 2002). Some of the important are identified using GWAS analysis presented in Table 3.

Proteomics: Utilization of Proteomics Knowledge

Salinity limits crop productivity and growth. Different complex processes occur during salt response signals in the cell, and metabolic processes take place simultaneously at the cellular and plant organ levels. The activation of transcription factors leads to the formation of specific proteins via the mechanism presented in Fig. 3. To produce effective salt tolerance mechanisms in crop plants, plant physiological and molecular processes should be investigated under different salinity levels. Nowadays, the advancement of proteomics research has provided a method of obtaining high-throughput data that are used to determine plant molecular networks (Zhang et al. 2012). Important proteins expressed under saline stress conditions at different growth stages in crop plants are presented in Table 3. Moreover, they also detected 2171 salt-responsive proteins, of which

561 were unique. These proteins were identified in leaves, roots, shoots seedlings, and other different growth stages. These proteins provide valuable a deeper insight into salt tolerance mechanisms related to photosynthesis, reactive oxygen species, signal transduction, ion homeostasis, and cytoskeleton dynamics under different salt stress conditions (Pang et al. 2010). However, the plants, i.e., glycophytes and halophytes respond differently under different salt stress conditions. Many studies have shown that *A. thaliana* (Pang et al., 2010), rice (*Oryza sativa*) (Kim et al. 2005), *Triticum durum* (Caruso et al. 2008), *Glycine Max* L. (Sobhanian et al. 2010), *Tabacum* (Razavizadeh et al. 2009), *T. aestivum* (Peng et al. 2009), *A. stolonifera* (Xu et al. 2010)(Xu et al., 2010), *P. cathayana* (Chen et al., 2012), *S. Europaea* (Wang et al., 2009), *P. coarctata* (Sengupta and Majumder 2009), and *D. salina* (Katz et al. 2007) induce photosynthesis-related proteins under salt stress conditions. Contrarily, salt-tolerant crops such as *T. halophila* (Katz et al., 2007), *S. salsa* (Li et al. 2011), and *S. aegyptiaca* (Askari et al. 2006) downregulate the expressions of salt-tolerant photosynthetic proteins under high salt stress conditions (Table 4). In some

Fig. 3 Schematic diagram of the protein modification process that allows plants to withstand saline environments (tolerance mechanism)

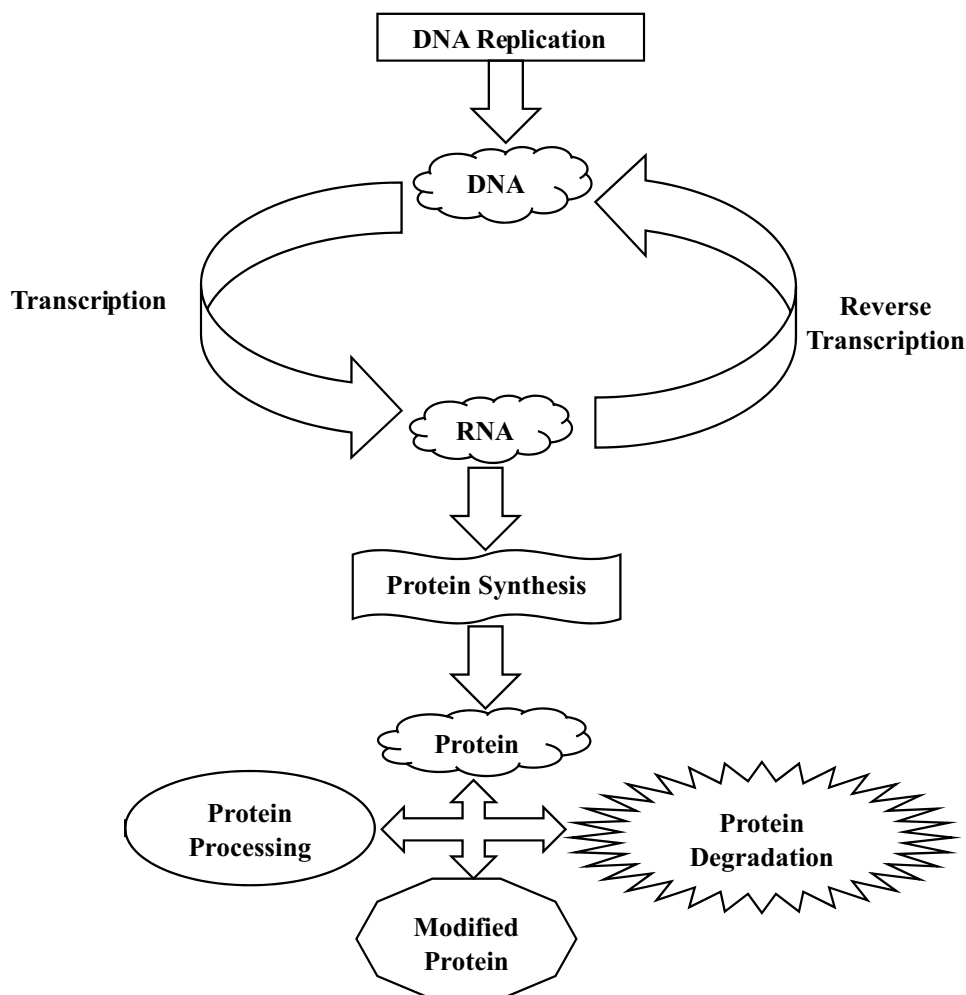


Table 4 Important proteins are expressed under saline stress conditions at different growth stages in crop plants

Crop	Genotype name	Stage	Plant Tissue	Quantification method	Biological replicates	Protein extraction	Validation	Source
Wheat	CS sensitive AMP tolerant	7 weeks	Shoot/Root	DIGE	3	Mitochondria	No	Jacoby et al. (2013)
	China-108, Yen- non-78, Norin-61, and Kantou-107	4 months	Seeds	2-DIGE	1	Total Protein	No	Kamal et al. (2010)
	Shanrong 3 toler- ant, Jinan 177 sensitive	Seedling	Shoot/Root	2-DGE	3	Total Protein	No	Peng et al. (2009)
Rice	Pokkali tolerant, IR29 sensitive	28 days	Roots	2-DIGE	3	Total Protein	No	Salekdeh et al. (2002)
Soybean	Jackson sensitive, Lee tolerant	21 days	Leaves	2-DIGE	3	Total Protein	No	Ma et al. (2012)
Barley	Morax tolerant, Steptoe sensitive	Seedlings	Roots	2-DIGE IPG 3–10	5	Total Protein	Yes	Witzel et al., (2009)
	Morax tolerant, Steptoe sensitive	Seedling	Leaves	2-DIGE	3	Total Protein	No	Witzel et al. (2014)
	Afzal tolerant, Line 527 sensitive	7 weeks	Leaves	2-DIGE	NS	Total Protein	No	Fatehi et al. (2012)
Tomato	Roma tolerant Supermundane sensitive	24 days	Leaves	2-DIGE	4	Total Protein	No	Manaa et al. (2013)

cases, proteins related to carbohydrate and energy metabolism are also induced under saline conditions in glycophytes, while the opposite is seen in halophytes (*S. salsa*) (Li et al. 2011).

Under salt stress, many proteins are expressed at the pre-transcriptional, post-transcriptional, and translational levels. The ability to distinguish plant stress proteins and identify suitable genes can enhance resistance to stress (Barkla et al. 2009). These complex regulatory pathways involve during TFs, osmolyte synthesis, ROS, kinase cascades, antioxidants, and iron homeostasis (Yin et al. 2015). The combined efforts of organ-specific and sub-cellular organelle-specific proteomic studies of the developmental mechanisms at different locations (leaf and roots) provide information on cellular and sub-cellular processes that regulate stress responses and signal transduction in various organelles (Hossain and Komatsu 2013). Proteomic approaches have been taken in studies of both halophytes and glycophytes. Plants using proteomics study include *Arabidopsis thaliana* (Razavizadeh et al. 2009), grass pea (Chattopadhyay et al. 2011), *Populus cathayana* (Chen et al. 2012), *Sorghum bicolor* (Ngara et al. 2012), tomato (Manaa et al. 2011), cucumber (Du et al. 2010), peanut (Jain et al. 2006), canola (Bandehagh et al. 2011), and durum wheat (Jacoby et al. 2010). Lectins are another type of protein induced by salinity and are involved in protein saccharide interactions and stress signaling. Jacalin domains work together with small lectins under stress conditions and serve as a plant tolerance mechanism (Zhang et al. 2000). Osmoticin is another type of protein that has

also been linked in plants used for salt stress resilience and enhances osmotic stress in potatoes and mangroves when treated with salt stress (Tada and Kashimura 2009). Moreover, plant tolerance mechanisms include different types of proteins such as ribosomal proteins (Chattopadhyay et al., 2011), poly-A binding proteins (Witzel et al. 2009), startup translation factors (Pang et al. 2010), translation elongation factors (Sobhanian et al. 2010), tumor-controlled proteins (during translation) (Yu et al. 2011), RNA recognition motif (RRM) (Pang et al., 2010), and tRNA syntheses (Wen et al. 2010) that can help to adopt certain defense mechanism.

Transcription Factors in Crop Plants in Response to Salt Stress

Tolerance mechanisms of crops against abiotic stresses are complicated and affect plant development at different growth stages (Chinnusamy et al. 2004). Tolerance mechanisms involve changes at the cell, tissue, and whole-plant level, and it is necessary to understand the response at the physiological and molecular levels (Farooq et al. 2009). Plant responses determined using different molecular approaches provide deep insight to figure out gene expression and signal transduction pathways and helps to find the metabolic changes that occur at different stress levels. Further, this information is used to enhance the tolerance mechanism in crop plants (Amirbakhtiar et al. 2021). Transcription factors are proteins linked to transcriptional regulators involved in chromatin remodeling or protein modification (Udvardi

et al. 2007). Transcription factors link cis-elements in the promoter regions of genes (which is stress induced) and trigger the upregulation of downstream genes that play an important role in abiotic stress tolerance (Agarwal and Jha 2010). Riechmann et al. (2000) identified 1500 TFs involved in stress response genes in *Arabidopsis*. Moreover, it has also been reported that tolerance or susceptibility is controlled at the transcriptional level, and plants respond independently to stressful conditions (Umezawa et al. 2006). Many genes are activated at the transcriptional level under salinity, which causes many metabolic proteins alteration produced under salt stress condition that regulate downstream genes and enhance stress tolerance mechanisms (Kavar et al. 2008). Vysotskaya et al. (2010) determine barley's physiological behavior and water retention under salt conditions and found that saline conditions limit the transpiration and hydraulic conductivity (HC) in salt-tolerant barley cultivars, unlike in more sensitive cultivars. Moreover, aquaporin (AQP) down-regulation was observed in salt-sensitive genotypes when salt treatment was delayed for up to 24 h. Greater tolerance was characterized by less inhibition of leaf area, greater root fresh weight, increased leaf water content, and greater chlorophyll concentration. The positive and negative effects of AQP expression have been determined at the gene expression level under saline conditions, while water transport depends on plant and cell–cell pathway interactions (López-Pérez et al. 2009). Aquaporin (*HVPIP2;1*) overexpression results in reduced salt sensitivity in transgenic rice at

100-mM NaCl (Katsuhara et al. 2003). Similarly, in maize, the expression of the AQP gene was enhanced by adding to a nutrient solution (Zhu et al. 2005). Fowler and Thomashow (2002) revealed that characterized gene products are of two types: genes that encode proteins and prevent water deficit within cells and genes induced by abiotic stress (regulatory proteins) that regulate stress signal transduction and alter the expressions of genes that could benefit the stress response (Shinozaki and Yamaguchi-Shinozaki 2007). Some important transcription factors (TFs) induced under salinity stress and salt related genes engineered and other abiotic stress conditions are presented in Tables 5 and 6 respectively.

Genome Editing and Salt Stress Tolerance

The new genomic era has brought nuclease systems with non-specific domains bonded to specific DNA sequence-binding domains. Such bonded nucleases can cut specific target genes and repair them through non-homologous end joining (NHEJ), known as genome editing (GE) (Gaj et al. 2013). First-generation GE technology includes meganucleases, i.e., ZFNs and TALENs, but achieving a specific target was difficult, labor exhaustive, and time consuming compared to second-generation genome editing techniques i.e., CRISPR/Cas9. Second-generation sequencing is easier to design and is easier, requires less time, and is cost effective. TALENs have greater binding specificity than ZFNs due to their length. TALENs have been successfully used in

Table 5 Important transcription factors (TFs) induced by salinity are used for improving salt tolerance in crop plants

Family	Gene	Stress	Crop name	Source
ZIP	<i>ZmbZIP17</i>	Drought, salt, heat	Maize	Jia et al. (2009)
	<i>OsbZIP23</i>	Drought, salt, heat	Rice	Xiang et al. (2008)
MYC	<i>AtMYC2</i>	Drought, salt, heat	Arabidopsis	Abe et al. (1997)
MYB	<i>AtMYB2</i>	Salt	Arabidopsis	Abe et al. (1997)
	<i>MYB15</i>	Salt and drought	Arabidopsis	Ding et al. (2009)
	<i>GmMYB76</i>	Salt	Soybean	Liao et al. (2008)
	<i>OsMYB3R-2</i>	Salt, drought, cold	Rice	Dai et al. (2007)
	<i>DREB2A</i>	Salt	Arabidopsis	Liu et al. (1998)
CBF/DREB	<i>OsDREB1A</i>	Salt, cold	Rice	Dubouzet et al. (2003)
	<i>WDREB2</i>	Salt	Wheat	Egawa et al. (2006)
	<i>HvDRF1</i>	Drought, salt	Barley	Xu et al. (2009)
	<i>PgDREB2A</i>	Drought, salt, cold	Pearl-millet	Agarwal et al. (2007)
	<i>GmDREBa</i>	Drought, Salt, Cold	Soybean	Li et al. (2005)
NAC	<i>AtNAC2</i>	Salt	Arabidopsis	He et al. (2005)
	<i>OsNAC6</i>	Cold, Drought, salt	Rice	Nakashima et al. (2007)
	<i>SNAC1</i>	Cold, Drought, salt	Rice	Hu et al. (2006)
	<i>GhNAC4</i>	Cold, Drought, salt	Cotton	Hu et al. (2006)
bZIP	<i>GmbZIP44</i>	Salinity, Freezing	Arabidopsis	Liao et al. (2008)
	<i>AtbZIP60</i>	Salinity	Arabidopsis	Fujita et al. (2007)
	<i>Wlip19</i>	Salinity	Rice	Zou et al. (2008)

Table 6 Important genes and their function used genome editing technique for stress tolerance in crop plants

Plants Name	Gene of interest	Gene function	Used Method	Stress	Reference
Rice	<i>RAV2</i>	Salinity Stress Response	CRISPR/Cas9	Salinity	Takagi et al. (2015)
Rice	<i>SAPK2</i>	ABA signaling	CRISPR/Cas9	Drought/Salinity	Zhang et al. (2019)
Rice	<i>OsRR22</i>	Cytokinin's signaling and metabolism	CRISPR/Cas9	Salinity	Kumar et al. (2013)
Rice	<i>DST</i>	Zinc finger TFs	CRISPR/Cas9	Salinity	Duan et al. (2016)
Tomato	<i>HyPRP1</i>	Key role in plant developmental process and stress amelioration	CRISPR/Cas9	Salinity	Lou et al. (2017)
Rice	<i>miR535</i>	microRNA maintains the salt-responsive gene at post-transcriptional level	CRISPR/Cas9	Salinity	Santosh Kumar et al. (2020)

Arabidopsis sp. (Cermak et al. 2011), tobacco (Zhang et al. 2013), rice (Li et al. 2012), and *Brachypodium sp.* (Shan et al. 2013). New genome editing technology has provided opportunities to breed crops with desirable traits (Jaganathan et al. 2018), and CRISPR/Cas9 uses Cas9 with guided RNAs (gRNA) to target multiple sites within the genome. GE crops have advantages over transgenic plants because they transfer edited DNA for specific traits (Malzahn et al. 2017). CRISPR technology has been used in model plant species such as *Arabidopsis sp.*, tobacco, rice, and some other crop plants are being considered for CRISPR technology (Jiang et al. 2013). A recent report also stated that around 20 crop species have been gene edited (Ricroch et al. 2017) for various agronomic traits as well as abiotic stress management so far. However, many of the published articles are proof of concept for CRISPR application, as they focused on knocking out specific genes that play important roles in biotic and abiotic stress tolerance. To enhance the resistance of rice salinity, Zhang et al. (2019) use a genome editing technique by engineering a Cas9-*OsRR22*-gRNA expressing vector for the rice *OsR22* gene. Of 14 transgenic T0 plants, nine mutant plants have been recognized. Six mutation forms were detected at the target site by sequencing, all of which were transferred successfully to the next generations. In T1 generations, mutant plants without transfer DNA (T-DNA) have been obtained through segregation. For their salinity tolerance and agronomic characteristics, two homozygous T2 mutant lines were studied further. In the seedling stage, the results show that the T2 homozygous mutant lines have significantly increased their salinity tolerance relative to wild plants. The Dystonia (*DST*) knockdown mutant gene is effective in improving salt tolerance. It has a major modification in agricultural characteristics, including leaf width, plant panicle count, and panicle longitudinal (Huang et al. 2009). Likewise, another study also indicated that *OsRR22*, but no improvements in other agronomic features could significantly boost the salt tolerance (Takagi et al. 2015). CRISPR/Cas9 provides the potential to shorten breeder time, dramatically lowering cost compared to traditional breeding methodology (Lee et al. 2016).

Future Research Directions

Genetic engineering for tolerance to salinity shows promise when overcoming obstacles to hybridization for introgression of appropriate genes helping to interpret the results for the salinity tolerance process. In addition, the integration of the physiological, metabolic, and biochemical characteristics of salinity tolerance is important to resolve the information issues in response to the stress of the entire plant phenotype. Salinity tolerance can be enhanced using knowledge about the morphology, physiology, and genetics of the crop plant that offers a selective landscape context within which scientists must maneuver crop plants. In a way, the result after introgression of the genes responsible for salinity tolerance in crops appears to be highly divergent, especially from the establishment and evolution perspective. Much advancement in adaptation to saline conditions in crop production will be anticipated with efficient molecular-aided approaches to breeding complemented by a framework incorporating multiple components, such as molecular next-generation sequencing (NGS) technologies, cost-efficient protocols, and precise quantitative trait expression determination. High-level tolerance to salinity includes several gene modifications, such as those involving the transportation and division of KCl, NaCl, and Cl at genetic and epigenetic stages and those that include morphological and anatomical variations. Manipulation of several intervarietal crosses to pyramid QTLs by the QTL tool can be implemented in nature. Within taxonomic families of economically significant crop species, i.e., grass (Poaceae, Gramineae), wide pools of genetic variance for salinity tolerance can be exploited significantly by introgression by interspecific hybridization and transgenic approaches. Examples include genomic and multiple gene selection where it is possible to exploit the combination of MAS and traditional backcross and pedigree analysis approaches to pyramidal multiple genes responsible for tolerance. New genomics and GE technologies provide options for a biologist to enhance salt tolerance using CRISPR-based GE techniques. NBT provides a platform for scientists to identify desirable genes and insert them into target crops

more quickly than conventional breeding. Knowledge about GWAS needs to expand to figure out a greater number of proteins family members, TFs, and a group of genes that played a significant role under salinity stress condition. Furthermore, the 3D protein structure deeply explained the protein structure and provides crucial information for subsequent research on biological functions. The major research aims in future should be to increase yield, nutritional factors, and biotic and abiotic stress tolerance (salinity and drought). CRISPR-based genome editing is a breakthrough technique that needs further modification to increase target efficiency. Trails from the past five years have been preliminary, and further improvement is needed to achieve a zero hunger goal and maintain food supplies for future populations.

Conclusion

Osmotic and ionic stress are caused by salt stress, and plants respond differently when salt stress occurs. Proline, ABA, and $\text{Na}^+:\text{K}^+$ ratio determination are essential, and these could be exploited to increase crop plant tolerance mechanisms. Many genes are activated that regulate plant tolerance mechanisms under salt stress. Understanding the molecular mechanisms behind salt stress is crucial for improving and introducing new salt-tolerant cultivars of crop plants into the environment. It is also essential to consider physiological, biochemical, and molecular factors for adaptation to salt stress. Furthermore, integrated plant omics approaches are crucial for genetic engineering to cope with the problem and vast knowledge for tolerance mechanisms. Due to its efficiency, simplicity, and specificity, genome editing is a valuable tool for crop development initiatives. Functional genomics and plant breeding it have opened new possibilities. Preliminary research has found that genome editing is a viable method for developing abiotic stress-resistant crops in future to combat hunger. However, significant technological and legislative barriers must be overcome before GE can be used to reshape global agriculture. It is also necessary to identify and characterize transcription factors and their products to exploit the gene products essential for salt-tolerant lines that improve adaptation under saline conditions. Moreover, TFs, as potential genes for use in breeding and crop improvement programs, provide insight into the abiotic stress mechanisms, physiological mechanisms, and molecular mechanisms (signal transduction and metabolic alteration) that could help to produce new resistant varieties and enhance salt tolerance through genetic modification.

Acknowledgements Deanship of Scientific Research King Saud University: The initiative of the DSR Graduate Students Research Support

(GSR) “The authors thank the Deanship of Scientific Research and RSSU at King Saud University for their technical support.”

Author Contributions Conceptualization, M. Afzal, Salah El Sayed Hindawi, Hussein H Migdadi, & Muhammad Habib ur Rehman; Supervision and review, Salem S Alghamdi, & Muhammad Habib ur Rehman, Muhammad Altaf Khan; writing and review, M. Afzal, Muhammad Usama Husnain, Muhammad Habib ur Rehman, Muhammad Arslan & Muhammad Shoab.

Funding Open Access funding enabled and organized by Projekt DEAL.

Declarations

Conflicts of interest The authors declare no conflict of interest.

Ethics Approval and Consent to Participate We all declare that manuscript reporting studies do not involve any human participants, human data, or human tissue. So, it is not applicable.

Consent for Publication Our manuscript does not contain data from any person, so it is “Not applicable.”

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abdelgawad H, Zinta G, Hegab MM, Pandey R, Asard H, Abuelsoud W (2016) High salinity induces different oxidative stress and antioxidant responses in maize seedlings organs. *Front Plant Sci* 7:276
- Abe H, Yamaguchi-Shinozaki K, Urao T, Iwasaki T, Hosokawa D, Shinozaki K (1997) Role of Arabidopsis MYC and MYB homologs in drought- and abscisic acid-regulated gene expression. *Plant Cell* 9(10):1859–1868
- Afzal M, Alghamdi SS, Migdadi HH, El-Harty E, Al-Faifi SA (2022a) Agronomical and physiological responses of faba bean genotypes to salt stress. *Agriculture* 12(2):235
- Afzal M, Alghamdi SS, Nawaz H, Migdadi HH, Altaf M, El-Harty E, Al-Faifi SA, Sohaib M (2022b) Genome-wide identification and expression analysis of CC-NB-ARC-LRR (NB-ARC) disease-resistant family members from soybean (*Glycine max* L.) reveal their response to biotic stress. *J King Saud Univ Sci* 34(2):101758
- Agarwal P, Jha B (2010) Transcription factors in plants and ABA dependent and independent abiotic stress signalling. *Biol Plant* 54(2):201–212
- Agarwal P, Agarwal PK, Nair S, Sopory S, Reddy M (2007) Stress-inducible DREB2A transcription factor from *Pennisetum*

- glaucum* is a phosphoprotein and its phosphorylation negatively regulates its DNA-binding activity. *Mol Genet Genom* 277(2):189–198
- Ahanger MA, Tomar NS, Tittal M, Argal S, Agarwal R (2017) Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. *Physiol Mol Biol Plants* 23(4):731–744
- Ahmadi-Ochtapeh H, Soltanloo H, Ramezani S, Naghavi M, Nikkhah H, Yoosefi Rad S (2015) QTL mapping for salt tolerance in barley at seedling growth stage. *Biol Plant* 59(2):283–290
- Ahmed SM, Alsamman AM, Jighly A, Mubarak MH, Al-Shamaa K, Istanbuli T, Momtaz OA, AllaliEl Hamwieh AA (2021) Genome-wide association analysis of chickpea germplasm differing for salinity tolerance based on DArTseq markers. *PLoS ONE* 16(12):e0260709
- Akbarimoghaddam H, Galavi M, Ghanbari A, Panjehkeh N (2011) Salinity effects on seed germination and seedling growth of bread wheat cultivars. *Trakia J Sci* 9(1):43–50
- Akram NA, Jamil A (2007) Appraisal of physiological and biochemical selection criteria for evaluation of salt tolerance in canola (*Brassica napus* L.). *Pak J Bot* 39(5):1593–1608
- Al-Barakah FN, Sohaib M (2019) Evaluating the germination response of *Chenopodium quinoa* seeds to bacterial inoculation under different germination media and salinity conditions. *Seed Sci Technol* 47(2):161–169
- Ali S, Gautam R, Mahajan R, Krishnamurthy S, Sharma S, Singh R, Ismail A (2013) Stress indices and selectable traits in SALTOL QTL introgressed rice genotypes for reproductive stage tolerance to sodicity and salinity stresses. *Field Crop Res* 154:65–73
- Ali Z, Merrium S, Habib-ur-Rahman M et al (2022) Wetting mechanism and morphological adaptation; leaf rolling enhancing atmospheric water acquisition in wheat crop—a review. *Environ Sci Pollut Res* 29:30967–30985. <https://doi.org/10.1007/s11356-022-18846-3>
- Amirbakhtiar N, Ismaili A, Ghaffari M-R, Mirdar Mansuri R, Sanjari S, Shobbar Z-S (2021) Transcriptome analysis of bread wheat leaves in response to salt stress. *PLoS ONE* 16(7):e0254189
- Angessa TT, Zhang X-Q, Zhou G, Broughton S, Zhang W, Li C (2017) Early growth stages salinity stress tolerance in CM72 x Gairdner doubled haploid barley population. *PLoS ONE* 12(6):e0179715
- Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar Na⁺/H⁺ antiporter in *Arabidopsis*. *Science* 285(5431):1256–1258
- Arzani A (2008) Improving salinity tolerance in crop plants: a biotechnological view. *In Vitro Cell Dev Biol Plant* 44(5):373–383
- Arzani A, Ashraf M (2016) Smart engineering of genetic resources for enhanced salinity tolerance in crop plants. *Crit Rev Plant Sci* 35(3):146–189
- Ashraf M, Foolad MR (2013) Crop breeding for salt tolerance in the era of molecular markers and marker-assisted selection. *Plant Breed* 132(1):10–20
- Ashraf M, Harris P (2004) Potential biochemical indicators of salinity tolerance in plants. *Plant Sci* 166(1):3–16
- Askari H, Edqvist J, Hajheidari M, Kafi M, Salekdeh GH (2006) Effects of salinity levels on proteome of *Suaeda aegyptiaca* leaves. *Proteomics* 6(8):2542–2554
- Atienza SG, Jafary H, Niks RE (2004) Accumulation of genes for susceptibility to rust fungi for which barley is nearly a nonhost results in two barley lines with extreme multiple susceptibility. *Planta* 220(1):71–79
- Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. *J Exp Bot* 63(10):3523–3543
- Atwell S, Huang YS, Vilhjálmsson BJ, Willems G, Horton M, Li Y, Meng D, Platt A, Tarone AM, Hu TT (2010) Genome-wide association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. *Nature* 465(7298):627–631
- Bahieldin A, Atef A, Sabir JS, Gadalla NO, Edris S, Alzohairy AM, Radhwan NA, Baeshen MN, Ramadan AM, Eissa HF (2015) RNA-Seq analysis of the wild barley (*H. spontaneum*) leaf transcriptome under salt stress. *CR Biol* 338(5):285–297
- Ball MC, Farquhar GD (1984) Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. *Plant Physiol* 74(1):1–6
- Bandehagh A, Salekdeh GH, Toorchi M, Mohammadi A, Komatsu S (2011) Comparative proteomic analysis of canola leaves under salinity stress. *Proteomics* 11(10):1965–1975
- Bano A, Fatima M (2009) Salt tolerance in *Zea mays* (L.) following inoculation with *Rhizobium* and *Pseudomonas*. *Biol Fertil Soils* 45(4):405–413
- Barati A, MOGHADAM M, Mohammadi S, Ghazvini H, Sadeghzadeh B (2017) Identification of QTLs associated with agronomic and physiological traits under salinity stress in barley
- Barkla BJ, Vera-Estrella R, Hernández-Coronado M, Pantoja O (2009) Quantitative proteomics of the tonoplast reveals a role for glycolytic enzymes in salt tolerance. *Plant Cell* 21(12):4044–4058
- Bashan Y (1998) Inoculants of plant growth-promoting bacteria for use in agriculture. *Biotechnol Adv* 16(4):729–770
- Bashan Y, de-Bashan LE, Prabhu S, Hernandez J-P (2014) Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). *Plant Soil* 378(1):1–33
- Buchanan CD, Lim S, Salzman RA, Kagiampakis I, Morishige DT, Weers BD, Klein RR, Pratt LH, Cordonnier-Pratt M-M, Klein PE (2005) Sorghum bicolor's transcriptome response to dehydration, high salinity and ABA. *Plant Mol Biol* 58(5):699–720
- Buckler ES IV, Thornsberry JM (2002) Plant molecular diversity and applications to genomics. *Curr Opin Plant Biol* 5(2):107–111
- Byrt CS, Xu B, Krishnan M, Lightfoot DJ, Athman A, Jacobs AK, Watson-Haigh NS, Plett D, Munns R, Tester M (2014) The Na⁺ transporter, Ta hkt 1; 5-d, limits shoot na⁺ accumulation in bread wheat. *Plant J* 80(3):516–526
- Caruso G, Cavaliere C, Guarino C, Gubbiotti R, Foglia P, Laganà A (2008) Identification of changes in *Triticum durum* L. leaf proteome in response to salt stress by two-dimensional electrophoresis and MALDI-TOF mass spectrometry. *Anal Bioanal Chem* 391(1):381–390
- Cattivelli L, Baldi P, Crosatti C, Di Fonzo N, Faccioli P, Grossi M, Mastrangelo AM, Pecchioni N, Stanca AM (2002) Chromosome regions and stress-related sequences involved in resistance to abiotic stress in Triticaceae. *Plant Mol Biol* 48(5):649–665
- Cermak T, Doyle EL, Christian M, Wang L, Zhang Y, Schmidt C, Baller JA, Somia NV, Bogdanove AJ, Voytas DF (2011) Efficient design and assembly of custom TALEN and other TAL effector-based constructs for DNA targeting. *Nucleic Acids Res* 39(12):e82
- Chakraborty K, Sairam RK, Bhattacharya R (2012) Differential expression of salt overly sensitive pathway genes determines salinity stress tolerance in Brassica genotypes. *Plant Physiol Biochem* 51:90–101
- Chattopadhyay A, Subba P, Pandey A, Bhushan D, Kumar R, Datta A, Chakraborty S, Chakraborty N (2011) Analysis of the grasspea proteome and identification of stress-responsive proteins upon exposure to high salinity, low temperature, and abscisic acid treatment. *Phytochemistry* 72(10):1293–1307
- Chaudhary R, Baranwal VK, Kumar R, Sircar D, Chauhan H (2019) Genome-wide identification and expression analysis of Hsp70, Hsp90, and Hsp100 heat shock protein genes in barley under stress conditions and reproductive development. *Funct Integr Genom* 19(6):1007–1022
- Chen S, Xing J, Lan H (2012) Comparative effects of neutral salt and alkaline salt stress on seed germination, early seedling growth

- and physiological response of a halophyte species *Chenopodium glaucum*. *Afr J Biotech* 11(40):9572–9581
- Chinnusamy V, Schumaker K, Zhu JK (2004) Molecular genetic perspectives on cross-talk and specificity in abiotic stress signalling in plants. *J Exp Bot* 55(395):225–236
- Close TJ, Wanamaker SI, Caldo RA, Turner SM, Ashlock DA, Dickerson JA, Wing RA, Muehlbauer GJ, Kleinhofs A, Wise RP (2004) A new resource for cereal genomics: 22K barley GeneChip comes of age. *Plant Physiol* 134(3):960–968
- Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol* 11(1):1–14
- Dai X, Xu Y, Ma Q, Xu W, Wang T, Xue Y, Chong K (2007) Over-expression of an R1R2R3 MYB gene, OsMYB3R-2, increases tolerance to freezing, drought, and salt stress in transgenic *Arabidopsis*. *Plant Physiol* 143(4):1739–1751
- De Leon TB, Linscombe S, Subudhi PK (2017) Identification and validation of QTLs for seedling salinity tolerance in introgression lines of a salt tolerant rice landrace ‘Pokkali.’ *PLoS ONE* 12(4):e0175361
- Diatchenko L, Lau Y, Campbell AP, Chenchik A, Moqadam F, Huang B, Lukyanov S, Lukyanov K, Gurskaya N, Sverdlov ED (1996) Suppression subtractive hybridization: a method for generating differentially regulated or tissue-specific cDNA probes and libraries. *Proc Natl Acad Sci* 93(12):6025–6030
- Ding Z, Li S, An X, Liu X, Qin H, Wang D (2009) Transgenic expression of MYB15 confers enhanced sensitivity to abscisic acid and improved drought tolerance in *Arabidopsis thaliana*. *J Genet Genom* 36(1):17–29
- Du C-X, Fan H-F, Guo S-R, Tezuka T, Li J (2010) Proteomic analysis of cucumber seedling roots subjected to salt stress. *Phytochemistry* 71(13):1450–1459
- Duan Y-B, Li J, Qin R-Y, Xu R-F, Li H, Yang Y-C, Ma H, Li L, Wei P-C, Yang J-B (2016) Identification of a regulatory element responsible for salt induction of rice OsRAV2 through ex situ and in situ promoter analysis. *Plant Mol Biol* 90(1):49–62
- Dubouzet JG, Sakuma Y, Ito Y, Kasuga M, Dubouzet EG, Miura S, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2003) OsDREB genes in rice, *Oryza sativa* L., encode transcription activators that function in drought-, high-salt- and cold-responsive gene expression. *Plant J* 33(4):751–763
- Egawa C, Kobayashi F, Ishibashi M, Nakamura T, Nakamura C, Takumi S (2006) Differential regulation of transcript accumulation and alternative splicing of a DREB2 homolog under abiotic stress conditions in common wheat. *Genes Genet Syst* 81(2):77–91
- Fan L, Li H, Zhuo J, Zhang Y, Wang J, Chen L, Yang Z, Chu C, Xie S, Laird AR (2016a) The human brainnetome atlas: a new brain atlas based on connectonal architecture. *Cereb Cortex* 26(8):3508–3526
- Fan Y, Zhou G, Shabala S, Chen Z-H, Cai S, Li C, Zhou M (2016b) Genome-wide association study reveals a new QTL for salinity tolerance in barley (*Hordeum vulgare* L.). *Front Plant Sci* 7:946
- Farooq M, Wahid A, Kobayashi N, Fujita D, Basra S (2009) Plant drought stress: effects, mechanisms and management. *Sustainable agriculture*. Springer, Berlin, pp 153–188
- Fatehi F, Hosseinzadeh A, Alizadeh H, Brimavandi T, Struik PC (2012) The proteome response of salt-resistant and salt-sensitive barley genotypes to long-term salinity stress. *Mol Biol Rep* 39(5):6387–6397
- Fowler S, Thomashow MF (2002) *Arabidopsis* transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. *Plant Cell* 14(8):1675–1690
- Frisch M, Bohn M, Melchinger AE (1999) Comparison of selection strategies for marker-assisted backcrossing of a gene. *Crop Sci* 39(5):1295–1301
- Fujita M, Mizukado S, Fujita Y, Ichikawa T, Nakazawa M, Seki M, Matsui M, Yamaguchi-Shinozaki K, Shinozaki K (2007) Identification of stress-tolerance-related transcription-factor genes via mini-scale Full-length cDNA Over-eXpressor (FOX) gene hunting system. *Biochem Biophys Res Commun* 364(2):250–257
- Gaj T, Gersbach CA, Barbas CF III (2013) ZFN, TALEN, and CRISPR/Cas-based methods for genome engineering. *Trends Biotechnol* 31(7):397–405
- Gama PBS, Tanaka K, Eneji AE, Eltayeb AE, Siddig KE (2009) Salt-induced stress effects on biomass, photosynthetic rate, and reactive oxygen species-scavenging enzyme accumulation in common bean. *J Plant Nutr* 32(5):837–854
- Genc Y, Oldach K, Verbyla AP, Lott G, Hassan M, Tester M, Wallwork H, McDonald GK (2010) Sodium exclusion QTL associated with improved seedling growth in bread wheat under salinity stress. *Theor Appl Genet* 121(5):877–894
- Gharat SA, Parmar S, Tambat S, Vasudevan M, Shaw BP (2016) Transcriptome analysis of the response to NaCl in *Suaeda maritima* provides an insight into salt tolerance mechanisms in halophytes. *PLoS ONE* 11(9):e0163485
- Gong D, Wang G, Si W, Zhou Y, Liu Z, Jia J (2018) Effects of salt stress on photosynthetic pigments and activity of ribulose-1, 5-bisphosphate carboxylase/oxygenase in *Kalidium foliatum*. *Russ J Plant Physiol* 65(1):98–103
- Goyal E, Amit SK, Singh RS, Mahato AK, Chand S, Kanika K (2016) Transcriptome profiling of the salt-stress response in *Triticum aestivum* cv. Kharchia. *Local Sci Rep* 6(1):1–14
- Gregorio G, Islam M, Vergara G, Thirumeni S (2013) Recent advances in rice science to design salinity and other abiotic stress tolerant rice varieties. *Sabrao J Breed Genet* 45(1):31–41
- Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. *International journal of genomics* 2014
- Gupta P, Kumar J, Mir R, Kumar A (2010) 4 Marker-assisted selection as a component of conventional plant breeding. *Plant Breed Rev* 33:145
- Ha E, Ikhajagba B, Bamidele J, Ogic-Odia E (2008) Salinity effects on young healthy seedling of *Kyllingia peruviana* collected from escravos, Delta state. *Glob J Environ Res* 2(2):74–88
- Habib-ur-Rahman M, Raza A, Ahrends HE et al (2022) Impact of in-field soil heterogeneity on biomass and yield of winter triticale in an intensively cropped hummocky landscape under temperate climate conditions. *Precision Agric* 23:912–938. <https://doi.org/10.1007/s11119-021-09868-x>
- Halfter U, Ishitani M, Zhu J-K (2000) The *Arabidopsis* SOS₂ protein kinase physically interacts with and is activated by the calcium-binding protein SOS3. *Proc Natl Acad Sci* 97(7):3735–3740
- Hamamoto S, Horie T, Hauser F, Deinlein U, Schroeder JI, Uozumi N (2015) HKT transporters mediate salt stress resistance in plants: from structure and function to the field. *Curr Opin Biotechnol* 32:113–120
- Hampson C, Simpson G (1990) Effect of temperature, salt and water stress on early growth of wheat (*Triticum aestivum* L.) germination. *Can J Bot* 68:524–528
- Hanin M, Ebel C, Ngom M, Laplaze L, Masmoudi K (2016) New insights on plant salt tolerance mechanisms and their potential use for breeding. *Front Plant Sci* 7:1787
- Hasan A, Doubrovina E, Sottile R, Prockop S, Klatt MG, Heller G, Selvakumar A, Barnett L, Hsu KC, O'Reilly RJ (2022) Dominant epitopes presented by prevalent HLA alleles permit wide use of banked CMVpp65 T-cells in adoptive therapy. *Blood Adv*
- He XJ, Mu RL, Cao WH, Zhang ZG, Zhang JS, Chen SY (2005) AtNAC₂, a transcription factor downstream of ethylene and auxin

- signaling pathways, is involved in salt stress response and lateral root development. *Plant J* 44(6):903–916
- Hirt H (2009) *Plant stress biology: from genomics to systems biology*. Wiley, New York
- Horie T, Kaneko T, Sugimoto G, Sasano S, Panda SK, Shibasaka M, Katsuhara M (2011) Mechanisms of water transport mediated by PIP aquaporins and their regulation via phosphorylation events under salinity stress in barley roots. *Plant Cell Physiol* 52(4):663–675
- Horie T, Motoda J, Kubo M, Yang H, Yoda K, Horie R, Chan WY, Leung HY, Hattori K, Konomi M (2005) Enhanced salt tolerance mediated by AtHKT1 transporter-induced Na⁺ unloading from xylem vessels to xylem parenchyma cells. *Plant J* 44(6):928–938
- Hossain Z, Komatsu S (2013) Contribution of proteomic studies towards understanding plant heavy metal stress response. *Front Plant Sci* 3:310
- Hu H, Dai M, Yao J, Xiao B, Li X, Zhang Q, Xiong L (2006) Over-expressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. *Proc Natl Acad Sci* 103(35):12987–12992
- Huang X-Y, Chao D-Y, Gao J-P, Zhu M-Z, Shi M, Lin H-X (2009) A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. *Genes Dev* 23(15):1805–1817
- Inan G, Zhang Q, Li P, Wang Z, Cao Z, Zhang H, Zhang C, Quist TM, Goodwin SM, Zhu J (2004) Salt cress. A halophyte and cryophyte Arabidopsis relative model system and its applicability to molecular genetic analyses of growth and development of extremophiles. *Plant Physiol* 135(3):1718–1737
- Isah T (2019) Stress and defense responses in plant secondary metabolites production. *Biol Res* 52
- Jacoby RP, Millar AH, Taylor NL (2010) Wheat mitochondrial proteomes provide new links between antioxidant defense and plant salinity tolerance. *J Proteome Res* 9(12):6595–6604
- Jacoby RP, Millar AH, Taylor NL (2013) Investigating the role of respiration in plant salinity tolerance by analyzing mitochondrial proteomes from wheat and a salinity-tolerant Amphiploid (wheat × *Lophopyrum elongatum*). *J Proteome Res* 12(11):4807–4829
- Jaganathan D, Ramasamy K, Sellamuthu G, Jayabalan S, Venkataraman G (2018) CRISPR for crop improvement: an update review. *Front Plant Sci* 9:985
- Jain S, Srivastava S, Sarin NB, Kav NN (2006) Proteomics reveals elevated levels of PR 10 proteins in saline-tolerant peanut (*Arachis hypogaea*) calli. *Plant Physiol Biochem* 44(4):253–259
- James RA, Blake C, Byrt CS, Munns R (2011) Major genes for Na⁺ exclusion, Nax1 and Nax2 (wheat HKT1; 4 and HKT1; 5), decrease Na⁺ accumulation in bread wheat leaves under saline and waterlogged conditions. *J Exp Bot* 62(8):2939–2947
- Jamshidi A, Javanmard H (2018) Evaluation of barley (*Hordeum vulgare* L.) genotypes for salinity tolerance under field conditions using the stress indices. *Ain Shams Eng J* 9(4):2093–2099
- Janaki Ramayya P, Vinukonda VP, Singh UM, Alam S, Venkateshwarlu C, Vipparla AK, Dixit S, Yadav S, Abbai R, Badri J (2021) Marker-assisted forward and backcross breeding for improvement of elite Indian rice variety Naveen for multiple biotic and abiotic stress tolerance. *PLoS ONE* 16(9):e0256721
- Jia Z, Lian Y, Zhu Y, He J, Cao Z, Wang G (2009) Cloning and characterization of a putative transcription factor induced by abiotic stress in *Zea mays*. *Afr J Biotechnol* 8(24)
- Jiang W, Zhou H, Bi H, Fromm M, Yang B, Weeks DP (2013) Demonstration of CRISPR/Cas9/sgRNA-mediated targeted gene modification in Arabidopsis, tobacco, sorghum and rice. *Nucleic Acids Res* 41(20):e188
- Kamal AHM, Kim K-H, Shin K-H, Choi J-S, Baik B-K, Tsujimoto H, Heo HY, Park C-S, Woo S-H (2010) Abiotic stress responsive proteins of wheat grain determined using proteomics technique. *Aust J Crop Sci* 4(3):196–208
- Katsuhara M, Koshio K, Shibasaka M, Hayashi Y, Hayakawa T, Kasamo K (2003) Over-expression of a barley aquaporin increased the shoot/root ratio and raised salt sensitivity in transgenic rice plants. *Plant Cell Physiol* 44(12):1378–1383
- Katz A, Waridel P, Shevchenko A, Pick U (2007) Salt-induced changes in the plasma membrane proteome of the halotolerant alga *Dunaliella salina* as revealed by blue native gel electrophoresis and nano-LC-MS/MS analysis. *Mol Cell Proteomics* 6(9):1459–1472
- Kavar T, Maras M, Kidrič M, Šuštar-Vozlič J, Meglič V (2008) Identification of genes involved in the response of leaves of *Phaseolus vulgaris* to drought stress. *Mol Breed* 21(2):159–172
- Kazemi K, Eskandari H (2011) Effects of salt stress on germination and early seedling growth of rice (*Oryza sativa*) cultivars in Iran. *Afr J Biotech* 10(77):17789–17792
- Khan M, Gul B, Weber D (2002) Seed germination in relation to salinity and temperature in *Sarcobatus vermiculatus*. *Biol Plant* 45(1):133–135
- Khodarahmpour Z, Ifar M, Motamedi M (2012) Effects of NaCl salinity on maize (*Zea mays* L.) at germination and early seedling stage. *Afr J Biotechnol* 11(2):298–304
- Khosravinejad F, Heydari R, Farboodnia T (2008) Effects of salinity on photosynthetic pigments, respiration, and water content in two barley varieties. *Pak J Biol Sci* 11(20):2438–2442
- Kilian B, Graner A (2012) NGS technologies for analyzing germplasm diversity in genebanks. *Brief Funct Genom* 11(1):38–50
- Kim DW, Rakwal R, Agrawal GK, Jung YH, Shibato J, Jwa NS, Iwahashi Y, Iwahashi H, Kim DH, Shim IS (2005) A hydroponic rice seedling culture model system for investigating proteome of salt stress in rice leaf. *Electrophoresis* 26(23):4521–4539
- Kumar G, Purty RS, Sharma MP, Singla-Pareek SL, Pareek A (2009) Physiological responses among Brassica species under salinity stress show strong correlation with transcript abundance for SOS pathway-related genes. *J Plant Physiol* 166(5):507–520
- Kumar K, Kumar M, Kim S-R, Ryu H, Cho Y-G (2013) Insights into genomics of salt stress response in rice. *Rice* 6(1):1–15
- Kumar V, Singh A, Mithra SA, Krishnamurthy S, Parida SK, Jain S, Tiwari KK, Kumar P, Rao AR, Sharma S (2015) Genome-wide association mapping of salinity tolerance in rice (*Oryza sativa*). *DNA Res* 22(2):133–145
- Lang L, Xu A, Ding J, Zhang Y, Zhao N, Tian Z, Liu Y, Wang Y, Liu X, Liang F (2017) Quantitative trait locus mapping of salt tolerance and identification of salt-tolerant genes in *Brassica napus* L. *Front Plant Sci* 8:1000
- Lee CM, Cradick TJ, Bao G (2016) The Neisseria meningitidis CRISPR-Cas9 system enables specific genome editing in mammalian cells. *Mol Ther* 24(3):645–654
- Lee I, Seo Y-S, Coltrane D, Hwang S, Oh T, Marcotte EM, Ronald PC (2011) Genetic dissection of the biotic stress response using a genome-scale gene network for rice. *Proc Natl Acad Sci* 108(45):18548–18553
- Legay S, Lamoureux D, Hausman J-F, Hoffmann L, Evers D (2009) Monitoring gene expression of potato under salinity using cDNA microarrays. *Plant Cell Rep* 28(12):1799–1816
- Lewis CM (2002) Genetic association studies: design, analysis and interpretation. *Brief Bioinform* 3(2):146–153
- Li W, Zhang C, Lu Q, Wen X, Lu C (2011) The combined effect of salt stress and heat shock on proteome profiling in Suaeda salsa. *J Plant Physiol* 168(15):1743–1752
- Li T, Liu B, Spalding MH, Weeks DP, Yang B (2012) High-efficiency TALEN-based gene editing produces disease-resistant rice. *Nat Biotechnol* 30(5):390–392

- Li L, Li M, Qi X, Tang X, Zhou Y (2018) De novo transcriptome sequencing and analysis of genes related to salt stress response in *Glehnia littoralis*. *PeerJ* 6:e5681
- Liang W, Cui W, Ma X, Wang G, Huang Z (2014) Function of wheat Ta-UnP gene in enhancing salt tolerance in transgenic Arabidopsis and rice. *Biochem Biophys Res Commun* 450(1):794–801
- Liang W, Ma X, Wan P, Liu L (2018) Plant salt-tolerance mechanism: A review. *Biochem Biophys Res Commun* 495(1):286–291
- Liao Y, Zou H-F, Wang H-W, Zhang W-K, Ma B, Zhang J-S, Chen S-Y (2008) Soybean GmMYB76, GmMYB92, and GmMYB177 genes confer stress tolerance in transgenic Arabidopsis plants. *Cell Res* 18(10):1047–1060
- Liu J, Ishitani M, Halfter U, Kim C-S, Zhu J-K (2000) The Arabidopsis thaliana SOS2 gene encodes a protein kinase that is required for salt tolerance. *Proc Natl Acad Sci* 97(7):3730–3734
- Liu Y, Lai N, Gao K, Chen F, Yuan L, Mi G (2013) Ammonium inhibits primary root growth by reducing the length of meristem and elongation zone and decreasing elemental expansion rate in the root apex in Arabidopsis thaliana. *PLoS ONE* 8(4):e61031
- Liu C, Mao B, Ou S, Wang W, Liu L, Wu Y, Chu C, Wang X (2014) OsbZIP71, a bZIP transcription factor, confers salinity and drought tolerance in rice. *Plant Mol Biol* 84(1):19–36
- Liu C, Cheng Y-J, Wang J-W, Weigel D (2017) Prominent topologically associated domains differentiate global chromatin packing in rice from Arabidopsis. *Nature Plants* 3(9):742–748
- Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchi-Shinozaki K, Shinozaki K (1998) Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low-temperature-responsive gene expression, respectively. *Plant Cell* 10(8):1391–1406
- Long NV, Dolstra O, Malosetti M, Kilian B, Graner A, Visser RG, van der Linden CG (2013) Association mapping of salt tolerance in barley (*Hordeum vulgare* L.). *Theor Appl Genet* 126(9):2335–2351
- López-Pérez L, del Carmen M-B, Maurel C, Carvajal M (2009) Changes in plasma membrane lipids, aquaporins and proton pump of broccoli roots, as an adaptation mechanism to salinity. *Phytochemistry* 70(4):492–500
- Lou D, Wang H, Liang G, Yu D (2017) OsSAPK2 confers abscisic acid sensitivity and tolerance to drought stress in rice. *Front Plant Sci* 8:993
- Lowe R, Shirley N, Bleackley M, Dolan S, Shafee T (2017) Transcriptomics technologies. *PLoS Comput Biol* 13(5):e1005457
- Luan Z, Xiao M, Zhou D, Zhang H, Tian Y, Wu Y, Guan B, Song Y (2014) Effects of salinity, temperature, and polyethylene glycol on the seed germination of sunflower (*Helianthus annuus* L.). *Sci World J* 2014
- Luo Q, Teng W, Fang S, Li H, Li B, Chu J, Li Z, Zheng Q (2019) Transcriptome analysis of salt-stress response in three seedling tissues of common wheat. *The Crop Journal* 7(3):378–392
- Ma H, Song L, Shu Y, Wang S, Niu J, Wang Z, Yu T, Gu W, Ma H (2012) Comparative proteomic analysis of seedling leaves of different salt tolerant soybean genotypes. *J Proteomics* 75(5):1529–1546
- Mahajan S, Pandey GK, Tuteja N (2008) Calcium-and salt-stress signaling in plants: shedding light on SOS pathway. *Arch Biochem Biophys* 471(2):146–158
- Malzahn A, Lowder L, Qi Y (2017) Plant genome editing with TALEN and CRISPR. *Cell Biosci* 7(1):1–18
- Manaa A, Ben Ahmed H, Valot B, Bouchet J-P, Aschi-Smiti S, Causse M, Faurobert M (2011) Salt and genotype impact on plant physiology and root proteome variations in tomato. *J Exp Bot* 62(8):2797–2813
- Manaa A, Mimouni H, Wasti S, Gharbi E, Aschi-Smiti S, Faurobert M, Ahmed HB (2013) Comparative proteomic analysis of tomato (*Solanum lycopersicum*) leaves under salinity stress. *Plant Omics* 6(4):268–277
- Mano Y, Takeda K (1997) Mapping quantitative trait loci for salt tolerance at germination and the seedling stage in barley (*Hordeum vulgare* L.). *Euphytica* 94(3):263–272
- Martínez-Atienza J, Jiang X, Garcíadeblás B, Mendoza I, Zhu J-K, Pardo JM, Quintero FJ (2007) Conservation of the salt overly sensitive pathway in rice. *Plant Physiol* 143(2):1001–1012
- Memon SA, Hou X, Wang LJ (2010) Morphological analysis of salt stress response of Pak Choi. *Electron J Environ Agric Food Chem* 9(1)
- Mendoza I, Rubio F, Rodríguez-Navarro A, Pardo JM (1994) The protein phosphatase calcineurin is essential for NaCl tolerance of *Saccharomyces cerevisiae*. *J Biol Chem* 269(12):8792–8796
- Merriam S, Ali Z, Tahir M et al (2022) Leaf rolling dynamics for atmospheric moisture harvesting in wheat plant as an adaptation to arid environments. *Environ Sci Pollut Res*. <https://doi.org/10.1007/s11356-022-18936-2>
- Mirdar Mansuri R, Shobbar Z-S, Babaeian Jelodar N, Ghaffari M, Mohammadi SM, Daryani P (2020) Salt tolerance involved candidate genes in rice: an integrative meta-analysis approach. *BMC Plant Biol* 20(1):1–14
- Mitchell-Olds T (2010) Complex-trait analysis in plants. *Genome Biol* 11(4):1–3
- Mu C, Zhang S, Yu G, Chen N, Li X, Liu H (2013) Overexpression of small heat shock protein LimHSP16.45 in Arabidopsis enhances tolerance to abiotic stresses. *PLoS ONE* 8(12):e82264
- Munns R (2002) Comparative physiology of salt and water stress. *Plant Cell Environ* 25(2):239–250
- Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annu Rev Plant Biol* 59:651–681
- Munns R, James RA, Xu B, Athman A, Conn SJ, Jordans C, Byrt CS, Hare RA, Tyerman SD, Tester M (2012) Wheat grain yield on saline soils is improved by an ancestral Na⁺ transporter gene. *Nat Biotechnol* 30(4):360–364
- Mutz K-O, Heilkenbrinker A, Lönne M, Walter J-G, Stahl F (2013) Transcriptome analysis using next-generation sequencing. *Curr Opin Biotechnol* 24(1):22–30
- Mwando E, Han Y, Angessa TT, Zhou G, Hill CB, Zhang X-Q, Li C (2020) Genome-wide association study of salinity tolerance during germination in barley (*Hordeum vulgare* L.). *Front Plant Sci* 11:118
- Nakashima K, Tran LSP, Van Nguyen D, Fujita M, Maruyama K, Todaka D, Ito Y, Hayashi N, Shinozaki K, Yamaguchi-Shinozaki K (2007) Functional analysis of a NAC-type transcription factor OsNAC6 involved in abiotic and biotic stress-responsive gene expression in rice. *Plant J* 51(4):617–630
- Naranjo MA, Forment J, Roldan M, Serrano R, Vicente O (2006) Overexpression of Arabidopsis thaliana LTL1, a salt-induced gene encoding a GDSL-motif lipase, increases salt tolerance in yeast and transgenic plants. *Plant Cell Environ* 29(10):1890–1900
- Naveed SA, Zhang F, Zhang J, Zheng T-Q, Meng L-J, Pang Y-L, Xu J-L, Li Z-K (2018) Identification of QTN and candidate genes for salinity tolerance at the germination and seedling stages in rice by genome-wide association analyses. *Sci Rep* 8(1):1–11
- Negrão S, Courtois B, Ahmadi N, Abreu I, Saibo N, Oliveira M (2011) Recent updates on salinity stress in rice: from physiological to molecular responses. *Crit Rev Plant Sci* 30(4):329–377
- Netondo GW, Onyango JC, Beck E (2004) Sorghum and salinity: II. Gas exchange and chlorophyll fluorescence of sorghum under salt stress. *Crop Sci* 44(3):806–811
- Ngara R, Ndimba R, Borch-Jensen J, Jensen ON, Ndimba B (2012) Identification and profiling of salinity stress-responsive proteins in Sorghum bicolor seedlings. *J Proteomics* 75(13):4139–4150
- Nguyen VL, Ribot SA, Dolstra O, Niks RE, Visser RG, van der Linden CG (2013) Identification of quantitative trait loci for ion

- homeostasis and salt tolerance in barley (*Hordeum vulgare* L.). *Mol Breed* 31(1):137–152
- Othman F, Naufaliansyah MA, Hussain F (2019) Effect of water salinity on permeability alteration during CO₂ sequestration. *Adv Water Resour* 127:237–251
- Pang Q, Chen S, Dai S, Chen Y, Wang Y, Yan X (2010) Comparative proteomics of salt tolerance in *Arabidopsis thaliana* and *Thellungiella halophila*. *J Proteome Res* 9(5):2584–2599
- Parihar P, Singh S, Singh R, Singh VP, Prasad SM (2015) Effect of salinity stress on plants and its tolerance strategies: a review. *Environ Sci Pollut Res* 22(6):4056–4075
- Pastori GM, Foyer CH (2002) Common components, networks, and pathways of cross-tolerance to stress. The central role of “redox” and abscisic acid-mediated controls. *Plant Physiol* 129(2):460–468
- Patel PR, Kajal SS, Patel VR, Patel VJ, Khristi SM (2010) Impact of saline water stress on nutrient uptake and growth of cowpea. *Braz J Plant Physiol* 22(1):43–48
- Peng Z, Wang M, Li F, Lv H, Li C, Xia G (2009) A proteomic study of the response to salinity and drought stress in an introgression strain of bread wheat. *Mol Cell Proteomics* 8(12):2676–2686
- Puram VRR, Ontoy J, Subudhi PK (2018) Identification of QTLs for salt tolerance traits and prebreeding lines with enhanced salt tolerance in an introgression line population of rice. *Plant Mol Biol Rep* 36(5):695–709
- Putney SD, Herlihy WC, Schimmel P (1983) A new troponin T and cDNA clones for 13 different muscle proteins, found by shotgun sequencing. *Nature* 302(5910):718–721
- Quamruzzaman M, Manik S, Shabala S, Cao F, Zhou M (2021) Genome-wide association study reveals a genomic region on 5AL for salinity tolerance in wheat. *Theor Appl Genet* 1–13
- Rahman MHU, Ahmad A, Wang X, Wajid A, Nasim W, Hussain M, Awais M (2018) Multi-model projections of future climate and climate change impacts uncertainty assessment for cotton production in Pakistan. *Agric For Meteorol* 253:94–113. <https://doi.org/10.1016/j.agrformet.2018.02.008>
- Rahman MHU, Ahmad A et al (2019) Application of CSM-CROPGRO cotton model for cultivars and optimum planting dates: evaluation in changing semiarid climate. *Field Crops Res* 238:139–152. <https://doi.org/10.1016/j.fcr.2017.07.007>
- Rahman MHU, Ahmad I, Wang D et al (2020a) Influence of semi-arid environment on radiation use efficiency and other growth attributes of lentil crop. *Environ Sci Pollut Res* 28:13697–13711. <https://doi.org/10.1007/s11356-020-11376-w>
- Rahman MH et al (2020b) Climate resilient cotton production system: a case study in Pakistan. In: Ahmad S, Hasanuzzaman M (eds) *Cotton Production and Uses*. Springer, Singapore. https://doi.org/10.1007/978-981-15-1472-2_22
- Razavizadeh R, Ehsanpour AA, Ahsan N, Komatsu S (2009) Proteome analysis of tobacco leaves under salt stress. *Peptides* 30(9):1651–1659
- Ren Z-H, Gao J-P, Li L-G, Cai X-L, Huang W, Chao D-Y, Zhu M-Z, Wang Z-Y, Luan S, Lin H-X (2005) A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nat Genet* 37(10):1141–1146
- Ribaut J-M, Ragot M (2007) Marker-assisted selection to improve drought adaptation in maize: the backcross approach, perspectives, limitations, and alternatives. *J Exp Bot* 58(2):351–360
- Ricroch A, Clairand P, Harwood W (2017) Use of CRISPR systems in plant genome editing: toward new opportunities in agriculture. *Emerg Top Life Sci* 1(2):169–182
- Riechmann JL, Heard J, Martin G, Reuber L, Jiang C-Z, Keddie J, Adam L, Pineda O, Ratcliffe O, Samaha R (2000) *Arabidopsis* transcription factors: genome-wide comparative analysis among eukaryotes. *Science* 290(5499):2105–2110
- Rivandi J, Miyazaki J, Hrmova M, Pallotta M, Tester M, Collins N (2011) A SOS3 homologue maps to HvNax4, a barley locus controlling an environmentally sensitive Na⁺ exclusion trait. *J Exp Bot* 62(3):1201–1216
- Rivelli AR, James RA, Munns R, Condon AT (2002) Effect of salinity on water relations and growth of wheat genotypes with contrasting sodium uptake. *Funct Plant Biol* 29(9):1065–1074
- Rivera-Ingraham GA, Lignot J-H (2017) Osmoregulation, bioenergetics and oxidative stress in coastal marine invertebrates: raising the questions for future research. *J Exp Biol* 220(10):1749–1760
- Roy S, Huang W, Wang X, Evrard A, Schmöckel S, Zafar Z, Tester M (2013) A novel protein kinase involved in Na⁺ exclusion revealed from positional cloning. *Plant Cell Environ* 36(3):553–568
- Russell J, Dawson IK, Flavell AJ, Steffenson B, Weltzien E, Booth A, Ceccarelli S, Grand S, Waugh R (2011) Analysis of > 1000 single nucleotide polymorphisms in geographically matched samples of landrace and wild barley indicates secondary contact and chromosome-level differences in diversity around domestication genes. *New Phytol* 191(2):564–578
- Sabagh AE, Mbarki S, Hossain A, Iqbal MA, Islam MS, Raza A, Llanes A, Reginato M, Rahman MA, Mahboob W, Singhal RK, Kumari A, Rajendran K, Wasaya A, Javed T, Shabbir R, Rahim J, Barutçular C, Habib Ur Rahman M, Raza MA, Ratnasekera D, Konuskan Öl, Hossain MA, Meena VS, Ahmed S, Ahmad Z, Mubeen M, Singh K, Skalicky M, Brestic M, Sytar O, Karademir E, Karademir C, Erman M, Farooq M (2021) Potential role of plant growth regulators in administering crucial processes against abiotic stresses. *Fron. Agron* 3:648694. <https://doi.org/10.3389/fagro.2021.648694>
- Salekdeh GH, Siopongco J, Wade L, Ghareyazie B, Bennett J (2002) A proteomic approach to analyzing drought- and salt-responsiveness in rice. *Field Crop Res* 76(2–3):199–219
- Santosh Kumar V, Verma RK, Yadav SK, Yadav P, Watts A, Rao M, Chinnusamy V (2020) CRISPR-Cas9 mediated genome editing of drought and salt tolerance (OsDST) gene in indica mega rice cultivar MTU1010. *Physiol Mol Biol Plants* 26(6):1099–1110
- Saradadevi R, Mukankusi C, Li L, Amongi W, Mbiu JP, Raatz B, Ariza D, Beebe S, Varshney RK, Huttner E (2021) Multivariate genomic analysis and optimal contributions selection predicts high genetic gains in cooking time, iron, zinc, and grain yield in common beans in East Africa. *The Plant Genome* 14(3):e20156
- Saravanavel R, Ranganathan R, Anantharaman P (2011) Effect of sodium chloride on photosynthetic pigments and photosynthetic characteristics of *Avicennia officinalis* seedlings. *Recent Res Sci Technol* 3(4)
- Sayar R, Bchini H, Mosbahi M, Ezzine M (2010) Effects of salt and drought stresses on germination, emergence and seedling growth of durum wheat (*Triticum durum* Desf.). *Afr J Agric Res* 5(15):2008–2016
- Sen Raychaudhuri S, Deng XW (2000) The role of superoxide dismutase in combating oxidative stress in higher plants. *Bot Rev* 66(1):89–98
- Sengupta S, Majumder AL (2009) Insight into the salt tolerance factors of a wild halophytic rice, *Porteresia coarctata*: a physiological and proteomic approach. *Planta* 229(4):911–929
- Shahid M, Ameen F, Maheshwari HS, Ahmed B, AlNadhari S, Khan MS (2021) Colonization of *Vigna radiata* by a halotolerant bacterium *Kosakonia sacchari* improves the ionic balance, stressor metabolites, antioxidant status and yield under NaCl stress. *Appl Soil Ecol* 158:103809
- Shan Q, Wang Y, Chen K, Liang Z, Li J, Zhang Y, Zhang K, Liu J, Voytas DF, Zheng X (2013) Rapid and efficient gene modification in rice and *Brachypodium* using TALENS. *Mol Plant* 6(4):1365–1368
- Shavrukov Y, Langridge P, Tester M, Nevo E (2010) Wide genetic diversity of salinity tolerance, sodium exclusion and growth

- in wild emmer wheat. *Triticum Dicoccoides* Breed Sci 60(4):426–435
- Shavrukov Y, Shamaya N, Baho M, Edwards J, Ramsey C, Nevo E, Langridge P, Tester M (2011) Salinity tolerance and Na⁺ exclusion in wheat: variability, genetics, mapping populations and QTL analysis. *Czech J Genet Plant Breed* 47:S85–S93
- Shehzad M, Zhou Z, Ditta A, Cai X, Khan M, Xu Y, Hou Y, Peng R, Hao F, Wang K (2019) Genome-wide mining and identification of protein Kinase Gene Family impacts salinity stress tolerance in highly dense genetic map developed from interspecific cross between *G. hirsutum* L. and *G. darwinii* G. Watt. *Agronomy* 9(9):560
- Sheldon AR, Dalal RC, Kirchoff G, Kopittke PM, Menzies NW (2017) The effect of salinity on plant-available water. *Plant Soil* 418(1):477–491
- Shen T, Horwitz KB, Lange CA (2001) Transcriptional hyperactivity of human progesterone receptors is coupled to their ligand-dependent downregulation by mitogen-activated protein kinase-dependent phosphorylation of serine 294. *Mol Cell Biol* 21(18):6122–6131
- Shi H, Quintero FJ, Pardo JM, Zhu J-K (2002) The putative plasma membrane Na⁺/H⁺ antiporter SOS1 controls long-distance Na⁺ transport in plants. *Plant Cell* 14(2):465–477
- Shinde H, Tanaka K, Dudhate A, Tsugama D, Mine Y, Kamiya T, Gupta SK, Liu S, Takano T (2018) Comparative de novo transcriptomic profiling of the salinity stress responsiveness in contrasting pearl millet lines. *Environ Exp Bot* 155:619–627
- Shinozaki K, Yamaguchi-Shinozaki K (2007) Gene networks involved in drought stress response and tolerance. *J Exp Bot* 58(2):221–227
- Shrivastava P, Kumar R (2015) Soil salinity: a serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi J Biol Sci* 22(2):123–131
- Silva P, Gerós H (2009) Regulation by salt of vacuolar H⁺-ATPase and H⁺-pyrophosphatase activities and Na⁺/H⁺ exchange. *Plant Signal Behav* 4(8):718–726
- Singer SD, Laurie JD, Bilichak A, Kumar S, Singh J (2021) Genetic variation and unintended risk in the context of old and new breeding techniques. *Crit Rev Plant Sci* 40(1):68–108
- Singh U, Dar M, SINGH S, Zaidi N, Bari M, Mackill D, Collard B, Singh V, Singh J, Reddy J (2013) Field performance, dissemination, impact and tracking of submergence tolerant (Sub1) rice varieties in South Asia. *SABRAO J Breed Genet* 45(1)
- Sobhanian H, Motamed N, Jazii FR, Nakamura T, Komatsu S (2010) Salt stress induced differential proteome and metabolome response in the shoots of *Aeluropus lagopoides* (Poaceae), a halophyte C4 plant. *J Proteome Res* 9(6):2882–2897
- Sohaib M, Zahir ZA, Khan MY, Ans M, Asghar HN, Yasin S, Al-Barakah FN (2020) Comparative evaluation of different carrier-based multi-strain bacterial formulations to mitigate the salt stress in wheat. *Saudi J Biol Sci* 27(3):777–787
- Song N-H, Ahn Y-J (2010) DcHsp17.7, a small heat shock protein from carrot, is upregulated under cold stress and enhances cold tolerance by functioning as a molecular chaperone. *HortScience* 45(3):469–474
- Steele K, Price A, Witcombe J, Shrestha R, Singh B, Gibbons J, Virk D (2013) QTLs associated with root traits increase yield in upland rice when transferred through marker-assisted selection. *Theor Appl Genet* 126(1):101–108
- Su P, Yan J, Li W, Wang L, Zhao J, Ma X, Li A, Wang H, Kong L (2020) A member of wheat class III peroxidase gene family, TaPRX-2A, enhanced the tolerance of salt stress. *BMC Plant Biol* 20(1):1–15
- Sunkar R, Zhu JK (2007) Micro RNAs and short-interfering RNAs in plants. *J Integr Plant Biol* 49(6):817–826
- Supplitt S, Karpinski P, Sasiadek M, Laczanska I (2021) Current achievements and applications of transcriptomics in personalized cancer medicine. *Int J Mol Sci* 22(3):1422
- Sze H, Li X, Palmgren MG (1999) Energization of plant cell membranes by H⁺-pumping ATPases: regulation and biosynthesis. *Plant Cell* 11(4):677–689
- Tada Y, Kashimura T (2009) Proteomic analysis of salt-responsive proteins in the mangrove plant. *Bruguiera Gymnorhiza* *Plant Cell Physiol* 50(3):439–446
- Takagi H, Tamiru M, Abe A, Yoshida K, Uemura A, Yaegashi H, Obara T, Oikawa K, Utsushi H, Kanzaki E (2015) MutMap accelerates breeding of a salt-tolerant rice cultivar. *Nat Biotechnol* 33(5):445–449
- Tanaka Y, Hibino T, Hayashi Y, Tanaka A, Kishitani S, Takabe T, Yokota S (1999) Salt tolerance of transgenic rice overexpressing yeast mitochondrial Mn-SOD in chloroplasts. *Plant Sci* 148(2):131–138
- Thomson MJ, de Ocampo M, Egdane J, Rahman MA, Sajise AG, Adorada DL, Tumimbang-Raiz E, Blumwald E, Seraj ZI, Singh RK (2010) Characterizing the SaltQ quantitative trait locus for salinity tolerance in rice. *Rice* 3(2):148–160
- Thornsberry JM, Goodman MM, Doebley J, Kresovich S, Nielsen D, Buckler ES (2001) Dwarf8 polymorphisms associate with variation in flowering time. *Nat Genet* 28(3):286–289
- Tian X, Wang Z, Zhang Q, Ci H, Wang P, Yu L, Jia G (2018) Genome-wide transcriptome analysis of the salt stress tolerance mechanism in *Rosa chinensis*. *PLoS ONE* 13(7):e0200938
- Tondelli A, Xu X, Moragues M, Sharma R, Schnaithmann F, Ingvarsdson C, Manninen O, Comadran J, Russell J, Waugh R (2013) Structural and temporal variation in genetic diversity of European spring two-row barley cultivars and association mapping of quantitative traits. *Plant Genome* 6(2):plantgenome2013.2003.0007
- Touchette B, Smith G, Rhodes K, Poole M (2009) Tolerance and avoidance: two contrasting physiological responses to salt stress in mature marsh halophytes *Juncus roemerianus* Scheele and *Spartina alterniflora* Loisel. *J Exp Mar Biol Ecol* 380(1–2):106–112
- Udvardi MK, Kakar K, Wandrey M, Montanari O, Murray J, Andriankaja A, Zhang J-Y, Benedito V, Hofer JM, Chueng F (2007) Legume transcription factors: global regulators of plant development and response to the environment. *Plant Physiol* 144(2):538–549
- Ul Hassan M, Rasool T, Iqbal C et al (2021) Linking plants functioning to adaptive responses under heat stress conditions: a mechanistic review. *J Plant Growth Regul.* <https://doi.org/10.1007/s00344-021-10493-1>
- Umezawa T, Fujita M, Fujita Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Engineering drought tolerance in plants: discovering and tailoring genes to unlock the future. *Curr Opin Biotechnol* 17(2):113–122
- Velculescu VE, Zhang L, Vogelstein B, Kinzler KW (1995) Serial analysis of gene expression. *Science* 270(5235):484–487
- Vysotskaya L, Hedley PE, Sharipova G, Veselov D, Kudoyarova G, Morris J, Jones HG (2010) Effect of salinity on water relations of wild barley plants differing in salt tolerance. *AoB Plants* 2010
- Wang X, Fan P, Song H, Chen X, Li X, Li Y (2009) Comparative proteomic analysis of differentially expressed proteins in shoots of *Salicornia europaea* under different salinity. *J Proteome Res* 8(7):3331–3345
- Wang Z, Cheng J, Chen Z, Huang J, Bao Y, Wang J, Zhang H (2012) Identification of QTLs with main, epistatic and QTL× environment interaction effects for salt tolerance in rice seedlings under different salinity conditions. *Theor Appl Genet* 125(4):807–815
- Wen F-P, Zhang Z-H, Bai T, Xu Q, Pan Y-H (2010) Proteomics reveals the effects of gibberellic acid (GA3) on salt-stressed rice (*Oryza sativa* L.) shoots. *Plant Sci* 178(2):170–175

- Witzel K, Weidner A, Surabhi G-K, Börner A, Mock H-P (2009) Salt stress-induced alterations in the root proteome of barley genotypes with contrasting response towards salinity. *J Exp Bot* 60(12):3545–3557
- Witzel K, Matros A, Strickert M, Kaspar S, Peukert M, Mühling KH, Börner A, Mock H-P (2014) Salinity stress in roots of contrasting barley genotypes reveals time-distinct and genotype-specific patterns for defined proteins. *Mol Plant* 7(2):336–355
- Xiang Y, Tang N, Du H, Ye H, Xiong L (2008) Characterization of OsbZIP23 as a key player of the basic leucine zipper transcription factor family for conferring abscisic acid sensitivity and salinity and drought tolerance in rice. *Plant Physiol* 148(4):1938–1952
- Xu C, Sibicky T, Huang B (2010) Protein profile analysis of salt-responsive proteins in leaves and roots in two cultivars of creeping bentgrass differing in salinity tolerance. *Plant Cell Rep* 29(6):595–615
- Xu J, Wang B, Wu Y, Du P, Wang J, Wang M, Yi C, Gu M, Liang G (2011) Fine mapping and candidate gene analysis of ptgms2–1, the photoperiod-thermo-sensitive gene in rice (*Oryza sativa* L.). *Theor Appl Genet* 122(2):365–372
- Xu C, Tang X, Shao H, Wang H (2016) Salinity tolerance mechanism of economic halophytes from physiological to molecular hierarchy for improving food quality. *Curr Genomics* 17(3):207–214
- Xu L, Wu C, Oelmueller R, Zhang W (2018) Role of phytohormones in *Piriformospora indica*-induced growth promotion and stress tolerance in plants: more questions than answers. *Front Microbiol* 9:1646
- Xu Y, This D, Pausch RC, Vonhof WM, Coburn JR, Comstock JP, McCouch SR (2009) Leaf-level water use efficiency determined by carbon isotope discrimination in rice seedlings: genetic variation associated with population structure and QTL mapping. *Theor Appl Genet* 118(6):1065–1081
- Xue D, Huang Y, Zhang X, Wei K, Westcott S, Li C, Chen M, Zhang G, Lance R (2009) Identification of QTLs associated with salinity tolerance at late growth stage in barley. *Euphytica* 169(2):187–196
- Yang Q, Chen Z-Z, Zhou X-F, Yin H-B, Li X, Xin X-F, Hong X-H, Zhu J-K, Gong Z (2009) Overexpression of SOS (Salt Overly Sensitive) genes increases salt tolerance in transgenic Arabidopsis. *Mol Plant* 2(1):22–31
- Yang Y, Wang Q, Chen Q, Yin X, Qian M, Sun X, Yang Y (2017) Genome-wide survey indicates diverse physiological roles of the barley (*Hordeum vulgare* L.) calcium-dependent protein kinase genes. *Sci Rep* 7(1):1–15
- Yin C-C, Ma B, Collinge DP, Pogson BJ, He S-J, Xiong Q, Duan K-X, Chen H, Yang C, Lu X (2015) Ethylene responses in rice roots and coleoptiles are differentially regulated by a carotenoid isomerase-mediated abscisic acid pathway. *Plant Cell* 27(4):1061–1081
- Yu J, Chen S, Zhao Q, Wang T, Yang C, Diaz C, Sun G, Dai S (2011) Physiological and proteomic analysis of salinity tolerance in *Puccinellia tenuiflora*. *J Proteome Res* 10(9):3852–3870
- Yu J, Zhao W, Tong W, He Q, Yoon M-Y, Li F-P, Choi B, Heo E-B, Kim K-W, Park Y-J (2018) A genome-wide association study reveals candidate genes related to salt tolerance in rice (*Oryza sativa*) at the germination stage. *Int J Mol Sci* 19(10):3145
- Zeng A, Chen P, Korth KL, Ping J, Thomas J, Wu C, Srivastava S, Pereira A, Hancock F, Brye K (2019) RNA sequencing analysis of salt tolerance in soybean (*Glycine max*). *Genomics* 111(4):629–635
- Zhang W, Peumans WJ, Barre A, Houles Astoul C, Rovira P, Rougé P, Proost P, Truffa-Bachi P, Jalali AA, Van Damme EJ (2000) Isolation and characterization of a jacalin-related mannose-binding lectin from salt-stressed rice (*Oryza sativa*) plants. *Planta* 210(6):970–978
- Zhang A, Sun H, Wang P, Han Y, Wang X (2012) Modern analytical techniques in metabolomics analysis. *Analyst* 137(2):293–300
- Zhang Y, Zhang F, Li X, Baller JA, Qi Y, Starker CG, Bogdanove AJ, Voytas DF (2013) Transcription activator-like effector nucleases enable efficient plant genome engineering. *Plant Physiol* 161(1):20–27
- Zhang M, Kong X, Xu X, Li C, Tian H, Ding Z (2015) Comparative transcriptome profiling of the maize primary, crown and seminal root in response to salinity stress. *PLoS ONE* 10(3):e0121222
- Zhang W, Liu Y, Wang L, Wang H, Ma M, Xu M, Xu X, Gao Z, Duan J, Cram DS (2016) Clinical application of next-generation sequencing in preimplantation genetic diagnosis cycles for Robertsonian and reciprocal translocations. *J Assist Reprod Genet* 33(7):899–906
- Zhang B, Chen X, Lu X, Shu N, Wang X, Yang X, Wang S, Wang J, Guo L, Wang D (2018a) Transcriptome analysis of *Gossypium hirsutum* L. reveals different mechanisms among NaCl, NaOH and Na₂CO₃ stress tolerance. *Sci Rep* 8(1):1–14
- Zhang M, Cao Y, Wang Z, Zq W, Shi J, Liang X, Song W, Chen Q, Lai J, Jiang C (2018b) A retrotransposon in an HKT1 family sodium transporter causes variation of leaf Na⁺ exclusion and salt tolerance in maize. *New Phytol* 217(3):1161–1176
- Zhang A, Liu Y, Wang F, Li T, Chen Z, Kong D, Bi J, Zhang F, Luo X, Wang J (2019) Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the OsRR22 gene. *Mol Breed* 39(3):1–10
- Zhao S, Fung-Leung W-P, Bittner A, Ngo K, Liu X (2014) Comparison of RNA-Seq and microarray in transcriptome profiling of activated T cells. *PLoS ONE* 9(1):e78644
- Zheng J, Zhao J, Zhang J, Fu J, Gou M, Dong Z, Hou W, Huang Q, Wang G (2006) Comparative expression profiles of maize genes from a water stress-specific cDNA macroarray in response to high-salinity, cold or abscisic acid. *Plant Sci* 170(6):1125–1132
- Zhou J, Wang X, Jiao Y, Qin Y, Liu X, He K, Chen C, Ma L, Wang J, Xiong L (2007) Global genome expression analysis of rice in response to drought and high-salinity stresses in shoot, flag leaf, and panicle. *Plant Mol Biol* 63(5):591–608
- Zhou M, Johnson P, Zhou G, Li C, Lance R (2012) Quantitative trait loci for waterlogging tolerance in a barley cross of Franklin × Yu Yao Xiang Tian Erleng and the relationship between waterlogging and salinity tolerance. *Crop Sci* 52(5):2082–2088
- Zhu J-K, Liu J, Xiong L (1998) Genetic analysis of salt tolerance in Arabidopsis: evidence for a critical role of potassium nutrition. *Plant Cell* 10(7):1181–1191
- Zhu C, Schraut D, Hartung W, Schaffner AR (2005) Differential responses of maize MIP genes to salt stress and ABA. *J Exp Bot* 56(421):2971–2981
- Zhu C, Gore M, Buckler ES, Yu J (2008) Status and prospects of association mapping in plants. *Plant Genome* 1 (1)
- Zou M, Guan Y, Ren H, Zhang F, Chen F (2008) A bZIP transcription factor, OsABI5, is involved in rice fertility and stress tolerance. *Plant Mol Biol* 66(6):675–683

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.