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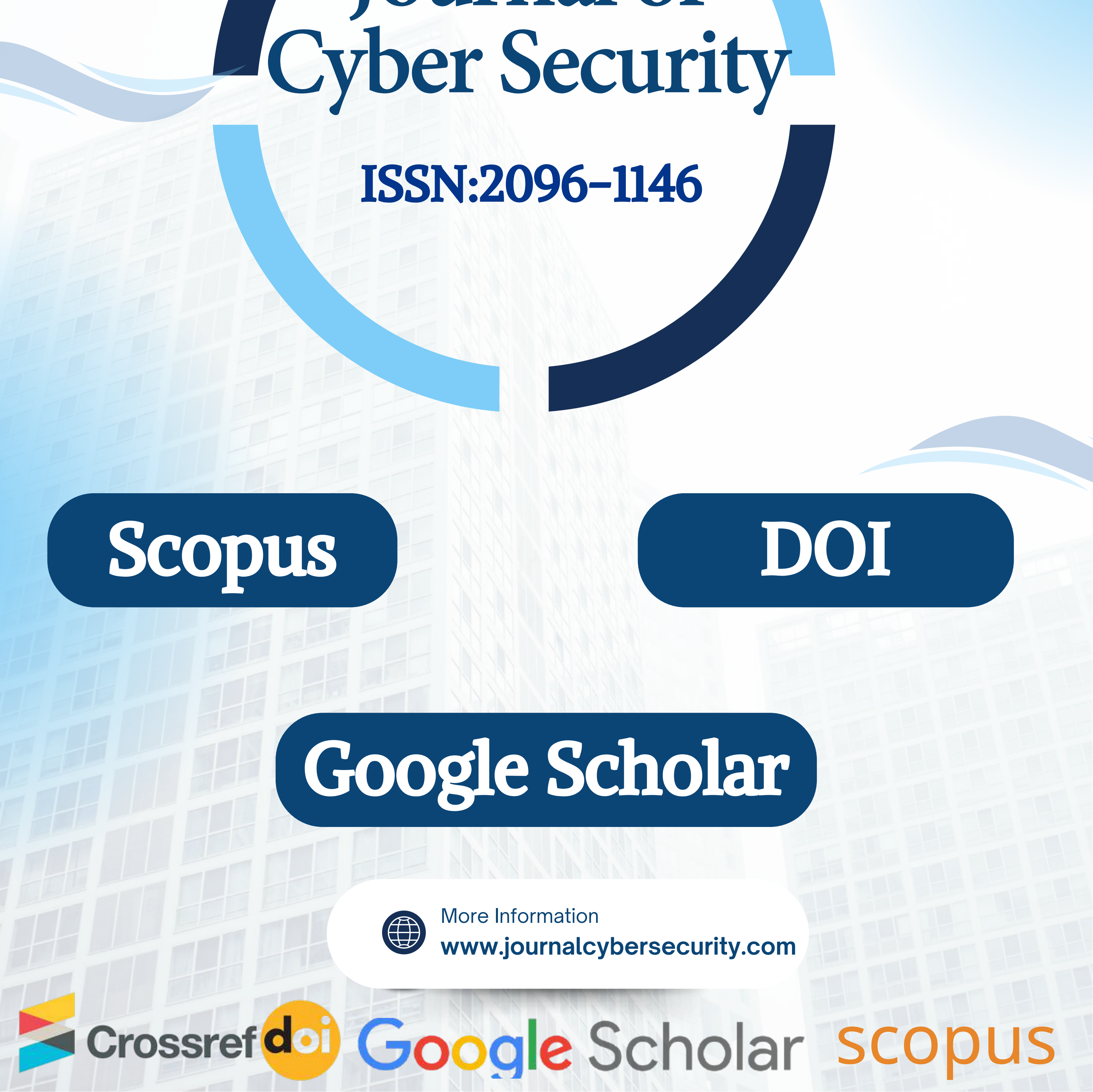

Genetic and Molecular Mechanisms for Stress Tolerance in Fruit Crops: A Review

***Ashok Kumar*[1]*, S.R. Singh*[2]*, M.C. Yadav*[3]*, Arvind Kumar*[4]*, Vijay Kumar Yadav*[5]*, Anupam Yadav*[6]*, Alkesh Khakre*[7]*, and Tanisha Jain*[8]**

1. *Professor & Dean Agriculture, JNCTPU, New Chouksey Nagar, Bhopal, India.*
2. *Principal Scientist, Indian Institute of Sugarcane Research (ICAR), Lucknow, U.P., India.*
3. *Principal Scientist, NBPGR (ICAR), Pusa Campus, New Delhi-110012, India.*
4. *Principal Scientist, ICAR Head Quarters, Pusa Campus, New Delhi -110012, India*
5. *Professor Genetics & Plant Breeding, CSAUA&T—Kanpur, U.P., India.*

***6, 7, & 8.** Assistant Professor, Agriculture, JNCTPU, New Chouksey Nagar, Bhopal, India.*

****Corresponding Author:***

Prof. (Dr.) Ashok Kumar
Professor & Dean Agriculture, JNCTPU, New Chouksey Nagar, Bhopal (M.P.) India.
Mobile:7819993411,8273847446

Abstract

Salinity is considered a global threat to agriculture and causes a significant reduction in crop yield. Major threats to global food security are abiotic stresses like salinity, drought, extreme temperatures, and hypoxia. Comprehending plant responses' molecular mechanisms to these stresses is essential for stress-tolerant crops. This article provides a comprehensive overview of plant abiotic stress responses, focusing on stress signal perception and transduction, gene expression regulation, and cellular and physiological adaptation mechanisms. It emphasizes advancements in identifying key factors for stress tolerance and in omics technologies facilitating these. The article also discusses applying this knowledge to develop stress-tolerant crops via genetic engineering and other means. However, it acknowledges challenges in translating molecular knowledge into practical breeding outcomes, such as stress tolerance trait complexity, genotype-by-environment interactions, and trade-offs with other agronomic traits. The article emphasizes the need for a multidisciplinary approach integrating molecular biology, genomics, biotechnology, and traditional breeding to address these challenges. It also highlights the importance of exploring and using genetic diversity in wild relatives and landrace collections and the potential of emerging technologies like systems biology and AI in speeding up stress-tolerant crop development. The review concludes by calling for continued investment in R&D, capacity building, and collaboration among researchers, breeders, policymakers, and stakeholders to ensure a food-secure future faced with global climate change.

Key Words: Abiotic stress, Molecular mechanisms, Stress tolerance, Crop improvement, Sustainable agriculture

1. Introduction: The negative effect of stress on the crops depends on the severity and intensity. In the cropping systems the abiotic stresses can induce losses that range from 50% to 70%. The most common abiotic stresses are represented by drought, salinity, high temperature, high irradiance, nutrient deficiency, flooding, cold, and heavy metals. Climate change can increase the stressful conditions in some geographical stress and some stresses can act synergistically on crop response. Understanding the molecular mechanisms behind the crop responses and adaptation strategies can lead to the identification of some key regulatory genes associated with abiotic stress tolerance. New biotechnological tools such as transcriptional studies and CRISPR-cas9 can help to identify target genes that can lead to achieve tolerance and help breeders to develop novel stress-tolerant crops. Physiological, biochemical, molecular biology and proteomic data can greatly help in understanding crop responses to abiotic stresses. Therefore, research papers and reviews related to abiotic stress tolerance or response in horticultural crops are welcome for this Special Issue. Fruit crops provide various kinds of fruit commodities that are of significant nutritional benefit and economic value to humans (Tanou, G.; Ziogas, V.; Molassiotis, A. ,2017). Fruits provide essential and valuable nutrition to humans, and they have an increasingly crucial role in helping humans respondto numerous disorders and diseases (Li, S.; Chen, H.; Yu, H.; Li, Y.; Wang, L. ,2023; Li, J.; Yan, G.; Duan, X.; Zhang, K.; Zhang, X.; Zhou, Y.; Wu, C.; Zhang, X.; Tan, S.; Hua, X.; et al. ,2022). The beautiful colors and fragrant scents of different fruits well fulfil our aesthetic and sensory enjoyment. Currently, fruit commodities with good appearance and high quality bring us considerable economic interest. However, fruit quantity, appearance, and nutritional qualities, including the contents of their diverse primary and secondary metabolites, namely amino acids, organic acids, flavonoids, an-thocyanins, soluble sugars, vitamins, etc., are determined by the growth status of fruit trees, including the phenotypes dictated by genetic characteristics, tree nutrition, and biotic and abiotic stimuli (Li, J.; Yan, G.; Duan, X.; Zhang,

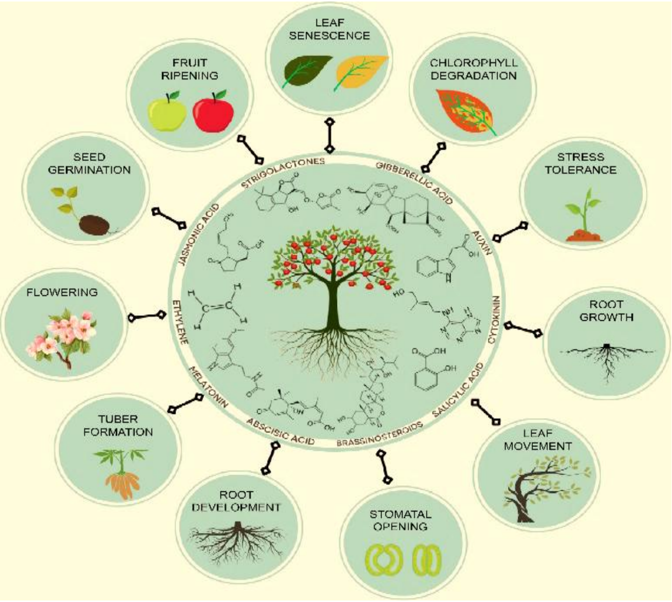

Figure 1: Diagram illustrating the chemical structures and functions of hormones utilized to promote the growth/development and productivity of fruit crops.

Sources: Manzoor MA, Xu Y, Iv Z, Xu J, Wang Y, et al. 2023

K.; Zhang, X.; Zhou, Y.; Wu, C.; Zhang, X.; Tan, S.; Hua, X.; et al. ,2022). So far, numerous pieces of literature, including those in this Special Issue, have highlighted the physiological and molecular response of the abiotic stresses, new progresses of physiological response, and underlying molecular mechanisms of fruit crops in response to environmental stresses, such as mineral nutrient decencies toxicities, osmotic stress, heavy metal stress, temperature stress, and light stress, aswell as the strategies aiming at improving the stress tolerance of fruit crops and selecting the resistant varieties by screening the biomarker compounds and resistance molecular breeding (Habibi, F.; Liu, T.; Shahid, M.A.; Schaffer, B.; Sarkhosh, A. ,2023; Kumar, R.; Berwal, M.; Saroj, P.,2019; Molassiotis, A.; Tanou, G.; Filippou, P.; Fotopoulos, V.,2013; Nawaz, R.; Abbasi, N.A.; Hafiz, I.A.; Khalid, A.,2020; Yang, L.T.; Pan, J.F.; Hu, N.J.; Chen, H.H.; Jiang, H.X.; Lu, Y.B.; Chen, L.S. ,2022; Lu, F.; Hu, P.; Lin, M.; Ye, X.; Chen, L.; Huang, Z.,2022).

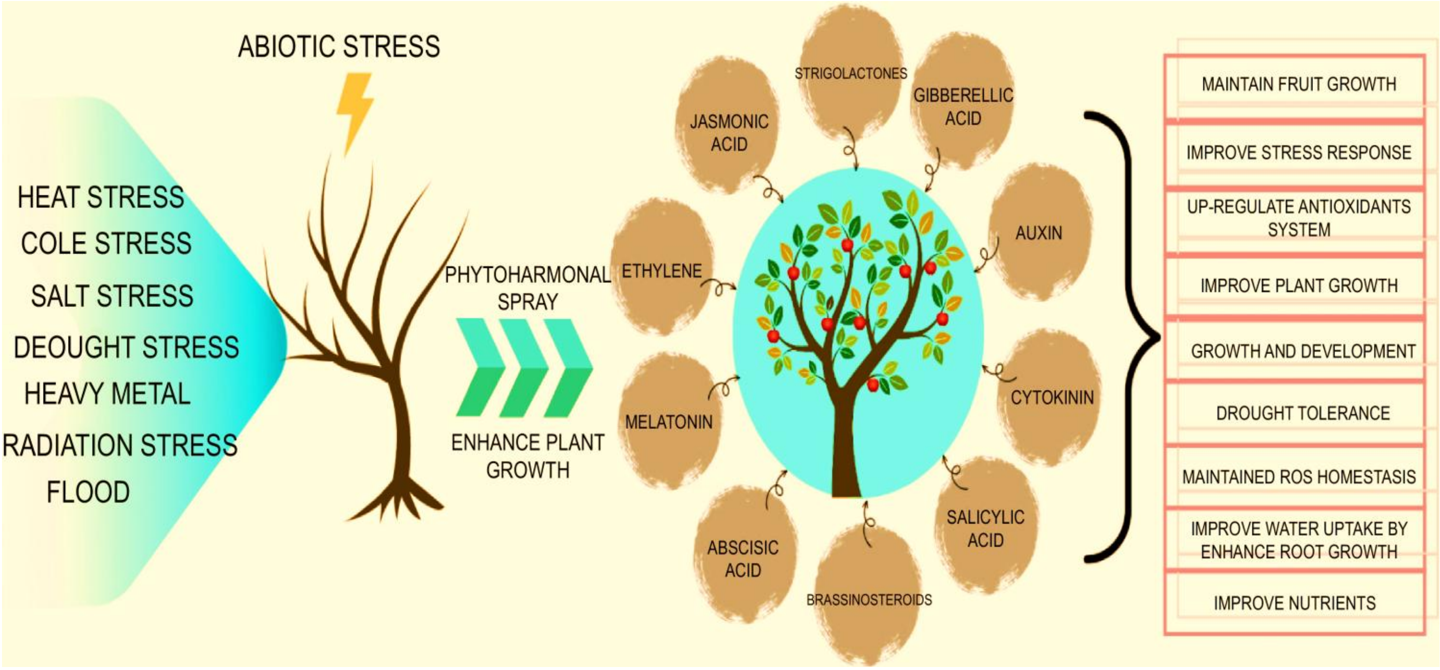

Figure 2: Phytohormones have been recognized as major regulators in facilitating the adaptive responses of plants to diverse abiotic stress conditions, thereby playing a crucial role not only in stress tolerance but also in promoting growth, development, and ultimately enhancing the overall productivity of horticultural crops. Through intricate signaling pathways and molecular mechanisms, these phytohormones such as brassinosteroids (BRs), gibberellin (GA), jasmonates (JAs), salicylic acid (SA), strigolactones (SLs), abscisic acid (ABA), and melatonin (MEL) orchestrate a complex network that modulates physiological, biochemical, and morphological changes, enabling plants to overcome the detrimental effects of abiotic stressors. Therefore, understanding the multifaceted roles and interactions of phytohormones in horticultural crop systems represents a vital avenue for devising innovative strategies to enhance adaptability, optimize growth, and maximize yield under challenging environmental conditions. ***Sources: Manzoor MA, Xu Y, Iv Z, Xu J, Wang Y, et al. 2023***

Under the condition of global warming, with more frequent occurrences of extreme weather events, including exceptionally hot weather, drought, and/or rainstorms, the adverse effects of high temperatures, drought, and/or waterlogging on fruit growth and agricultural production are becoming increasingly severe, and they compromise both fruit yield and fruit quality. Detrimental weather conditions can cause reductions in fruit crop growth, affecting yield quality and quantity, and they can result in significant fruit losses. High-temperature-induced morphological, physiological, and molecular disorders have been reported in fruit trees (Li, S.; Chen, H.; Yu, H.; Li, Y.; Wang, L. ,2023). High temperatures can affect fruit tree growth and fruit characteristics in various aspects, including the flowering number, fruit drop and fruit deformities, and the slowdown of fruit growth. Drought also affects the normal growth of fruit crops. Zhang et al. showed that altered expression levels of genes related to photosynthesis, carbohydrate metabolism, oxidoreductase activities, nutrient metabolism, and senescence pathways were observed in drought-treated seedlings. Furthermore, the contents of some plant hormones, such as gibberellin and abscisic acid, were affected in drought-treated seedlings. This suggested that a widespread impact of drought existed in fruit crops (Zhang, X.; Lei, L.; Lai, J.; Zhao, H.; Song, W. ,2019). Waterlogging is another constraining factor for fruit crops. Zhang et al.reported that differentially expressed genes (DEGs) were differentially regulated between two apple cultivars (waterlogging-tolerant *Malus hupehensis* and sensitive *M. toringoides*) under waterlogging stress, especially those DEGs involved in flavonoids metabolism and hormone signaling, suggesting a possible link between flavonoids and hormone signaling and waterlogging tolerance (Zhang, K.; Chen, X.; Yuan, P.; Song, C.; Song, S.; Jiao, J.; Wang, M.; Hao, P.; Zheng, X.; Bai, T. ,20123). An experiment using kiwifruit plants under water logging and drought demonstrated that the contents of abscisic acid (ABA) and ABA responsive or biosynthesis genes, such as DRE-binding protein 2 (DREB2), “W-tryptophan, R-arginine, K-lysine, Y-tyrosine 40” (WRKY40), nine-cis-epoxy carotenoid dioxygenase 3 (NCED3), etc., were upregulated by these two water stresses, supporting the theory that kiwifruit plants can combat water stress extremes by regulating ABA metabolism and signaling (Wurms, K.V.; Reglinski, T.; Buissink, P.; Chee, A.A.; Fehlmann, C.; McDonald, S.; Cooney, J.; Jensen, D.; Hedderley, D.; McKenzie, C.; et al. ,2023).Except for weather conditions, geochemical factors and agronomic management can also bring on unfavorable factors in the cultivation of fruit crops. For instance, Lu et al. showed that the application of the copper-containing pesticide Bordeaux mixture increased the contents of leaf copper (Cu), decreased photosynthetic pigments, and decreased the efficiency of photo-electron transport, inducing leaf chlorosis and photosynthetic inhibition. The Cu-induced impairment of chloroplast ultrastructure and enhancement of antioxidant systems were different between Citrus grandis and C. sinensis, which conferreda higher tolerance of Cu toxicity to C. grandis (Lu, F.; Hu, P.; Lin, M.; Ye, X.; Chen, L.; Huang, Z. ,2022).

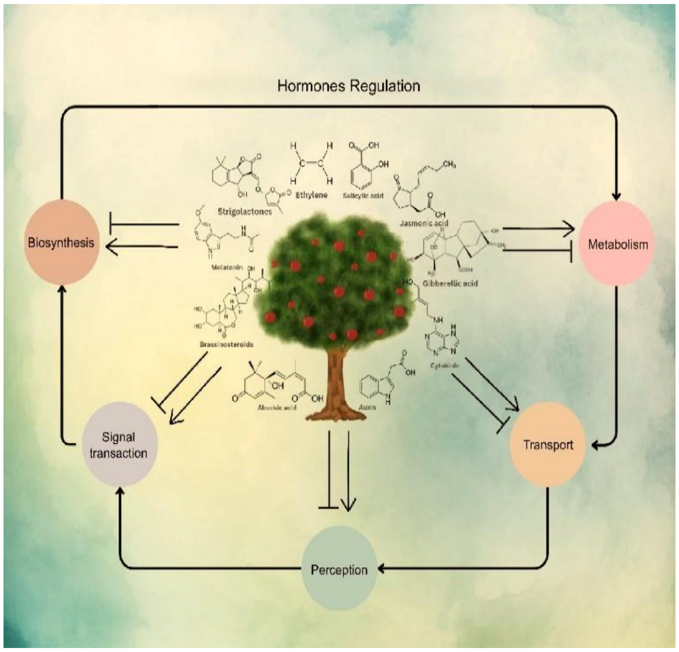

Figure 3: The role of plant hormones in regulating plant growth and development by manipulating biosynthesis, metabolism, transport, and signal transduction of plant phytohormones. *Sources: Manzoor MA, Xu Y, lv Z, Xu J, Wang Y, et al. 2023*

Some new biomarkers involving nutrient stress have been identified in the literature. For example, Liu et al. found that the overexpression of SlmiR319b-regulated Teosinte-Branched1/Cycloidea/PCF 10 (SlTCP10), which mediates Jasmonic Acid 2 (SlJA2) in roots, can enlarge root growth and potassium(K) absorption in tomato (Liu, X.; Pei, L.; Zhang, L.; Zhang, X.; Jiang, J. ,2023). The overexpression of Malus domestica Auxin/Indole-3-AceticAcid 27 (MdIAA27T) can improve the tolerance to phosphorus (P) deficiency in transgenic apple trees by growing longer and denser adventitious roots and taking up higher P con-tent than the control plants under low-P conditions (Zhao, S.; Zhao, X.; Xu, X.; Han, Z.; Qiu, C. ,2022). These studies could provide a new regulation mechanism for increasing K and P acquisition efficiency under low-K and low-P stress. Soil acidification caused by strong base leaching and decalcification/allitization in tropic and subtropical areas consequentially led to several metal stresses, such as aluminum (Al) and manganese

(Mn) stress and nutrient deficiency. Huge amounts of work have put forward extensive details of Al toxicity in fruit crops cultivated in acidic soil (Chandra, J.; Keshavkant, S. ,2021; Rahman, R.; Upadhyaya, H. ,2021). Physiological, transcriptomic, and proteomic studies have shown that both Al and Mn can affect the integrity of the cell wall and plasma membrane and disrupt the normal cellular processes of nucleic acids, amino acids, carbohydrates, energy metabolisms, growth regulation, and signal transduction (Chandra, J.; Keshavkant, S. ,2021; Rahman, R.; Upadhyaya, H. ,2021; Delhaize, E.; Ma, J.F.; Ryan, P.R. ,2012 Zheng, L.; Lan, P.; Shen, R.F.; Li, W.F. ,2014). To cope with Al toxicity, some plant species and cultivars have evolved mechanisms to detoxify Al, both externally and internally, through the exudation of organic acids or other secondary metabolites and the chelation of Al cations into nontoxic forms (Delhaize, E.; Ma, J.F.; Ryan, P.R. ,2012). In citrus plants, the enhancement of reactive oxygen species (ROS)metabolism and sulfur compound metabolism has also been proven to play important roles in Al tolerance. To effectively eliminate Al toxicity, except for liming, it is proposed that the application of some beneficial compounds such as melatonin, methyl jasmonate, and sulfur-containing fertilizer in the field could be practicable in the cultivation of fruit crops (Guo, P.; Li, Q.; Qi, Y.P.; Yang, L.T.; Ye, X.; Chen, H.H.; Chen, L.S. ,2017; Ren, J.; Yang, X.; Zhang, N.; Feng, L.; Ma, C.; Wang, Y.; Yang, Z.; Zhao, J. ,2021). In fields, the inappropriate application of chemical fertilizer and neglecting the application of organic manure can also lead to nutrient disorders such as magnesium deficiency, potassium deficiency, zinc deficiency, and boron stress in orchards (Yang, L.T.; Pan, J.F.; Hu, N.J.; Chen, H.H.; Jiang, H.X.; Lu, Y.B.; Chen, L.S., 2022). Mean-while, considering the complexities of outdoor conditions, more than one unfavorable factor is simultaneously applied to fruit crops, increasing the difficulty of finding coun-termeasures. Hence, a better understanding of the response mechanisms of fruit crops to adverse conditions is hugely significant for the sustainability of fruit production.

2. Abiotic stress-inducible genes

The complex plant response to abiotic stress involves many genes and biochemical-molecular mechanisms. The analyze of the functions of stress-inducible genes is an important tool not only to understand the molecular mechanisms of stress tolerance and the responses of higher plants, but also to improve the stress tolerance of crops by gene manipulation. Hundreds of genes are thought to be involved in abiotic stress responses (Seki, 2003, Avni Öktem et al., 2008). Many drought-inducible genes are also induced by salt stress and cold, which suggests the existence of similar mechanisms of stress responses. These genes are classified into three major groups: (1) those that encode products that directly protect plant cells against stresses such as heat stress proteins (HSPs) or chaperones, LEA proteins, Osmo protectants, antifreeze proteins, detoxification enzymes and free-radical scavengers (Bray et al., 2000, Wang et al., 2000); (2) those that are involved in signaling cascades and in transcriptional control, such as Mitogen-activated protein kinase (MAPK), Calcium-dependent protein kinase (CDPK) (Ludwig et al., 2004) and SOS kinase (Zhu et al., 2001), phospholipases (Frank et al., 2000) and transcriptional factors (Cho et al., 2000, Shinozaki et al., 2000); (3) those that are involved in water and ion uptake and transport such as aquaporins and ion transporters (Blumwald et al., 2000).

Advertisement

3. Transcriptional factor genes involved in abiotic stress

Plant growth and productivity are under constant threat from environmental changes in the form of various stress factors. The most common abiotic stresses are drought, flooding or submergence, salinity, extreme temperatures (heat and freezing) and high light. Furthermore, the continued modification of the atmosphere by human activities lead to increase in the concentration of ozone in the troposphere and this can generate oxidative stress, which leads to the destruction of proteins and cells, premature ageing and reduced crop yields.

Tolerance or susceptibility to these abiotic stresses is a very complex phenomenon, both because stress may occur at multiple stages of plant development and more than one stress simultaneously affects the plant. Therefore, the perception of abiotic stresses and signal transduction to switch on adaptive responses are critical steps in determining the survival and reproduction of plants exposed to adverse environments (Chinnusamy et al., 2004). During the past few years, transcriptome analysis has indicated that distinct environmental stresses induce similar responses. Overlap between stress responses can explain the phenomenon known as cross-tolerance, a capability to limit collateral damage inflicted by other stresses accompanying the primary stress. Responses to abiotic stresses require the production of important metabolic proteins such as those involved in synthesis of Osmo protectants and regulatory proteins operating in signal transduction pathways, that are kinases or transcription factors (TFs).

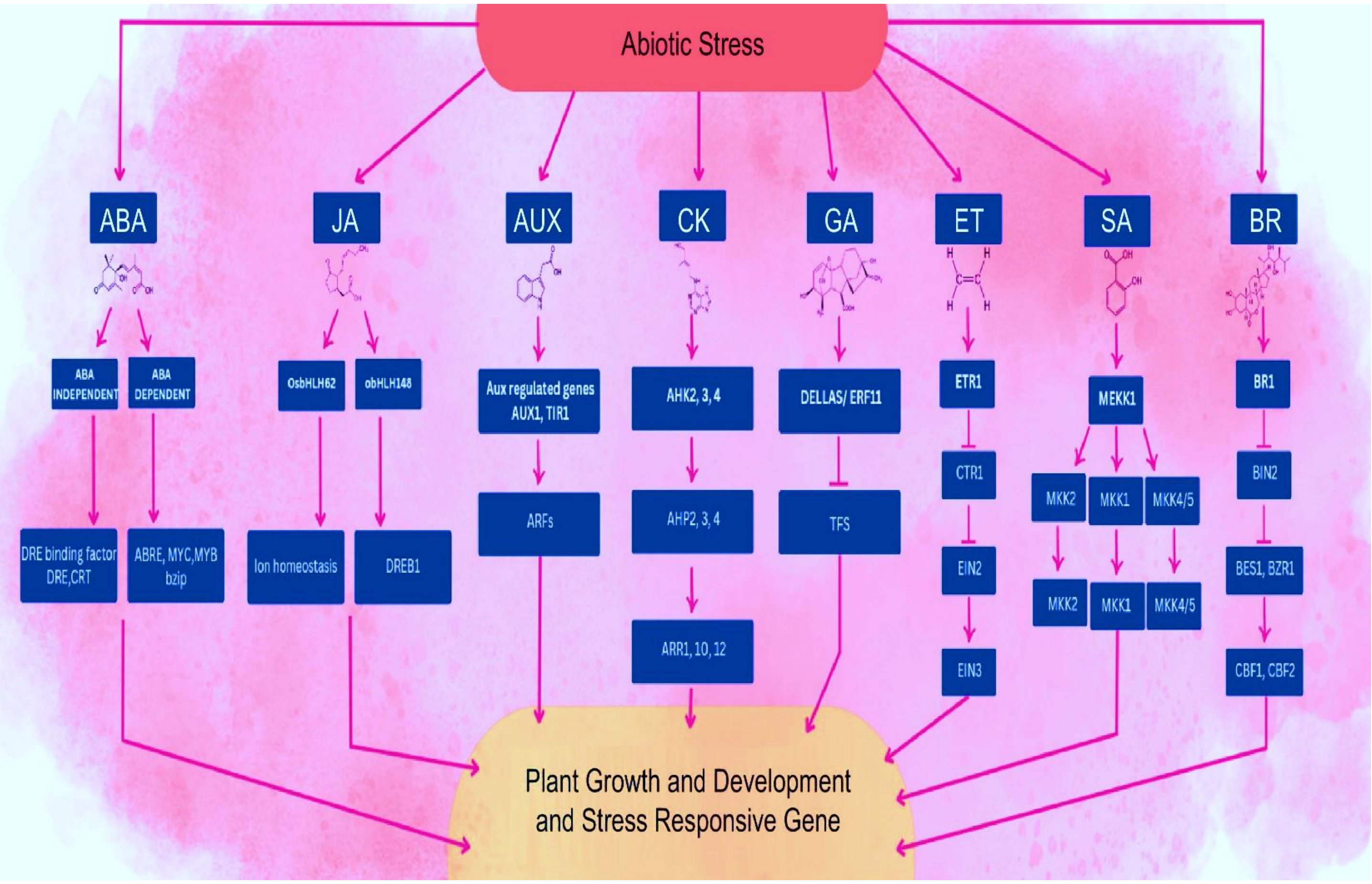

Figure 4: An overview of phytohormone crosstalk and their signaling networks in abiotic stress responses. Under various conditions of abiotic stress, plant growth, and development are impacted by changes in phytohormonal signaling. Biosynthesis and signaling pathways of hormones are altered, which can affect specific genes within this network that are responsible for improving plant growth and defensive mechanisms to confer abiotic stress tolerance. The arrows bar end and simple arrow suggest repression effect and activation, respectively. ***Sources: Manzoor MA, Xu Y, lv Z, Xu J, Wang Y, et al. 2023.***

The regulation of these responses requires proteins operating in the signal transduction pathways, such as transcriptional factors, which regulate gene expression by binding to specific DNA sequences in the promoters of respective target genes. This type of transcriptional regulatory system is called regulon. At least four different regulons that are active in response to abiotic stresses have been identified. Dehydration-responsive element binding protein 1 (DREB1)/C-repeat binding factor (CBF) and DREB2 regulons function in abscisic acid (ABA)-independent gene expression, whereas the ABA-responsive element (ABRE) binding protein (AREB)/ABRE binding factor (ABF) regulon functions in ABA-dependent gene expression (Saibo et al., 2009). In addition to these major pathways, other regulons, including the NAC (or NAM, No Apical Meristem) and Myeloblastosis-Myelocytomatosis (MYB/MYC) regulons, are involved in abiotic stress-responsive gene expression. Particularly, NAC- type TF OsNAC6 is induced by abiotic stresses, including cold, drought and high salinity. Microarray analysis showed that many abiotic inducible genes were up regulated in rice plants over-expressing OsNAC6 (Nakashima et al., 2007).

TFs are powerful targets for genetic engineering in abiotic stress resistance in crop plants and many studies have been done in the last two decades on this topic. Transcription factors are shown in ovals. Transcription factor-modifying enzymes are shown in circles. The small triangles correspond to post-translational modifications. Green squares with question marks represent putative MYC ICE1-like transcription factors that may activate CBF1/DREB1B and CBF2/DREB1C. The green boxes represent the *cis*-elements present in stress-responsive genes. The red dot corresponds to the sumoylation modification by SIZ1 of the ICE1 transcription factor. The dashed black line from SIZ1 to HOS1 represents competition for binding places on the ICE1 transcription factor. SIZ1 blocks the access of HOS1 to the ubiquitination sites on the ICE1. CBF4/DREB1D is a DRE cis-element binding factor that is ABA dependent.

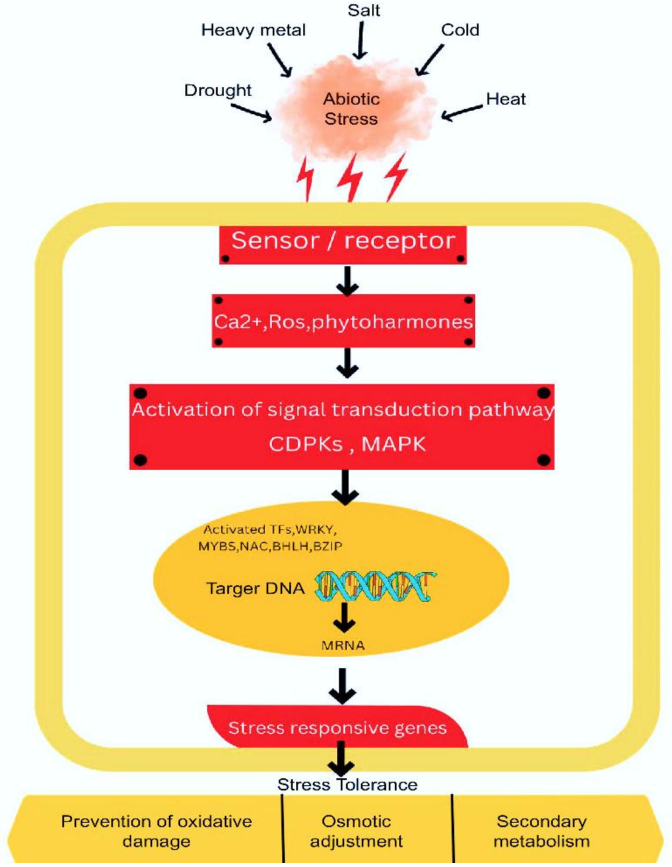

Figure 5: The diagram illustrates the generic signaling pathway that plants use to respond to abiotic stress. The pathway begins with the perception of signal and extends towards stress responses. Initially, receptors and sensors perceive stress and cascading downstream stress responses *via* reactive oxygen (ROS), Ca^{2+}, and phytohormones. Secondary messengers facilitate the transmission and amplification of signals in plants. This process involves the modulation of transcription factors and stress-responsive genes, which in turn triggers various molecular, biochemical, and physiological responses that contribute to enhancing stress tolerance in plants. The extension and transduction of signals are facilitated by secondary messengers. These secondary messengers result in the different regulation of stress-responsive genes and transcription factors. The regulation of TFs and genes leads to the adjustment of biochemical, physiological, and molecular responses that ultimately enhance stress tolerance in plants. ***Sources: Manzoor MA, Xu Y, lv Z, Xu J, Wang Y, et al. 2023.***

4. Drought stress transcriptional factors

The genome controls the regulation of the response to water deficit as well as the effectiveness of the response. Microarrays, largely performed using *Arabidopsis thaliana* as model plant, have been used to catalogue the many genes that are induced or repressed in response to conditions that may lead to cellular water-deficit stress (Seki et al., 2002). These genes can be placed in at least four different functional groups: signal transduction, transcriptional regulation, cellular metabolism and transport and protection of cellular structures.

There are at least six different classes of TFs that participate in gene induction or repression in response to water deficit. Homeobox domain and NAC domain containing TFs are induced by multiple treatments that mimic water-deficit stress. Accumulation of proteins which have metabolic or structural functions promote adaptation to stress. One class of genes that could play a role in protection is called the late embryogenesis abundant (*Lea*) genes. The *Lea* genes are also developmentally programmed for expression in desiccating seeds. These genes encode small hydrophilic proteins that are predicted to protect proteins and membranes through chaperone-like functions. These proteins were thought to improve the performance of rice plants by protecting cell membranes from injury under abiotic stress (Chandra et al., 2004).

4.1. Gene regulation and transcriptional factors in water deficit

A recent review (Shinozaki & Yamaguchi-Shinozaki, 2007) on analysis of gene expression during drought stress response in plants show and summarize the functions of some genes in both stress response and tolerance. Microarray analysis performed on wheat genome, showed that among 300 unique single expressed sequences tag (ESTs), the 30% of genes were significantly up-regulated and the 18% were down-regulated under drought stress (Way et al., 2005).

Potential functions of approximatively 130 genes of *A. thaliana* up-regulated in water-deficit was reported by Bray (2002). These genes are involved in cellular response to drought stress by signaling events, detoxification and other functions. cDNA microarray analysis on 7000 Arabidopsis full-length cDNAs clarify relationship between rehydratation-, proline- and water-treatment inducible genes. Among the 152 rehydratation-inducible genes, 58 genes conteined in their promoter regions the ACTCAT sequence involved in proline- and hypoosmolarity- inducible gene expression, suggesting that this motif is a major cis-activing element involved in rehydratation-inducible gene expression (Oono et al., 2003). Moreover, microarray analysis performed on two moderately drought-tolerant native Andeon potato clones revealed that there was 1713 differentially expressed genes with 186 up-regulated involved in drought tolerance by inducing of osmotic adjustment, changes in carbohydrate metabolism, membrane modifications and cell rescue mechanisms, such as detoxification of oxygen radicals and protein stabilization (Schafleitner et al., 2007).

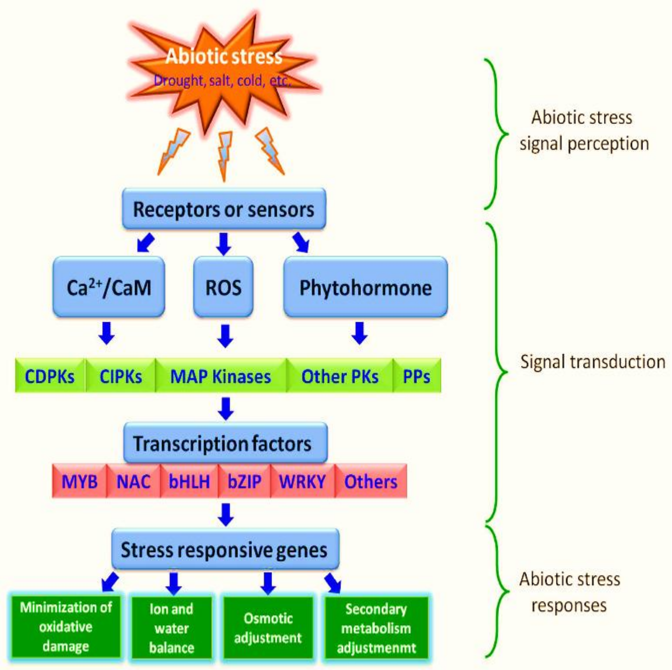

Figure 6: Model for transcription factors regulating abiotic stress-signaling pathways. ***Sources: Khan, Sardar-Ali, Meng-Zhan Li, Suo-Min Wang, and Hong-Ju Yin. 2018.***

These recent studies underline how the expression of genes in response to water deficit is complex and can be regulated at the transcriptional, post-transcriptional and translational levels. Two major transcriptional regulatory pathways of gene expression play an important role in response to water-deficit stress: the ABA-independent pathway and ABA-dependent pathway. The first is controlled largely by a family of TFs called dehydration response element binding protein (DREB), which contains a DNA binding motif originally identified in a flower patterning protein called APETALA2 (AP2) (Fig. 2), while transcription factor families known to be as the most responsive to ABA signaling under drought are NAC, AREB/ABF, and MYB.

4.1.1. ABA-independent pathway

DREB are important TFs which induce a set of abiotic stress-related genes and confer stress resistance to plants. The DREB TFs could be divided into two group: DREB1, involved signal transduction pathways under low temperature; DREB2, involved in signal transduction pathways under dehydration. They belong to the ethylene responsive element binding factors (ERF) family of TFs. ERF proteins are a sub-family of the AP2/ethylene responsive element binding protein (EREBP) TFs that is distinctive to plants. ERF proteins share a conserved 58–59 amino acid domain (the ERF domain) that binds to *cis*-elements, the GCC box, found in many pathogens related (PR) gene promoters conferring ethylene responsiveness (Gu et al., 2000), and to the C-repeat CRT/dehydration responsive element (DRE) motif involved in the expression of cold and dehydration responsive genes (Agarwal et al., 2006).

The DREB proteins contain an ERF/AP2DNA-binding domain quite conserved: amino acid alignment shows high sequence similarity in the nuclear localization signal at the N-terminal region and some similarity in the C-terminal acidic domain (Agarwal et al., 2006). Indeed, TFs containing ERF/AP2DNA-binding domain are widely found in many plants such as Arabidopsis (Okamuro et al., 1997), tomato (Zhou et al., 1997), tobacco (Ohme-Takagi & Shinshi, 1995), rice (Sasaki et al., 1994, Weigel, 1995) and maize (Moose & Sisco, 1996).

Another ABA-independent pathway was identified after the observation that Early Responsive to Dehydration Stress 1 (ERD1) gene transcripts accumulated before any increase of ABA in response to dehydration and high salinity (Nakashima et al., 1997). Promoter analysis of ERD1 revealed TFs belonging to the NAC family and zinc finger homeodomain (ZF-HD) as essential to the activation of the ERD1 gene (Tran et al., 2007). The increased drought tolerance may be due both to the reduced transpiration rate (increased stomatal closure) and to an increased ABA sensitivity.

Many genes (e.g. Aquaporin, ERD10, ERD13 and ERF) already described as being involved in plant response to water stress are down-regulated in drought stress (Cominelli et al., 2005). A member of the *A. thaliana* family of R2R3-MYB TFs, AtMYB61, is also specifically expressed in guard cells in a consistent manner, being involved in the regulation of stomatal aperture (Liang et al., 2005). The strong induction of Stress Responsive – NAC1 (SNAC1) gene expression by drought in guard cells suggests an effect in stomatal closure (Hu et al., 2006). It has been reported that modulation of transcription plays an important role in controlling guard cell activity. Recently two MYB-type TFs were identified as regulators of stomatal movements.

4.1.2. ABA-dependent pathway

ABA-dependent gene induction during water deficit is controlled by at least five different classes of TFs. The ABA response element (ABRE) with the consensus ACGTGG/TC is bound by basic Leucine Zipper Domain (bZIP-type) TFs. Three Arabidopsis bZIP TFs (AREB1/ABF2, AREB2/ABF4, and ABF3) are expressed in response to water-deficit stress and ABA treatment.

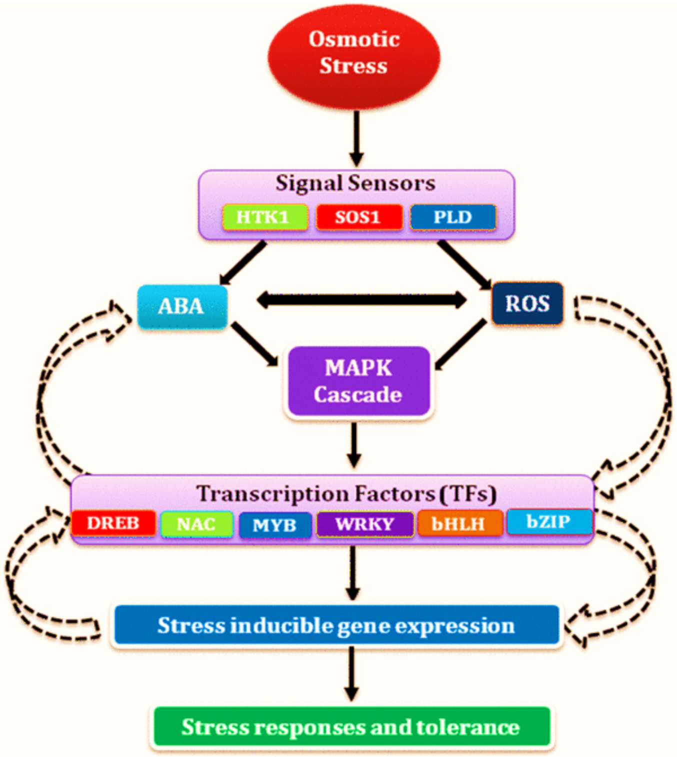

Figure 7: A representation of the transcriptionally mediated regulation of response, gene expression and tolerance to osmotic stress in wheat. TFs regulate osmotic stress via directly regulating gene expression by interacting with cis-elements in the promoter regions upstream of the target genes in wheat or indirectly through various signaling cascades. The solid lines represent direct regulation while dotted lines represent indirect regulation. For discussion, please see main text. ABA abscisic acid, ROS reactive oxygen species. *Sources: Shabir H. Wani, et al,2018*

Activation of the TFs requires ABA accumulation and the induction of an ABA-responsive protein kinase which activates the TF through phosphorylation. Other TFs are also involved in ABA regulation of gene expression during cellular water deficit. Three genes encoding a class of TFs that is unique to plants, the NAC domain proteins ANAC019, ANAC055, and ANAC072 are induced by water deficit and ABA treatment. The NAC domain is a 60 bp DNA binding domain that is predicted to form a helix-turn-helix motif. MYB, MYC and homeodomain TFs, and a family of transcriptional repressors (Cys2/His2-type zinc-finger proteins) are also involved in the ABA response to water deficit. Expression of the drought-inducible gene Responsive to Dehydration 22 (RD22) from Arabidopsis was found to be induced by ABA. The promoter region of RD22 contains MYC (CANNTG) and MYB (C/TAACNA/G) *cis*-element recognition sites. MYC and MYB TFs only accumulate after an increase of ABA concentration. Over-expression of these TFs result in enhanced sensitivity to ABA and drought tolerance (Abe et al., 2003).

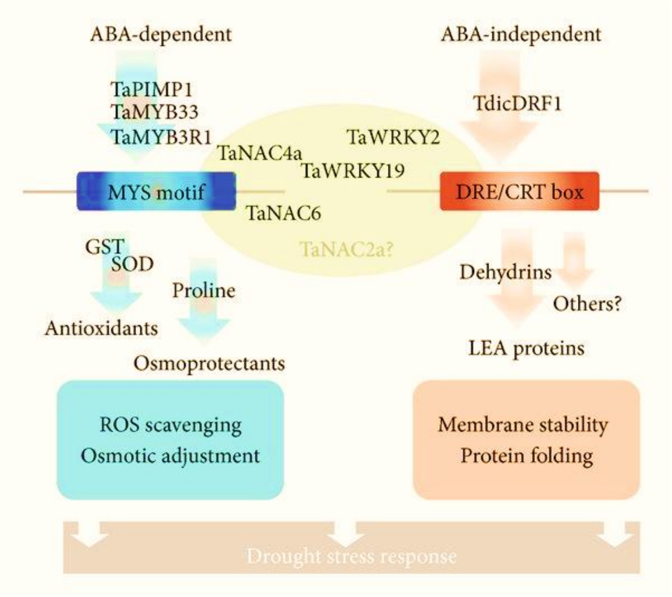

Figure 8: ABA-dependent and ABA-independent pathways of stress response. MYB and DREB TFs are given as examples to ABA-dependent and-independent routes. While ABA-dependent pathways appear to recruit antioxidant and Osmo protectant mechanisms, ABA-independent pathways generally involve protective proteins. NAC and WRKY TFs provide crosstalk between these pathways; where some members, such as TaNAC4 and TaNAC6, may predominantly act in an ABA-dependent fashion, some members may be closer to ABA-independent pathways. In several cases, such as TaWRKY19, both pathways are employed. It should be noted that both pathways are highly intermingled, and functions of several regulators, such as TaNAC2a, as well as entire pathways are yet to be elucidated.

5. Transcriptional factor involved in response to flooding stress

Flooding and submergence are two conditions that cannot be tolerated by most plants for periods of time longer than a few days. These stresses lead to anoxic conditions in the root system. At a critical oxygen pressure, mitochondrial respiration that provides the energy for growth in the photosynthetically inactive roots will decrease, then cease and the cells will die (Bray, 2004). Recent reviews on gene expression analysis performed by microarray tools reported as the expression of several transcription factors, such as heat shock factors, ethylene response-binding proteins, MADS-box proteins, AP2 domain, leucine zipper, zinc finger and WRKY factors, increases in response to various regimes of oxygen deprivation in Arabidopsis and rice (Loreti et al., 2005, Lasanthi-Kudahettige et al., 2007).

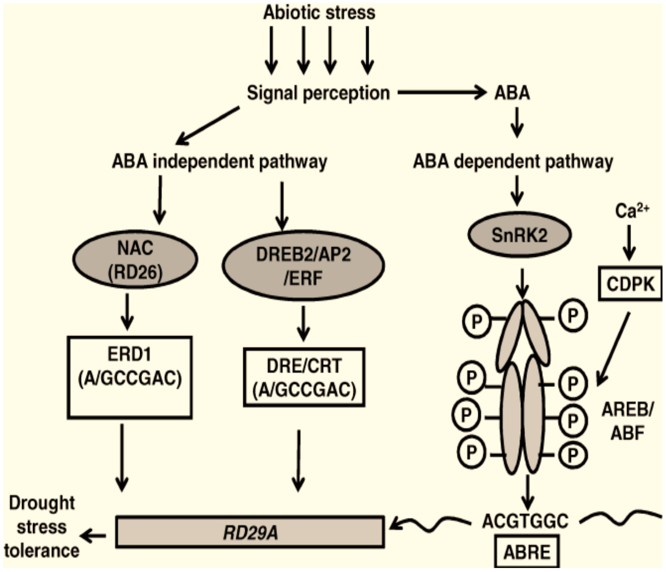

Figure 9: ABA-dependent and ABA-independent signaling in plants. DREB2 and NAC signal transduction pathways are induced in response to drought stress and are involved in the expression of downstream target genes responsive to drought stress both in Arabidopsis and maize. The NAC transcription factor and DREB2 are involved in ERD1 and RD29A gene expression, respectively. SnRK2 can interact physically and phosphorylate b-ZIP transcriptional activators that might also be phosphorylated by certain CPKs, which recognize similar or even identical C-domain motifs as the SnRK2s. The RD29 gene contains both ABRE and DRE/DRT cis elements in its promoter. DRE, drought-responsive, ABA, Abscisic acid (modified from Yamaguchi-Shinozaki and Shinozaki, 2006; Shinozaki and Yamaguchi-Shinozaki, 2007; Wasilewska et al., 2008).

Recently Licausi et al. (2010), using a qRT-PCR platform (Czechowski et al., 2002; Scheible et al., 2004, Morcuende et al., 2007, Osuna et al., 2007, Barrero et al., 2009), have identified TFs that are differentially expressed by hypoxic conditions. Among the TFs that have been characterized, members of the AP2/ERF-type family are the most commonly represented in the set of up-regulated TFs, followed by Zinc-finger and basic helix-loop-helix (bHLH-type) TFs, while TFs belonging to the bHLH family are the most commonly represented in the set of down-regulated TFs, together with members from the bZIP and MYB families.

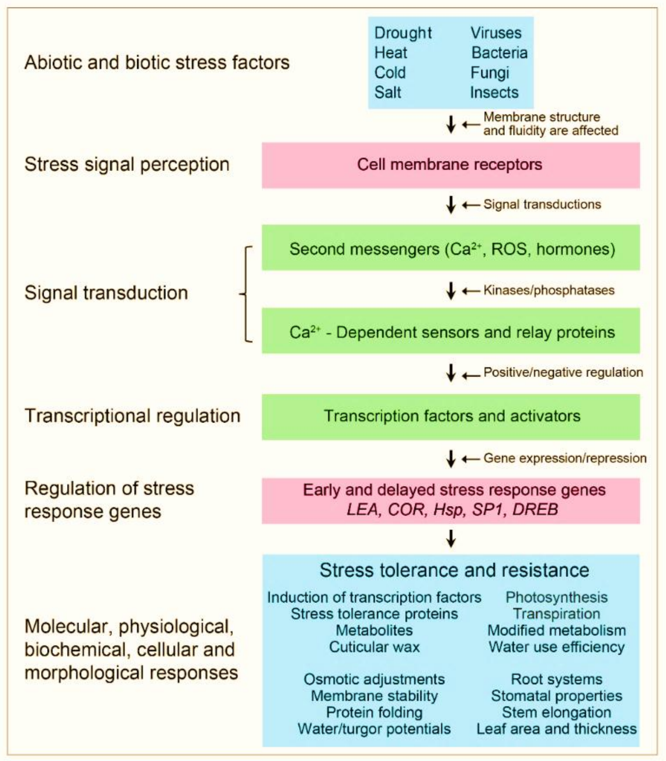

Figure 10: Plants respond to abiotic and biotic stresses through signal transduction pathways. An extracellular signal is perceived via receptors localized in membranes that lead to the activation of signal transduction pathways. The signal cascade (through second messengers, sensors, and kinases that activate a variety of TFs) results in the expression of multiple stress-responsive genes, which mediate stress tolerance and resistance, and restore the cellular and tissue homeostasis. *Sources: Hrmova, Maria, and Syed Sarfraz Hussain. 2021.*

In silico experiments and *trans*-activation assays shown that some TFs active in flooding stress are able to regulate the expression of hypoxia responsive genes. Particularly, five hypoxia-induced TFs (At4g29190; LBD41, At3g02550;HRE1, At1g72360; At1g69570; At5g66980) from different TF families [Zinc Finger, Ligand Binding Domain (LBD) or Lateral Organ Boundary Domain, ERF, DNA binding with one finger (DOF), ARF] showed this ability (Licausi et al., 2010).

Accumulation of ROS is a common consequence of biotic and abiotic stresses, including oxygen deprivation. There is evidence of redox-sensitive TFs, at least one of which might be involved in the adaptive response to low oxygen. ZAT12, a putative zinc finger-containing TF, is recognized as a component in the oxidative stress response signaling network of Arabidopsis (Rizhsky et al., 2004), promotes expression of other TFs and the upregulation of cytosolic ascorbate peroxidase 1, a key enzyme in the removal of H_2O_2. Advances have been made in molecular analyses of cDNAs and genes involved in the anaerobic response. Huq and Hodges (2000) reported early activation of a rice (*Oryza sativa* L.) gene by anoxia, the *aie* (anaerobically inducible early) gene. This gene encodes for a putative protein that shows short stretches of similarities to functionally interesting proteins (e. g. DNA binding proteins and nitric oxide synthase), indicating its putative involvement in signalling.

Advertisement

6. Salinity stress

High salinity is a critical environmental factor that inimically affects large areas of cultivated land. Plant growth, physiological and metabolic processes are affected, resulting in significant reductions in global crop productivity (Magomeet al., 2008, Zhang et al., 2009). Exposure to high levels of NaCl not only affects plant water relations but also creates ionic stress in the form of cellular accumulation of Cl^- and, in particular, Na^+ ions. Salt stress also changes the homeostasis of other ions such as Ca^{2+}, K^+, and NO^{3-}.

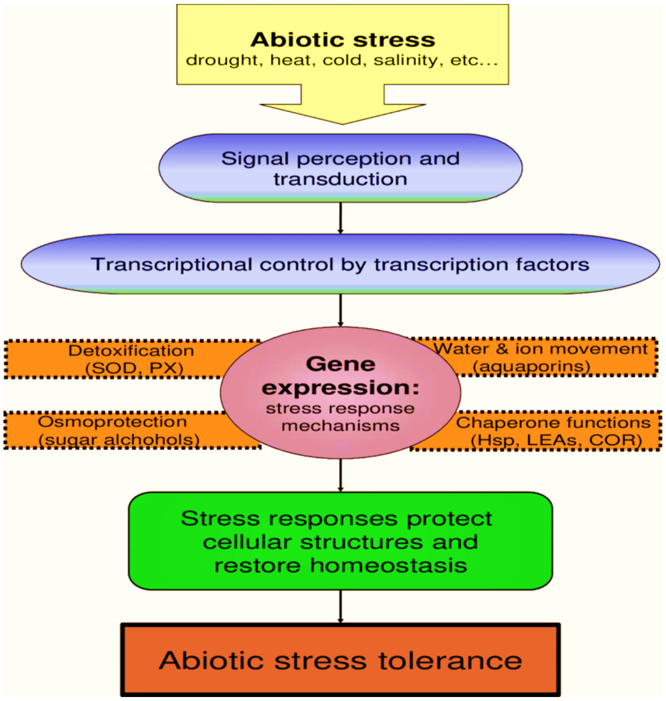

Figure 11: Plant response to abiotic stress. Transcription factors control signal transduction, leading to the expression of stress response genes. *Sources: Alina S Puig, 2010.*

Salt accumulation can modify plant cell plasma membrane lipid and protein composition, cause ion imbalance and hyperosmotic stress and eventually disturb normal growth and development (Fujii & Zhu 2009, López-Pérez et al., 2009). In general, high NaCl concentrations affect plant physiology and metabolism at different levels (water deficit, ion toxicity, nutrient imbalance, and oxidative stress; Vinocur & Altman, 2005), and at least two main responses can be expected: a rapid protective response together with a long term adaptation response. During initial exposure to salinity, plants experience water stress, which in turn reduces leaf expansion. During long-term exposure to salinity, plants experience ionic stress, which can lead to premature senescence of adult leaves, and thus a reduction in the photosynthetic area available to support continued growth (Cramer & Nowak, 1992). Salt tolerance determinants are categorized either as effectors that directly modulate stress etiology or attenuate stress effects, or as regulatory molecules that are involved in stress perception, signal transduction, or modulation of effector function. Genomics studies are focused on gene expression analysis following exposure of plants to high salinity, using salt shock experiments to mimic stresses that affect hydration and ion homeostasis.

The stress-responsive genes can be classified into two classes, i.e. early and delayed response genes (Sairam & Tyagi, 2004). The former are induced quickly and transiently, while the latter are activated more slowly and their expression is sustained. The early response genes encode transcription factors that activate downstream delayed response genes (Zhu, 2002). When microarray expression profiles of wild type plants, a T-DNA insertion knockout mutant of AtNHX1 (nhx1), and a rescued line (NHX1: nhx1) exposed to both short (12 h and 48 h) and long (one and two weeks) durations of a non-lethal salt stress were investigated, 147 transcripts showed both salt responsiveness and a significant influence of AtNHX1. Fifty-seven of these genes showed differential regulation across all salt treatments, while the rest were regulated as a result of a particular duration.

A large number of genes from a variety of biochemical pathways participate in responses conferring salt tolerance. These pathways include notably those involved in: signal transduction; carbon metabolism and energy production; oxidative stress protection; uptake, exclusion, transport and compartmentalization of sodium ions; modifications of structural components of cell walls and membranes. Several genes have been identified as functional components in the plant response to salt stress, including those encoding detoxifying enzymes like glutathione peroxidase (Roxas et al., 1997), Na^+/H^+ antiporter AtNHX1 (Apse et al., 1999), osmolytes such as glycine-betaine and LEA (late embryogenesis abundant protein) (Xu et al., 1996), flavoprotein AtHAL3 (Espinosa-Ruiz et al., 1999), signal mediator Ca2+/calmodulin-dependent protein phosphatase (Pardo et al., 1998) and transcription factor Alfin1 (Bastola et al., 1998). Analyses of complete transcriptomes suggest that systems like synthesis of osmolytes and ion transporters and regulation of transcriptional and translational machineries have distinct roles in salt-stress response. In particular, induction of transcripts of specific TFs, RNA-binding proteins, ribosomal genes and translation initiation and elongation factors has been reported to be important during salt stress (Sahi et al., 2006). Since not many stress-specific consensuses sequences were identified in promoters of stress specific genes to activate or repress transcription, transcription factors must be located in the nucleus, bind DNA and interact with the basal transcription apparatus. Transcription factors involved in stress responses include DRE-related binding factors, leucine zipper DNA-binding proteins, putative zinc finger proteins, myb proteins, bZIP/HD-ZIPs, and AP2/EREBP (Chen et al., 2002, Seki et al., 2002), interact with promoters of osmotic-regulated genes (Abe et al., 1997, Liu et al., 1998; Hasegawa et al., 2000a, 2000b). Particularly, AP2/ERF domain proteins include the DREB or CBF proteins binding to dehydration response elements (DRE) or C-repeats. A major transcriptional regulatory system is represented by DRE/C-repeat promoter sequences in stress-activated genes and DREBs/CBF factors that control stress gene expression (Stockinger et al., 1997, Liu et al., 1998). Several stress-inducible genes such as rd29A, Cor6.6, Cor15a and Kin1 are target genes of DREBs/CBFs in Arabidopsis and contain DRE/C-repeat sequences in their promoters.

Moreover, basic region leucine zipper (bZIP) proteins contain a DNA binding domain rich in basic residues that bind to an ACGT core sequence. One bZIP subfamily has been linked genetically to an ABA response: ABI5 and its homologs, the ABRE binding factors (ABFs/AREBs). ABRE binding factors (ABFs)/ABA-responsive element binding (AREBs) proteins respond at the transcriptional and post-transcriptional level to dehydration and salt stress (Choi et al., 2000, Uno et al., 2000). Other regulatory intermediates that modulate plant salt stress responses include SOS3 (Ca^{2+} -binding protein), SOS2 (Suc nonfermenting- like) kinase, Ca^{2+} -dependent protein kinases, and mitogen-activated protein kinases (Halfter et al., 2000). Genetic and physiological data indicate that SOS3, SOS2, and SOS1 are components of a signal pathway that regulates ion homeostasis and salt tolerance and their functions are Ca^{2+} dependent. In particular, SOS1, encoding a plasma membrane Na^+/H^+ antiporter, plays a critical role in sodium extrusion and in controlling long-distance Na^+ transport from the root to shoot (Liu & Zhu, 1998). This antiporter forms one component in a mechanism based on sensing of the salt stress that involves an increase of cytosolic $[Ca^{2+}]$ and reversible phosphorylation with SOS1 acting in concert with SOS2 and SOS3 (Shi et al., 2000). SOS2 encodes a Suc non-fermenting-like (SNF) kinase, and SOS3 encodes a Ca^{2+} -binding protein with sequence similarity to the regulatory subunit of calcineurin and neuronal Ca^{2+} sensors (Liu & Zhu, 1998, Liu et al., 2000). In yeast, co-expression of SOS1, SOS2, and SOS3 increases the salt tolerance of transformed yeast cells much more than expression of one or two SOS proteins (Shi et al., 2000), suggesting that the full activity of SOS1 depends on the SOS2/SOS3 complex.

Several studies have shown that reactive oxygen species (ROS) and oxidative stress may be mediating at least some of the toxic effects of NaCl on legumes (Jungklang et al., 2004) and other vascular plants (Attia et al., 2008). ROS are predominantly generated in the chloroplast by direct transfer of excitation energy from chlorophyll to produce singlet oxygen, or by univalent oxygen reduction at photosystem I, in the Mehler reaction (Allen, 1995) and to some extent in mitochondria. ROS have the potential to interact non-specifically with many cellular components, triggering peroxidative reactions and causing significant damage to proteins, lipids, and nucleic acids. To cope with ROS and to maintain redox homeostasis, living organisms evolved antioxidant defense systems, comprised of enzymatic and non-enzymatic components, which normally maintain ROS balance within the cell. Major nonenzymatic antioxidants include ascorbate (vitamin C) and glutathione in plants, although tocopherol (vitamin E), flavonoids, alkaloids, and carotenoids can also act as antioxidants. Intracellular ROS can also influence the ROS induced MAPK signal pathway through inhibition of phosphatases or downstream transcription factors (Mittler et al., 2004) (Fig. 3).

8. Heavy metal accumulation and metal stress

Uptake of excess metal ions is toxic to most plants. Phytotoxicity of heavy metals can be attributed to symplastic accumulation of heavy metals, particularly in the plasmatic compartments of the cells, such as the cytosol and chloroplast stroma (Brune et al., 1995). Metal-induced changes in development are the result of either a direct and immediate impairment of metabolism (Van Assche & Clijsters, 1990) or signaling processes that initiate adaptive or toxicity responses that need to be considered as active processes of the organism (Jonak et al., 2004). The detoxification of heavy metals by plants is achieved by uptake and translocation, sequestration into the vacuole and metabolization, including oxidation, reduction or hydrolysis and conjugation with glucose, glytanyl cysteine syntase (GSH) or amino acids (Salt et al., 1998, Meagher, 2000, Dietz & Schnoor, 2001).

So, in order to determine genes involved in response to heavy metal, recently, several studies, based on use of *A. thaliana* as model plant, performed the analysis of global gene expression after exposure to salts of lead (Pb) and cadmium (Cd). The analysis revealed 65 and 338 up- and down-regulated genes by Cd and 19 and 76 by Pb (Kovalchuk et al., 2005). Particularly, it was found that ABC transporters were differentially regulated after Cd treatments, suggesting for some plant ABC transponders a key role in glutathione-Cd or phytochelatins-Cd complex transport both into cellular compartments and outside of the cell (Bovet et al., 2005).

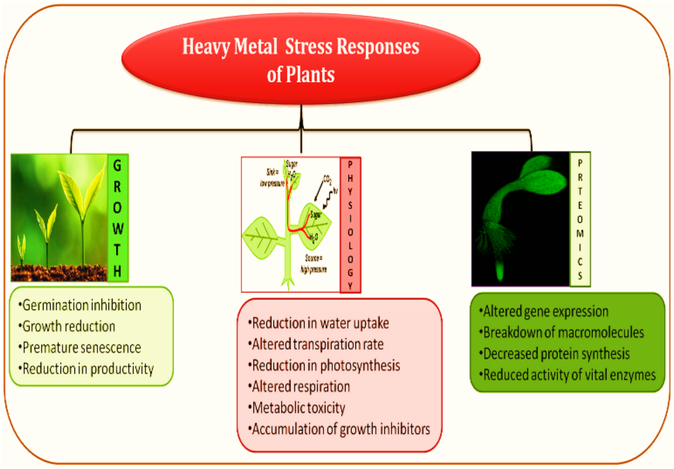

Figure 12: Diagrammatic representation of heavy metal effects on plant growth and development.(Accumulation of metals instigates direct or indirect harmful effects causing morpho-physiological abnormalities (decreased photosynthesis, plant growth, biomass, and yield), giving rise to the formation of ROS resulting in redox homeostasis disruption, damaging plasma membrane of cells, proteins, lipids, and nucleic acids, and causing disorder in metabolic activities that ultimately lead to reduced agricultural productivity). ***Sources: Faizan, Mohammad, Pravej Alam, Vishnu D. Rajput, Ahmad Faraz, Shadma Afzal, S. Maqbool Ahmed, Fang-Yuan Yu, Tatiana Minkina, and Shamsul Hayat. 2023***

Subsequently studies performed on Arabidopsis, using microarray tools, demonstrated that exist a complex regulatory network which differentially modulates gene expression in a tissue-specific manner. Responses observed in roots included the induction of genes involved in Sulphur assimilation-reduction and glutathione metabolism. Therefore, it was suggested that plants activate the Sulphur assimilation pathway by increasing transcription of related genes to provide an enhanced supply of glutathione for phytochelatin biosynthesis.

Nonspecific defense mechanisms include accumulation of osmolytes, antioxidants, amino acids and changes in hormonal balances.

The significance of glutathione and the metal-induced phytochelatins (PCs) in heavy metal tolerance has been summarized intensely in excellent reviews (Rauser, 1995, 1999, Hall, 2002). Depletion of glutathione appears to be a major mechanism in short-term heavy metal toxicity and in accordance with this hypothesis, a good correlation between glutathione contents and tolerance index was observed with 10 pea genotypes differing in Cd sensitivity (Metwally et al., 2005).

In roots, after Cd exposure, three categories of genes were identified from transcriptome analysis: (1) common responses conserved across species; (2) metallophyte-specific responses representing candidate genes for Cd hyper tolerance; (3) specific responses to Cd (Weber et al., 2006).

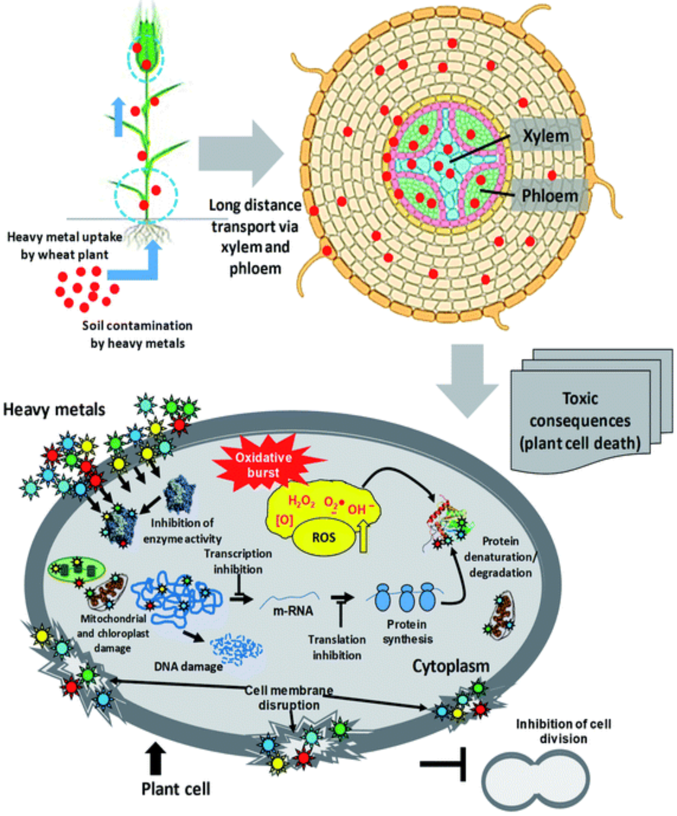

Figure 13: Sequence of events from metal entry into a plant cell to the death of the plant. ***Sources: Asfa Rizvi, Almas Zaidi, Fuad Ameen, Bilal Ahmed, Muneera D. F. AlKahtani c and Mohd. Saghir Khan.2020.***

9. High light stress

Light plays a critical role in regulating plant growth and development through the modulation of expression levels of light-responsive genes that regulate developmental and metabolic processes. Light signals are perceived through at least four distinct families of photoreceptors, which include phytochromes (Phy), cryptochromes, phototropins and unidentified ultraviolet B (UVB) photoreceptor(s). For each developmental response, more than one photoreceptor can contribute to the perception of light signals, indicating that signal integration points for different light signals must exist in transcriptional hierarchies. Light can modulate photoreceptor activity by inducing changes that alter their cellular localization. The best characterized light receptor is Phy, which exists in two photochemically interconvertible forms, Pr and Pfr, and is encoded by a small family of genes in angiosperms. Phytochromes are synthesized in the inactive Pr form, that absorbs red light, (660 nm), and are activated on light absorption by conversion to the biologically active Pfr form, that absorbs far-red light (730 nm). The photoconversion of phytochromes results in their translocation from the cytoplasm into the nucleus, which is crucial for allowing them to interact with transducers in initiating downstream transcriptional cascades (Quail, 2002).

The responses of plants to light are complex: seed germination, seedlings photomorphogenesis, chloroplast development and orientation, photodinesis, stem growth, pigment biosynthesis, flowering and senescence (Kendrick & Kronenberg, 1994). Collectively these processes are known as photomorphogenesis. Besides excess light, a range of abiotic environmental conditions such as O_3, salt, toxic metals, and temperature can induce increased production of ROS by limiting the ability of a plant to utilize light energy through photosynthesis (Shinozaki & Yamaguchi-Shinozaki, 2000). Exposure of a plant to light exceeding what is utilized in photochemistry leads to inactivation of photosynthetic functions and the production of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide ($O_2{}^{-}$), hydroxyl radicals, and singlet oxygen ($^1O_2$; Niyogi, 1999). Indeed, high light drove change in the redox potential of plastoquinone (PQ) regulating the expression of two cytosolic peroxidases during HL stress (Karpinski et al., 1999). Furthermore, the redox state of PQ has been shown to be involved in the expression of chloroplast encoded genes (Pfannschmidt et al., 1999).

Classical genetic and molecular approaches have identified various regulators downstream of photoreceptors. Many of these encode TFs, as well as kinases, phosphatases and degradation-pathway proteins. Although some of these regulators are specific for light quality, others regulate signal transduction networks in response to various light signals, representing potential signal integration points. Several basic post-translational mechanisms are involved in regulating TF activities and the subcellular localization in response to light. The phosphorylation of TFs is a common modification that can influence their ability to bind to promoters. For example, the level of G-Box Binding Factor 1 (GBF1) is constant, but its affinity for the G-box is modulated by its phosphorylation status: its phosphorylation by nuclear Casein Kinase II (CKII) enables G-box binding (Klimczak et al., 1995). In the dark, some TFs that positively regulate gene expression in response to light, such as Long After Farred Light 1 (LAF1), are ubiquitylated by Constitutive Photomorphogenic 1 (COP1), a ring-finger-type ubiquitin E3 ligase. In darkness, COP1 acts as E3 ligase in the nucleus, targeting TFs like Long Hypocotyl5 (HY5) and LAF1 to degradation via the 26S proteasome. Upon exposure to light, COP1 migrates from the nucleus to the citosol. The study by Ulm and coworkers (2004) established that HY5, a bZIP transcription factor that is one of the key regulators of cryptochrome and phytochrome controlled photomorphogenesis, is an important component of the UVB-induced signalling network. UVB promotes rapid transcriptional activation of HY5 (and its interacting partner Long Hypocotyl5-Like [HYH]) independently of all known photoreceptors, and loss of HY5 results in the impairment of the transcriptional induction of a subset of UVB-responsive genes. Taken together, these observations demonstrate that UVB up-regulates HY5 transcription by yet-unknown signalling pathway (s), and that the signalling cascades that mediate responses to visible light and long-wavelength UVB (300–320 nm) use shared components.

Additional studies suggested that HY5 also regulates the transcription of several photosynthesis-related genes, such as the ribulose bisphosphate carboxylase small subunit (RbcS1A) (Lee et al., 2007). Given that HY5 appears to regulate the expression of several Arabidopsis genes known to respond to abiotic stress conditions (e.g. CBF1, DREB2A, RD20 and MYB59) (Lee et al., 2007), it is inferred that HY5 could also be involved in the regulation of photosynthesis by adverse environmental conditions. In vitro analysis showed that HY5 directly binds to the promoters of several light-inducible genes (Hiltbrunner et al., 2006) and a recent chromatin immuno-precipitation analysis in combination with a whole-genome tiling microarray revealed that HY5 binds directly to a large number of genomic sites, mainly at the promoter regions of annotated genes. HY5 interacts specifically with the G-box (CACGTG) and is required for normal control by light of promoters bearing this sequence (Lee et al., 2007). Recently, some review showed as DNA *cis*-elements responsible for light regulated transcription are located within 5' upstream sequences. The evolution of regulatory sequences, which determine where, when, and the level at which genes are transcribed, has been largely neglected. In the case of the photosynthesis-associated nuclear genes (PhANGs) from higher plants, interesting evolutionary aspects of the molecular mechanisms by which transcription is activated by light receptors (e.g. phytochrome) could be addressed through the comparative analysis of promoter sequences. For instance, why does light profoundly affect transcription of PhANGs in monocotyledonous and dicotyledonous plants, while PhANG promoters in conifers, ferns, and mosses are either light insensitive or, at most, weakly photoresponsive (Mukai et al., 1992). Light-responsive Transcriptor Factors (TFs) have been identified through screens for light-responsive *cis*-element (LRE)-binding proteins and through genetic analyses of mutants that are deficient in their response to specific types of light. A combination of various methods has been used to identify these LREs. Such analyses have been successfully performed in identifying *cis*-acting elements involved in the light responsiveness of PhANGs, such as the G-box and I-box elements from rbcS genes (Giuliano et al., 1988) and the GATA motifs of Lhcb1 genes (Gidoni et al., 1989, Millar et., 1994). Although many LREs and their binding proteins have been identified, no single element is found in all light-regulated promoters, suggesting a complex light-regulation network and a lack of a universal switch (Jiao et al., 2007). Sequence heterogeneity of regulatory elements may be functionally overcome if multiprotein regulatory complexes facilitate binding to imperfect target sites (Miner et. 1991). The individual elements found within a multipartite *cis*-regulatory region are termed phylogenetic footprints (PFs); they share high conservation over a segment of 6 contiguous base pairs in alignments of orthologous upstream sequences and represent potential binding sites for transcription factors (Gumucio et al., 1993). The “phylogenetic-structural method” is based on the search of “homologous” (rather than “similar”) DNA sequences of a functionally characterized promoter. Two sequences are homologous when they share common ancestry, regardless of the degree of similarity between them (Doolittle et al., 1987).

10. Physiological and biochemical responses

Drought is multifaceted stress for plants and can cause a critical impact on the metabolism of crop plants (Farooq M, Basra S, Wahid A, et al.,2009; Bhargava S, Sawant K. ,2013; Rahdari P, Hoseini SM. ,2012) and trigger remarkable limitation of crop production (Amelework B, Shimelis H, Tongoona P, et al. ,2015; Boyer JS, Westgate ME. ,2004). Water deficit conditions are the most common edaphic stress that is harmful to cellular homeostasis and obstructs plant development (Pandey V, Shukla A. ,2015). The water requirement for irrigation is ceaselessly expanding while there is a serious decrease in water accessibility. This is unfavorable in semi-arid and arid conditions (Rostamza M, Chaichi M-R, Jahansooz MR, et al. ,2011). Water scarcity in fields expressed by the absence of adequate moisture in the soil results in a delay and or failure of crop maturation and development. Water deficiency affects the biochemical, morphological and physiological processes in crop plants. Drought causes loss of turgor, disorganizes the activities of enzymes, and reduces the energy transfer from photosynthesis, which causes a negative impact on cell multiplication, elongation and specialization, thereby affecting plant growth and development (Bhargava S, Sawant K. ,2013; Ayub M, Ashraf MY, Kausar A, et al.,2021; Jaleel CA, Manivannan P, Wahid A, et al.,2009; Osakabe Y, Osakabe K, Shinozaki K, et al.,2014).

Remarkable effects of drought on plants also include reduced cell expansion and division rate, decreased germination rate, reduced leaf area, disturbed stomatal responses and reduced chlorophyll levels. However, plants can circumvent water deficiency by decreasing water depletion (e.g. closing stomata, reducing leaf surface area, etc.) or increasing uptake of water (by deep roots) (Kozlowski TT, Pallardy SG. ,2002). An essential reaction of plants exposed to water deficit conditions is growth arrest. Restricted shoot development in the presence of drought stress diminishes the metabolic demands of the plant. It assembles the metabolites for the formation of defensive compounds, which are needed for osmotic adjustment. Constricted root development regulates the root meristem’s function and promotes root growth when the stress soothed (Hsiao TC, Xu LK. ,2000) (Aslam M, Zamir MSI, Afzal I, et al. ,2014; Farooq M, Basra S, Wahid A, et al. ,2009).

The response of plants towards water deficit conditions is extremely intricate. It fundamentally fluctuates amongst different plants and between their development stages and extent of water deficiency (Aslam M, Zamir MSI, Afzal I, et al. ,2014; Farooq M, Basra S, Wahid A, et al. ,2009). Water scarcity causes a remarkable impediment of root and shoots development, and leaf area which is followed by reduced growth and development of plants (Anjum SA, Xie XY, Wang LC, et al. ,2011b) (Anjum SA, Xie XY, Wang LC, et al.,2011b). Besides these alterations, plants engage various metabolic processes extending from photosynthesis to antioxidant and solute accumulation as constituents of water deficit resistance. Plants respond to drought stress by modifying the gene expression through complex transcriptional networks (Singh D, Laxmi A., 2015). According to Joshi et al.,2016b, although efficient adaptation mechanisms are highly conserved among stress susceptible genotypes, the tolerant genotypes, however, evolved additional regulatory mechanisms that improve their ability to manage severe abiotic stresses. With the availability of diverse omics tools including genomics, transcriptomics and proteomics, major progress has been made for understanding the interaction and complexity of the stress adaptive mechanisms and their respective signaling pathways (Liu JH, Peng T, Dai W. ,2016). Many of the transcriptional network genes specified in several molecular studies have been noticed to contribute to drought stress tolerance in transgenic plants (Todaka D, Shinozaki K, Yamaguchi-Shinozaki K., 2015). The signaling pathway of any abiotic stress comprises fundamental steps like signal perception, transduction, responsiveness, together with physiological and metabolic reaction activation (Liu JH, Peng T, Dai W. ,2016; Pérez-Clemente RM, Vives V, Zandalinas SI, et al. ,2013).

Signaling processes require the perception of stress stimulus by plant cells *via* sensors or receptors that are located at the cellular membranes. The receptor then activates the second messengers such as calcium ions, inositol phosphate, reactive oxygen species (ROS), cyclic nucleotides (cAMP and cGMP), sugars and nitric oxide inside the cells. These second messengers then instigate signaling pathways and transduce the signals (Bhargava S, Sawant K. ,2013). The modulation of phosphorylation and dephosphorylation of proteins by protein kinases and phosphatases, respectively, is an essential and noticeable mechanism in various signal transduction pathways, for example, the MAPKs and CDPKs, which have been established to play an essential role in drought stress signaling pathways (Huang GT, Ma SL, Bai LP, et al.,2012). After a phosphorylation cascade, TFs activation or suppression by protein kinases or phosphatases occurs, and TFs interact with distinct *cis*-elements in the promoter region and thus directly regulate the expression of a range of downstream genes (Danquah A, de Zelicourt A, Colcombet J, et al. ,2014). Additionally, at the transcriptional level these TFs are modulated by other upstream components (Hirayama T, Shinozaki K., 2010) and at the post-transcription level, their alteration by ubiquitination and SUMOylation, leads to the formation of a complex regulatory network which modulates the expression of stress responsive genes, regulating various physiological and metabolic processes (Mizoi J, Ohori T, Moriwaki T, et al. ,2013).

Substantial work has been carried out towards the identification and characterization of different TFs that impart drought tolerance. Water deficit conditions, if persisting for longer duration, result in a notable decrease in growth and development, as reported in pepper (*Piper nigrum*) (Anjum SA, Farooq M, Xie XY, et al. ,2012). The effects of water scarcity on plant growth and development are outlined in Table 1. The following subchapters present the effects of drought stress on some physio-biochemical reactions of plants.

11. Drought: physiological responses

11.1. Mineral nutrition

Several environmental stresses like drought may cause deficiency of nutrients, even in agricultural fields, as the individual nutrient absorption depends on the physicochemical properties of soil (Amtmann A, Blatt MR.,2009; Nawaz F, Shehzad MA, Majeed S, et al., 2020). With the reduction in water availability, nutrient availability in the soil decreases so the nutrient concentration in the plant tissues decreases (Kheradmand MA, Fahraji SS, Fatahi E, et al. ,2014). Water deficit conditions cause a significant impact on the uptake of nutrients by the roots and their translocation to the shoots. It has been noted that drought stress causes an enhancement of N, decreases P content, and generally has no consequence on the K content in plants (Farooq M, Basra S, Wahid A, et al., 2009). Reduction in plant Ca levels under drought stress has also been revealed (Bhargava S, Sawant K., 2013). The stability of membranes in the roots had an important function in the proper mineral nutrition of plants. However, cell membranes are the earliest subjects of various stresses including water stress. Hence, proper maintenance of the membrane stability is an essential element for drought tolerance in plants. Disintegrated cell membranes under drought stress are a key factor which causes disorganized ion balance in plants (Farooq M, Basra S, Wahid A, et al., 2009; Rahdari P, Hoseini SM. ,2012; Kheradmand MA, drought stress conditions, insufficient root functionality and slow water diffusion rates, make roots ineffective in absorbing nutrients from the soil (Dubey RS, Pessarakli M., 2001). Water deficit conditions also lead to stomatal closure as well as decreasing transpiration and limited translocation of nutrients from the root to the upper parts of plants (Bhargava S, Sawant K., 2013; Hu Y, Schmid halter U.,2005). Hence, water deficit conditions result in lesser availability of soil nutrients and reduced nutrient translocation consistency in plants (Nawaz F, Shehzad MA, Majeed S, et al. ,2020; Ahanger MA, Morad-Talab N, Abd-Allah EF, et al. ,2016; Hu Y, Burucs Z, von Tucher S, et al., 2007). All these elements have a grave effect on plant development, impacting several physiological processes. The closure of stomata is the chief physiological reaction of plants to water deficiency. By decreasing transpirational water losses, plants conserve water levels in cells and this is generated by either hydro passive or hydro active processes (Murata Y, Mori IC. ,2014). Water deficit conditions can induce abscisic acid (ABA) generation, which leads to stomatal closure and stimulates the expression of drought stress-associated genes for the regulation of plant responses.

Fahraji SS, Fatahi E, et al.,2014). Under

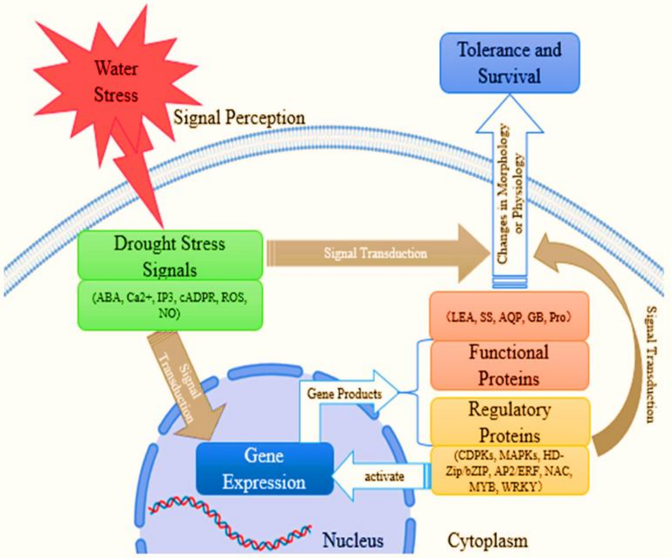

Figure 14: The process of plant drought-tolerance development. *Sources: Yang, Xinyi, Meiqi Lu, Yufei Wang, Yiran Wang, Zhijie Liu, and Su Chen. 2021*

11.2. Stomatal movement

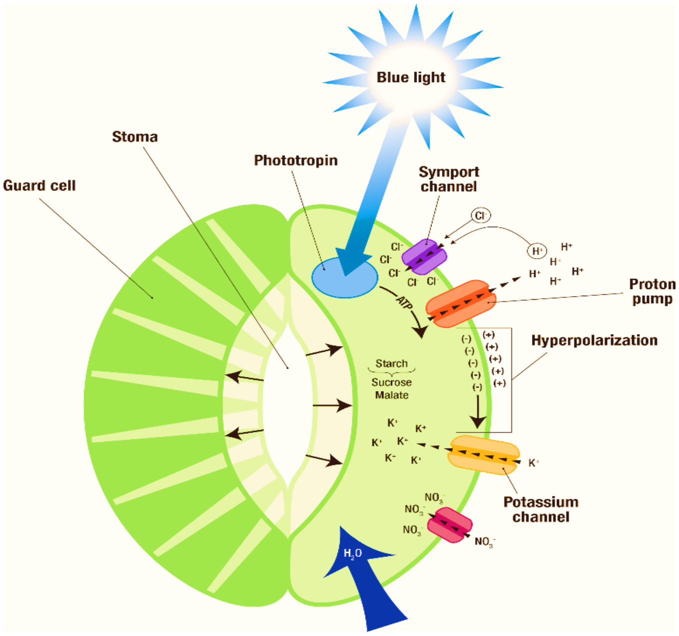

Figure 15: Phytotropins respond to blue light and signal to the proton pump to export protons. This active transport is fueled by the ATP produced in the light-dependent reactions of photosynthesis. This causes the cell to become hyperpolarized, stimulating an influx of potassium ions. At the same time, chloride is symported into the guard cell with protons as they reenter the cell. Nitrate (NO_3^-) also enters the cell. Starch breaks down, producing sucrose and malate. These, along with the influx of ions, increases the solute concentration inside of the guard cells, driving water into the cells. This increases turgor pressure and causes the guard cells to expand. Due to their radial cell wall thickenings, the guard cells curve when they expand, opening the stoma (plural: stomata). Image by Jen Valenzuela (CC-BY-NC).

Accumulation of ABA in plant cells leads to the ROS production (Liu Y, Ye N, Liu R, et al. ,2010; Taiwo AF, Daramola O, Sow M, et al. 2020). H_2O_2, an important ROS, participates in various plant metabolic reactions, stress responses and apoptosis (Apel K, Hirt H. ,2004; Foyer CH, Noctor G. ,2005). Additionally, H_2O_2 takes part in the modulation of stomatal movement. ABA and H_2O_2 relationship play an essential part under water deficit conditions. ABA stimulates H_2O_2 production in guard cells through NADPH oxidase, and H_2O_2 imparts ABA-generated closure of stomata. H_2O_2 induced stomatal closure has been noticed in broad bean (*Vicia faba*) and tobacco (*Nicotiana tabacum*) epidermis.

11.3. Stomatal Closure

When water is low, roots synthesize **abscisic acid** (ABA), which is transported through the xylem to the leaves.

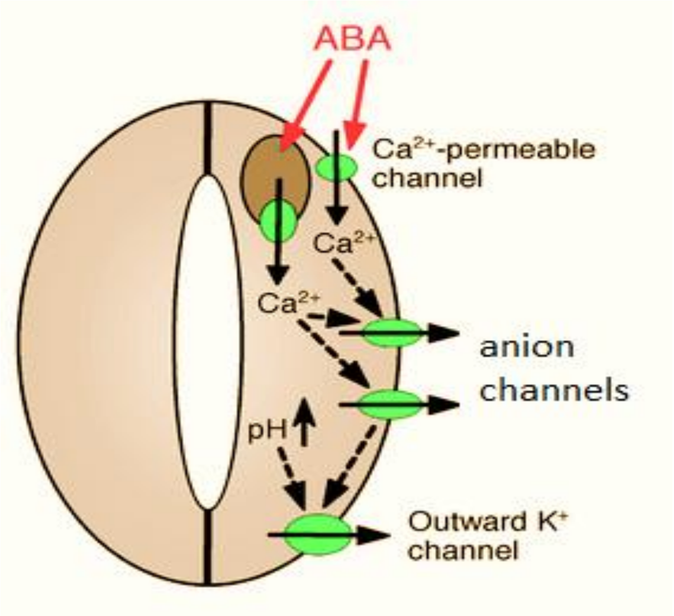

Figure 16: Stomatal closure is triggered by abscisic acid (ABA), which causes calcium (Ca^{2+}) ions to enter the cell. These open anion channels. At this point, the cytoplasm is not as negatively charged as it was before. The change in charge opens potassium (K^+) channels, and potassium leaves the cell as well. Water leaves the cells, causing them to loose turgor pressure. The stoma then closes. Image modified from June Kwak (public domain).

There, abscisic acid causes calcium channels to open. Calcium (Ca^{2+}) opens anion channels, and malate, chloride, and nitrate exit the cell. The membrane potential decreases (the difference in charge across the membrane becomes less pronounced) as anions leave the cell.

Potassium exits the cell in response to this decrease in membrane potential (called **depolarization**). The loss of these solutes in the cytosol results in water leaving the cell and a decrease in turgor pressure. The guard cells regain their original shape, and the stoma closes.

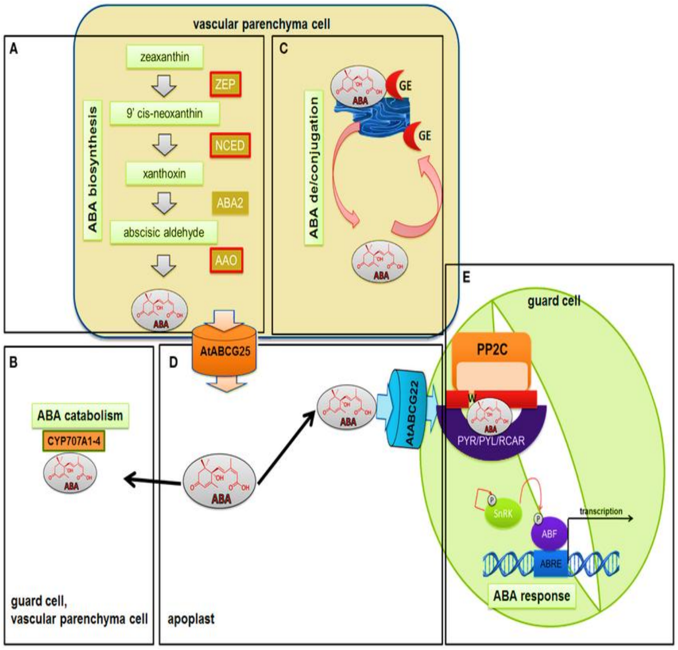

Figure: Abscisic acid biosynthesis, catabolism, deconjugation, transport, and signaling. ABA biosynthesis (A) is mainly induced by upregulating NCED3, ZEP, and AAO genes. At the same time as the biosynthesis of ABA is induced, the catabolism (B) that is performed by CYP707A1-4 is inhibited. The balance between active and inactive ABA in the cell is achieved not only by the regulation of biosynthesis and catabolism but also by ABA conjugation and deconjugation. The most widespread conjugate is the ABA glucosyl ester (ABA-GE), which is catalyzed by ABA glucosyltransferase (C). ABA delivery to the guard cells via ABCG transporters such as AGCG22 (D) promotes a cascade of reactions. The core of early ABA signaling involves ABA receptors – PYR/PYL/RCAR proteins, PP2Cs, and SnRKs (E). After binding ABA to the receptor, the negative regulatory action of PP2Cs is inhibited and SnRKs are able to phosphorylate and activate downstream targets in order to transduce the ABA signal. ***Sources: Agata Daszkowska-Golec, Iwona Szarejko,2013***

Stomata are specialized epidermal structures that are essential for plant survival and productivity. These structures consist of two guard cells around a pore. Every stoma is a molecular valve that acts in gas exchange, mainly CO2 and O2, which is necessary for optimal photosynthesis and which restricts water loss by modulating the transpiration level. The genes that are involved in the process of stomata development were crucial for the movement of plants from water to land during evolution since stomata facilitated gas exchange while limiting desiccation. The stomatal morphogenesis pathway has been identified in detail in Arabidopsis thaliana through in vesting at ions of many mutants with an impaired stomatal pattern or with other morphological defects in their epi dermal cells. Cell distribution and differentiation require a balance between proliferation and cell specification in time and space. The differentiation of stomata is preceded by at least one asymmetric as well as a few symmetric cell divisions. It requires three different types of precursor cells: the meristemoids mother cell (MMC), meristemoids and the guard mother cell (GMC).

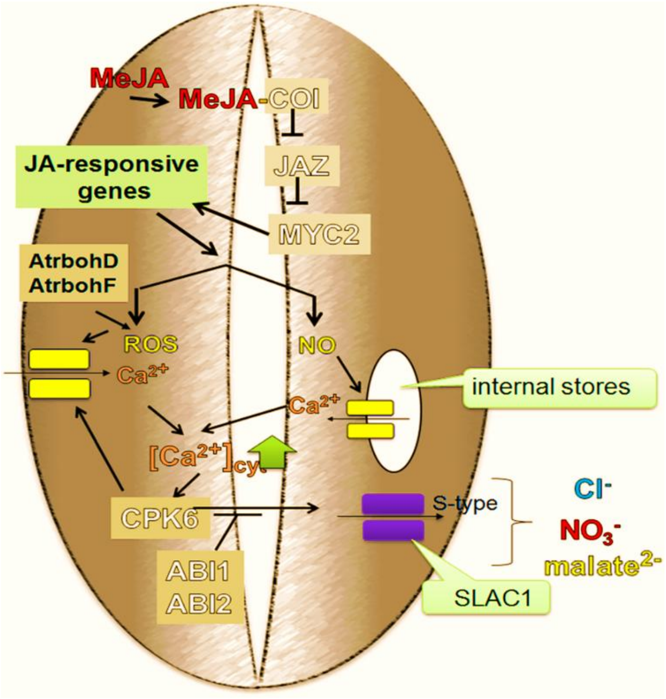

Figure 17: Me-JA regulated stomatal closure during drought stress. MeJA, before it can be bound by a receptor in the plant cell, is converted into a biologically active form (+)-7-iso-Jasmonoyl-l-isoleucine (JA-lle). JA-lle is then bound by the receptor SCFCOI complex that contains the coronatine insensitive1 (COI1) F-box protein. This interaction leads to the JAZ degradation which is negative regulator of MYC2. Inactive JAZ is not able to repress MYC2 function which in turn activates JA-responsive genes. MeJA induces the formation of ROS and NO, which activate the efflux of Ca^{2+} from internal stores and the influx from the apoplast by channels in plasma membrane. CPK6 acts downstream of NO and ROS signaling and therefore

may be the target of an NO-stimulated influx of Ca^{2+} into the cytoplasm. As a feedback loop, MeJA-induced influx of Ca^{2+} into the cytoplasm activates CPK6, which in turn is able to activate the S-type anion channel – SLAC1, which then leads to the MeJA-stimulated stomatal closure. *Sources: Agata Daszkowska-Golec, Iwona Szarejko,2013*.

The last step of stomatal development is the differentiation of the stoma itself within the structure of the guard cells. The number and pattern of stomata varies in different organs in A. thaliana. A common feature of patterning is that stomata are separated from each other by at least one epidermal cell. This pattern ensures the presence of neighbor cells for ion exchange, which is necessary for the regulation of the aperture width. For this reason, neighbor cells are part of a stomatal complex. Recent research has shown that the mode of action of stomata depends on the integration of environmental and intracellular signals. Many environmental factors such as CO2 concentration, biotic and abiotic stresses, and additionally different plant hormones, can modulate stomatal reaction. For plants that encounter dehydration stress, the most essential factor is the ability of stomata to close and thus prevent excess water loss. Opening and closing is achieved by the swelling and shrinking of the guard cells, which is driven by ion exchange; cytoskeletal ton reorganization and metabolite production; the modulation of gene expression and the posttranslational modification of proteins. Swelling of the guard cells results in stomata opening since the content of ions and osmolites within them makes them bigger and thus able to move away from each other making the stomatal aperture larger. In contrast, closing is an opposite mechanism and results in the shrinking of the guard cells when the efflux of ions occurs.

11.4. Photosynthesis

Photosynthesis is an essential indicator of drought stress due to its severe susceptibility to numerous environmental stresses. Several reports describe that drought caused a decline in chlorophyll content, net photosynthetic rate, maximal quantum yield (Fv/Fm), stomatal conductance and transpiration, which ultimately reduces plant metabolism and production (Mathobo R, Marais D, Steyn JM. ,2017; Muhammad I, Shalmani A, Ali M, et al.,2021; Saeidi M, Abdoli M. ,2018). Under drought stress, stomatal and nonstomatal factors could be effectual in suppressing the photosynthetic rate (Bray EA. ,2001; Sapeta H, Costa JM, Lourenco T, et al. ,2013). Water scarcity prompts the synthesis of ABA, which leads to the closure of stomata and thereby decreasing the intercellular carbon dioxide concentrations and hindering photosynthesis. However, this suppression is reversible so photosynthesis can resume upon the removal of stress (Chaves MM, Flexas J, Pinheiro C., 2009). Decreased CO_2 which occurred due to the closing of stomata, also reduces the activity of enzymes taking part in several dark reactions. Decreased activity of light-independent reactions might cause disparity in the light and dark reactions, leading to ROS accumulation in plastids (Farooq M, Basra S, Wahid A, et al.,2009; Bhargava S, Sawant K. ,2013; Nezhad Ahmadi A, Hossain Prodhan Z, Faruq G. ,2013), thus causing indiscriminate impairment to the photosynthetic apparatus. Under water-scarce conditions, there is a prompt fall in the amount and activity of RuBisCO noticed in all the plants studied; however, the intensity of this reduction depends on the plant species) (Farooq M, Basra S, Wahid A, et al., 2009; Muhammad I, Shalmani A, Ali M, et al.,2021; Chernyad'ev II.,2005). Decreased activity of RuBisCO results from the acidification of chloroplast stroma, reduced quantity and action of ATPase and ATP synthase, configurational changes in chloroplasts and RuBisCO (Farooq M, Basra S, Wahid A, et al., 2009; Chernyad'ev II. ,2005; Bhargava S, Sawant K., 2013). Additionally, under drought conditions, activities of several other enzymes that take part in carbon fixation, like phosphoenolpyruvate carboxylase, NADP-malic enzyme, fructose-1,6-bisphosphatase, NADP-glyceraldehyde phosphate dehydrogenase, phosphoribulokinase, sucrose phosphate synthase, and pyruvate orthophosphate dikinase, also reduce with decreased leaf water potential (Farooq M, Basra S, Wahid A, et al., 2009 Chernyad'ev II., 2005). Electron transport reactions of photosynthesis are also disrupted under water deficit conditions (Salehi-Lisar SY, Motafakkerazad R, Hossain MM, et al. ,2912; Bhargava S, Sawant K. ,2013). An attempt has been made to summarize the important informative studies corresponding to the impact of water scarcity on photosynthesis and its associated attributes in Table 2.

Table 2. Impact of water scarcity on photosynthesis and its associated attributes.

12. Drought: biochemical reactions of plants

Oxidative stress and antioxidant system

Drought results in oxidation in plant cells by inducing the generation of ROS (superoxide radical, hydrogen peroxide, hydroxyl radical, and singlet oxygen). ROS generation in plants is detrimental to several physiological and metabolic processes like photosynthesis and antioxidant defense system, causing lipid peroxidation, the disintegration of chlorophyll, destabilization of the membrane, and ion spillage Hossain MA, (Mostofa MG, Fujita M.,2013; Zou YN, Wu QS, Kuča K. ,2021). Under normal conditions, a steady-state cellular ROS level occurs as a result of equilibrium occurring between ROS production and scavenging. However, this balance gets shifted under various stresses, including drought stress, where more production of ROS occurs than scavenged, hence generating oxidative stress. Moreover, an early rise in the generation of ROS, before reaching the stage when its production overcomes scavenging action, can act as a signaling system for defense reactions. The signaling function of ROS has been seen well in defense response against pathogens where the generation of oxidative stress trigger signaling mechanisms for defense (Lamb C, Dixon RA. ,1997). Besides playing a negative role induced by stresses, ROS also play a role in growth and development. Therefore, ROS, e.g. H_2O_2, have been revealed to take part in radicle emergence during seed germination (Chaudhuri A, Kar RK.,2008; Garnczarska M, Wojtyla L. ,2008), growth of roots, and root hair elongation (Foreman J, Demidchik V, Bothwell JH, Mylona P, et al. ,2003; Liszkay A, van der Zalm E, Schopfer P. ,2004) and also play a role in the defense against pathogens during seed germination (Schopfer P, Plachy C, Frahry G. ,2001). Compared with other ROS, the relative stability of H_2O_2 and its potential to pass through the cell membrane makes it suitable for signaling. The site and level of production of ROS should be strictly under control for signaling, either under stress conditions or growth and development responses.

The cell wall is one of the essential sites where defense response through ROS commences (Zou YN, Wu QS, Kuča K., 2021; Castro B, Citterico M, Kimura S, et al. ,2021). In this compartment, the most exposed enzyme for the generation of ROS is NADPH oxidase, which produces $O_2^{\bullet-}$, which spontaneously or by the action of cell-wall located SOD is dismutated to H_2O_2 (Liszkay A, van der Zalm E, Schopfer P., 2004). Apart from functioning as a ROS detoxifier, wall-bound peroxidases also play a role in ROS signaling by the production of ROS like $O_2^{\bullet-}$ and H_2O_2. The latter may also function as the substrate for lignin, which is essential for cell wall composition. Cellular ROS signal peculiarity can be ascertained by the site of its production, control and transduction (Foyer CH, Noctor Therefore, different plant cell compartments will have distinct impact on the regulation of cellular redox signals under water deficit conditions. Downstream signaling of ROS or hydrogen peroxide occurs through calcium and reversible protein phosphorylation (Hung SH, Yu CW, Lin CH. ,2005; Neill SJ, Desikan R, Clarke A, et al. ,2002). Under environmental stress conditions, alterations in cytosolic free calcium ([Ca^{2+}] cyt) have been described. To enhance the influx of Ca^{2+}, ROS (including H_2O_2) can stimulate plasma membrane-localized hyperpolarization-activated calcium channels (HACCs) (Demidchik V, Shabala SN, Davies JM., 2007). G. ,2003).

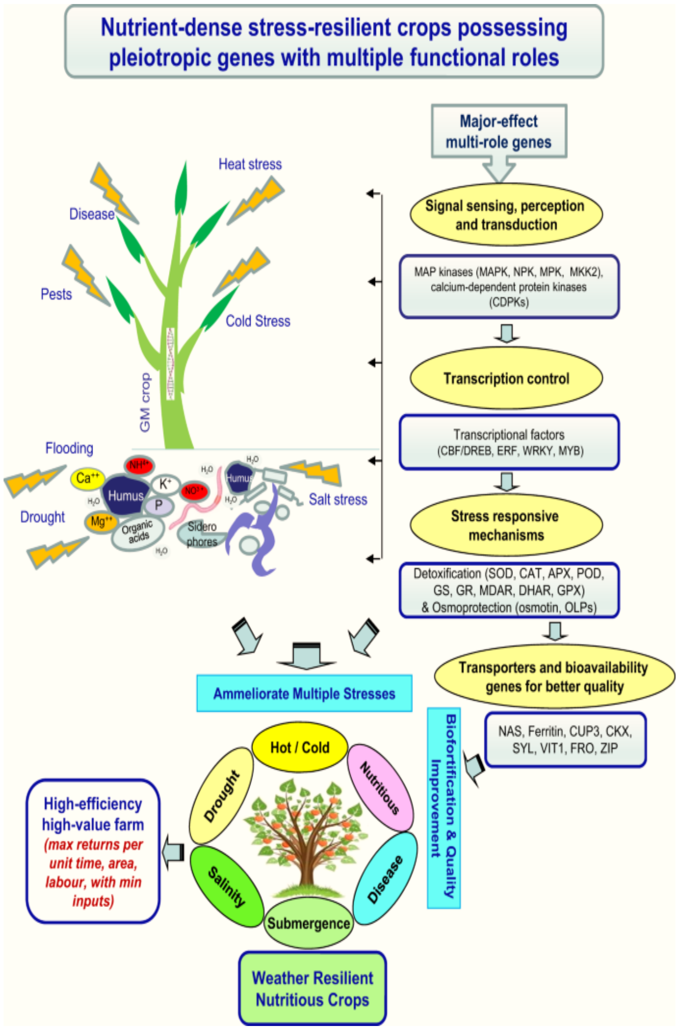

Figure 18: Crops can develop resilience towards stresses through genome engineering and increase uptake of nutrients through better nutrient use efficiency, and hence meet the food and nutritional security challenges. Such crops will support in establishing high-efficiency farms capable of giving better returns per unit of the applied input (time, space, labor, energy). *Sources: Husaini, A.M.,2022.*

Intracellular Ca^{2+} can also establish a positive feedback loop by prompting NADPH oxidase to generate ROS in the apoplast (Takeda S, Gapper C, Kaya H, et al., 2008). Reversible protein phosphorylation, on the other hand, is revealed to be required in downstream signaling after the production of ROS (Neill SJ, Desikan R, Clarke A, et al. ,2002), and a number of protein kinases have been exhibited to be induced by H_2O_2 (Hancock J, Desikan R, Harrison J, et al. ,2006); however, such activation does not occur by Ca^{2+}, as no Ca^{2+}- dependent kinase has been described under H_2O_2 regulation (Neill SJ, Desikan R, Clarke A, et al. ,2002). Moreover, various studies associate H_2O_2 with mitogen-activated kinase (MAPK) signaling cascade, which regulates gene expression through stimulation of transcription factors (Hung SH, Yu CW, Lin CH. ,2005; Neill SJ, Desikan R, Clarke A, et al. ,2002). Such modulated genes appear to play a role in cellular protection and repair process because some of the gene products are known for desiccation tolerance and DNA damage repair (Desikan R, Neill SJ, Hancock JT. ,2000). A cDNA microarray study in *Arabidopsis* has revealed the upregulation of 113 genes and downregulation of 62 genes by H_2O_2 suggesting a key role of H_2O_2 in governing plant drought responses regulating Ca^{2+} signaling, MAPK cascades and gene expression (Desikan R, Soheila AH, Hancock JT, et al. ,2001).

However, under water deficiency plants have developed several mechanisms to overcome this scarcity. Antioxidant system and osmotic regulation are chief defense systems that provide tolerance to crops against water stress conditions (Mahajan S, Tuteja N., 2005). Catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX), glutathione peroxidase (GPX) constitutes enzymatic antioxidants, and ascorbate, glutathione and phenolic compounds constitute non-enzymatic antioxidants. The magnitude of damage caused by ROS depends on the balance between the ROS generation and scavenging by the antioxidant system. SOD constitutes the first defense line in presence of ROS, which brings about dismutation of the O_2^- radicals to H_2O_2 (Carvalho MD ,2008). CAT and APX detoxify H_2O_2 and hamper its accretion. Several non-enzymatic antioxidants like flavonoids, tannins and lignin precursors take an active part in ROS detoxification (Kumar M, Tak Y, Potkule J, et al. ,2020), reducing oxidative stress. These antioxidants function cooperatively, engaging various redox reactions. Additionally, it has been noticed that phenolic compounds are crucial in detoxifying the hydrogen peroxide cascade in plant cells (Ali AA, Alqurainy F. ,2006). In rice (*Oryza sativa*), it was reported that total SOD activities and APX activities were enhanced with rises in water deficiency. Similarly, a rise in activities of SOD, CAT and APX was noticed in barley under drought stress (Harb A, Awad D, Samarah N. ,2015). In maize plants (*Zea mays*) (Noman A, Ali S, Naheed F, et al. ,2015) reported that drought stress enhances SOD and POD activities and treatment of as a further increases the enzyme activities.

13. Molecular mechanism for drought response in plants

Plants challenged with drought undergo many adaptive mechanisms at molecular levels to modulate the soil water content. under these conditions, up and down-regulation of many genes take place at the transcriptional level are induced in response to stress and the accumulation of stress proteins functions well in tolerance to drought. Signaling pathways during abiotic stress including drought shows the involvement of various dehydration-responsive element –binding genes (Agarwal PK, Agarwal P, Reddy MK, et al. ,2006. Plants exposed to drought stress experience negative effects like ROS-mediated cell injuries, enhanced cellular temperature and viscosity of cellular contents, altered interaction, aggregation, and denaturation of proteins (Farooq M, Basra SMA, Wahid A, et al. ,2008).

In order to tackle the toxic consequences of drought stress on crops, plant biotechnologists have developed new cultivars exhibiting high drought tolerance by using various molecular approaches, including transcriptomics, proteomics and metabolomics. Reports have revealed that in response to water stress conditions, plants modulate the expression of various drought-responsive genes whose regulation occurs *via* a complex transcriptome network (Singh D, Laxmi A. ,2015). A number of physiological, cellular and molecular processes are responsible for the enlargement of drought tolerance in plants, for instance, up-regulation or down-regulation of the expression of various genes accountable for the osmolyte accumulation, increased content of-enzymatic and enzymatic antioxidant system, decreased rate of transpiration, growth of shoot and tillering (Pareek A, Sopory SK, Bohnert HK, et al.,2010). Under water stress conditions, increased concentration of abscisic acid (ABA) plays a pivotal role in closing stomata. Also, it regulates the expression of various stress-responsive genes. However, the expression of drought receptive genes is also controlled by a system which is independent of ABA (Aguado A, Capote N, Romero F, et al., 2014). Numerous protein-coding key genes show drought-assisted expression and play a metabolic or regulatory role. For example, genes responsible for detoxification, biosynthesis of osmolytes, water channels, ion transporters, heat shock proteins, proteolysis of cellular substrates and proteins are related to late embryogenesis (Joshi R, Wani SH, Singh B, et al., 2016). Furthermore, the genes having regulatory roles mainly comprise transcription factors (i.e. AREB, NAC, AP2/ERF, MYC, MYB and bZIP), mitogen-activated protein kinases (MAPK); responsible for different cellular signalling pathways, protein kinases related to ribosomes, receptors and transcriptional regulated system and proteins responsible for synchronization of signal transduction (phosphatases) (Fàbregas N, Yoshida T, Fernie AR. ,2020). Various osmotic stress-responsive genes have been identified to play a vital role in the expression of enzymes responsible for the induction of the ABA biosynthetic pathway (Sah SK, Reddy KR, Li J. ,2016) and synthesis of different Osmo protectants like glycine betaine (GB), ectoine, mannitol, trehalose and proline, thereby maintaining the osmotic balance under stressful conditions.

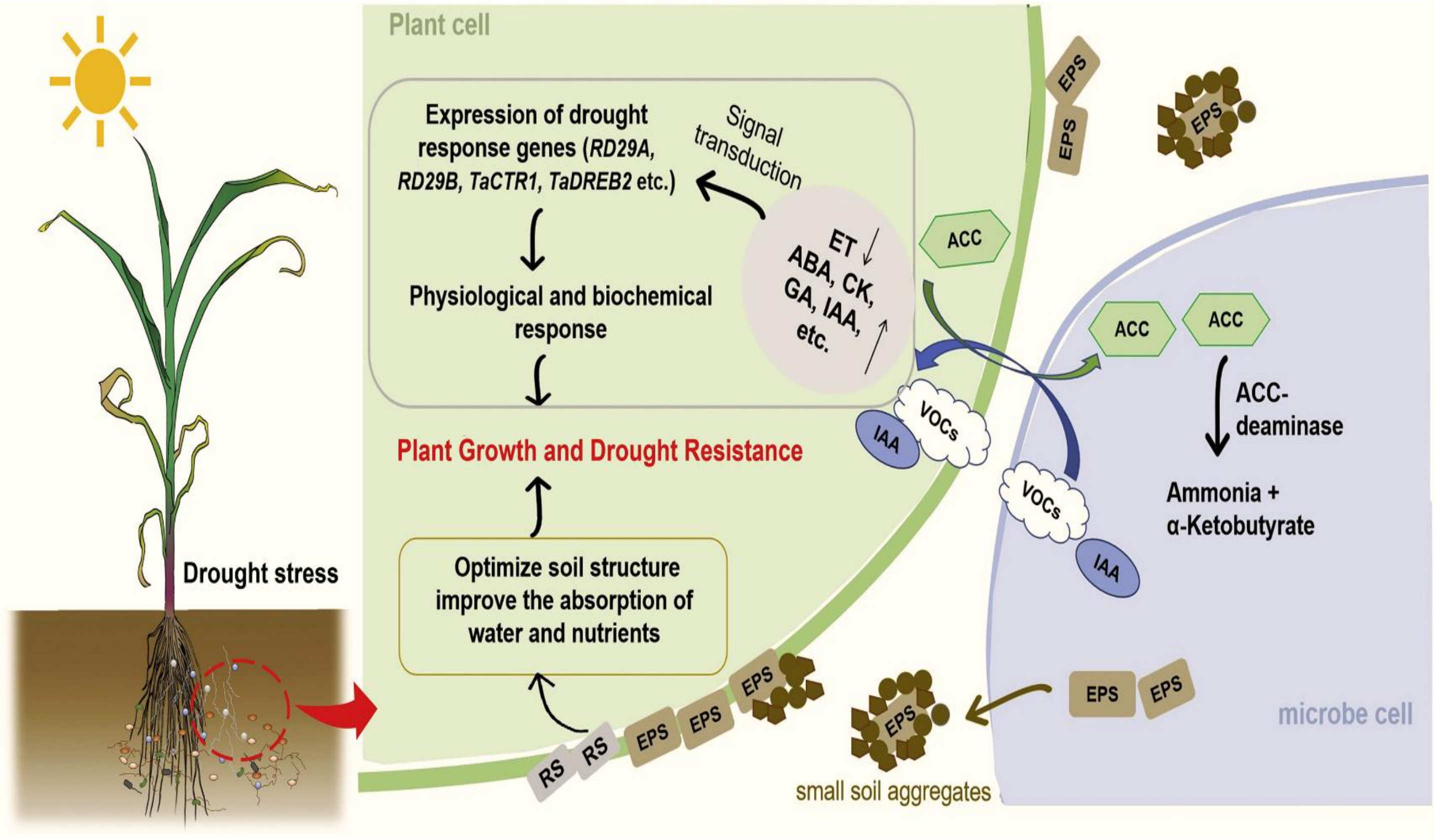

Figure 19: Mechanistic pathway for PGPR-mediated drought tolerance in plants. *Sources: Hui Zhang · Xiaopeng Sun · Mingqiu Dai.,2010*

The signaling pathways of various abiotic stresses, including drought stress, involve some common key steps. Foremost is the perception of stress stimulus *via* sensors or receptors which are localized in the plasma membrane or exist freely in the cytosol. The second is the transduction of the signalling *via* secondary messengers. Once the perception of stress stimulus occurs, it leads to the activation of secondary messengers like calcium ions, cyclic nucleotides (cAMP, cGMP), nitric oxide, sugars, ROS, etc. Secondary messengers thereafter activate the signalling pathway *via* modulating the expression or repression of various genes responsive to different stresses (Bhargava S, Sawant K. ,2013; Liu JH, Peng T, Dai W.,2016; Pérez-Clemente RM, Vives V, Zandalinas SI, et al.,2013). Protein kinases and phosphatases cause phosphorylation and de-phosphorylation respectively of the proteins involved in the signalling pathway (i.e. receptors, secondary messengers, transcription factors), and MAPKs and CDPKs are the two protein kinases that play a vital role in the regulation of the drought stress-mediated signalling pathway (Manna M, Thakur T, Chirom O, et al., 2021). Some transcription factors (TFs) directly communicate with the *cis*-acting elements incorporated in the promoter region of a group of downstream genes, hence synchronizing their expression (Danquah A, de Zelicourt A, Colcombet J, et al, 2014). Moreover, there are various TFs which are regulated *via* enhancers present in the upstream region of their gene (Danquah A, de Zelicourt A, Colcombet J, et al. ,2014). Ubiquitination and sumoylation, as modifications at the post transcriptional level, create a network of regulatory complex, which plays a pivotal role in the regulation of stress-responsive genes responsible for governing various plant physiological and metabolic processes (Mizoi J, Ohori T, Moriwaki T, et al. ,2013). Various TFs showing up-regulation in response to drought stress, such as AREB/ABF, AP2/ERF TFs, NAC TFs and Bzip, have been identified and characterized in several plants.

13.1. Effects of PGPRs on PGR levels in plants under drought stress

Under drought stress, PGPRs regulate the accumulation of PGRs in plant cells, and this is one of the main mechanisms by which root microbes promote plant drought resistance that inoculation of maize with the endophyte *Azospirillum lipoferum* enhanced the production of ABA, IAA, and GA in host plants and further improved plant drought resistance. IAA exists in both plants and microbes and plays important roles in the regulation of root development. Studies have shown that *Bacillus thuringiensis* and *Azospirillum* can synthesize IAA to promote the growth of lateral roots and root hairs in host plants, contributing to improved water absorption capacity and drought resistance. In addition, endophytes can promote root growth and reduce yield loss under drought conditions. For example, inoculation of wheat and maize plants with *Pantoea alhagi* or *Burkholderia phytofirmans* improved plant growth, root length, and drought resistance that arbuscular mycorrhizal fungi upregulated the expression of IAA biosynthesis genes and downregulated the expression of genes encoding outward IAA transporters in roots, thus improving IAA levels in roots, enhancing the growth of root hairs, and promoting plant drought resistance.

13.2. Effect of ACC deaminase-containing PGPRs on plant drought resistance

Ethylene, a plant hormone, is important for the normal growth and development of plants, and drought stress results in ethylene accumulation. Under stress, most plants secrete the ethylene synthesis precursor ACC as a root exudate. High levels of ethylene accumulation inhibit growth and development and may even lead to plant death ACC deaminase can degrade ACC into amines and Ket butyric acid, thereby reducing ethylene accumulation under drought stress, and this is one of the main mechanisms of PGPR-mediated plant drought resistance. Studies have shown that inoculation of tomato and pepper with *Achromobacter* ARV8, a PGPR that produces ACC deaminase, reduces ethylene levels and improves drought resistance of host plants. In addition, inoculation with ACC deaminase-producing PGPRs has positive effects on photosynthetic efficiency, stomatal conductance, water-use efficiency, transpiration rate, vapor pressure, chlorophyll content, and carbon content of maize plants under drought stress. ACC deaminase-producing PGPRs also enhance osmotic adjustment and antioxidant defenses of host plants under drought stress.

Effect of EPS-producing PGPRs on plant drought resistance

EPS is a polysaccharide macromolecule with high water-holding capacity produced by rhizobacteria. The EPS-producing bacteria *Pseudomonas putida* GAP-P45 can form a biofilm on the root surface, and plants inoculated with this strain show greater soil aggregation, more root-adhering soil, and high leaf RWC found that EPS-producing bacteria improved the photosynthetic rate, stomatal conductance, and other physiological characteristics of maize under drought stress. Studies showed that the integrated use of ACC deaminase-producing bacteria and EPS-producing bacteria had more beneficial effects on plant drought resistance than the use of either bacterium separately. Soil structure is very important for crop production. Drought stress can change the biochemical and physicochemical properties of soil, making it unsuitable for the growth of crops and bacteria. EPS-producing bacteria are conducive to the formation of small soil aggregates, which are important for the maintenance of soil structure and health. Inoculation with EPS-producing bacteria optimized soil structure, increased root adhering soil per unit root tissue, and further improved plant drought resistance. EPS is also conducive to the formation of rhizosheath structures on plant roots, which aid the absorption of nutrients and water. In addition, EPS-producing bacteria have been shown to participate in the regulation of osmotic adjustment and the antioxidant defense system. We may conclude that PGPR application in combination with EPS is a promising measure for combatting drought stress and thereby increasing global food security.

13.3. Drought stress responsive transcription factor family AREB/ABF

In response to drought-mediated osmotic stress, a key molecular complex known as AREB/ABFs (abscisic acid-responsive element-binding protein/ABRE binding factor) plays a significant role in the up-regulation of ABA responsive genes (Maruyama KY, Todaka DA, Mizoi JU, et al. 2012). A conserved sequence PyACGTGG/TC is present in the promoter region of ABA responsive genes, and the conserved *cis*-element functions in the expression of these genes in response to signalling switched on by ABA. Various ABRE or its coupling elements (CE) are involved in the regulation of ABA-dependent gene expression (Fujita Y, Yoshida T, Yamaguchi-Shinozaki K., 2016; Nakashima K, Yamaguchi-Shinozaki K. ,2016; Yao T, Zhang J, Xie M, et al. ,2020). Four SnRK2 phosphorylation sites present in the AREB/ABFs and containing a conserved domain have an essential role in regulating ABA-mediated gene expression (Fujita Y, Yoshida T, Yamaguchi-Shinozaki K. ,2013; Fujita Y, Fujita M, Shinozaki K, et al. ,2011). It has been found that vascular tissue and guard cells are the sources for the synthesis of ABA. Once ABA is synthesized, it is immediately transported to the target cells (Bauer H, Ache P, Lautner S, et al., 2013; Kuromori T, Sugimoto E, Shinozaki K. ,2014). Researches have revealed the existence of five NCED (9-*cis*-epoxy carotenoid dioxygenase) coding genes in *Arabidopsis*. Among these genes, *NCED3* has been shown to exhibit enhanced expression in response to dehydration. The

AG-box recognition sequence acts as a regulation site of the gene located up to 2248 bp upstream to its transcription start site (Behnam BA, Iuchi SA, Fujita MI, et al. ,2013). The ABA bound receptor complex PYL/PYR/RCARs then gets associated with PP2Cs and leads to the activation as well as the release of SnRK2 (Nakashima K, Yamaguchi-Shinozaki K. ,2013; Kuromori T, Sugimoto E, Shinozaki K. ,2014). Activated protein kinase SnRK2, in turn, activates the AREB/ABF TFs *via* phosphorylation, which eventually recognizes and binds to ABRE *cis*-element of ABA-responsive genes. In the absence or under low concentration of ABA, PP2Cs play a pivotal role in the down-regulation of ABA signaling *via* dephosphorylating the SnRK2 protein kinase. Among the nine members of AREB/ABF transcription factor family, AREB1/ABF2 functions in the regulation of drought-mediated ABA signaling, particularly at the vegetative stage (Fujita Y, Fujita M, Shinozaki K, et al. ,2011; Joo H, Baek W, Lim CW, et al., 2021). Increased transcriptome level of AREB1 has been reported to enhance drought tolerance in rice, soybean and *Arabidopsis* (Yao T, Zhang J, Xie M, et al. ,2020; Barbosa EGG, Leite JP, Marin SRR, et al. ,2013; Oh SJ, Song SI, Kim YS, Jang HJ, Kim SY, et al. ,2005).

13.4. Drought stress responsive transcription factor family AP2/ERF

AP2/ERF, referred to as APETALA2/Ethylene Response Element Binding Factors, is a large family of TFs comprising of numerous plant-specific TFs. Purification and characterization of these TFs has revealed the presence of conserved AP2/ERF DNA binding domain as well as recognition of the GC-box of ethylene-responsive genes (Rashid M, Guangyuan H, Guangxiao Y, et al. ,2012. AP2/ERFBP TFs are considered to play a significant role in the regulation of various plant physiological and biochemical processes like development of vegetative and reproductive stages, cellular proliferation, biotic or abiotic stress, and phytohormone-mediated responses. Based upon the number and similarity in the domains of AP2/ERF, this TFs family is further divided into four subfamilies, including AP2, ABI3/VP1 related TF RAV, ERF and DREB (dehydration responsive element binding protein) (Rashid M, Guangyuan H, Guangxiao Y, et al., 2012; Cao S, Wang Y, Li X, et al. ,2020; Ritonga FN, Ngatia JN, Wang Y, et al. ,2021). Eleven genes of DREB1/CBF and six genes of DREB2 have been reported in rice whose expression under cold and dehydration respectively was ABA independent (Nakashima K, Yamaguchi-Shinozaki K, Shinozaki K. ,2014). In *Arabidopsis*, the A/GCCGAC sequence has been found to be incorporated in the promoter region of drought-responsive genes, whose *cis*-element is recognized as DRE/CRT (Lucas S, Durmaz E, Akpınar BA, et al. ,2011). DRE/CRT is the specific binding site for DREB1/CBF TFs and governs the expression of various abiotic stress responsive genes, including drought stress (Lucas S, Durmaz E, Akpınar BA, et al. ,2011; Ritonga FN, Ngatia JN, Wang Y, et al. ,2021; Dong MA, Farré EM, Thomashow MF. 2011; Qin F, Shinozaki K, Yamaguchi-Shinozaki K.,2011). Overexpression of DREB1/CBF TFs leads to increased transcriptome level of various stress responsive genes, ultimately increasing drought tolerance in rice (*Oryza sativa*) (Datta K, Baisakh N, Ganguly M, et al. ,2012; Paul S, Gayen D, Datta SK, et al. ,2015), tomato (*Solanum lycopersicum*), potato (*solanum tuberosum*), chrysanthemum (*Chrysanthemum indicum*) (Iwaki T, Guo L, Ryals JA, et al. ,2013), tobacco (*Nicotiana*), peanut (*Arachis hypogaea*) (Bhatnagar-Mathur P, Rao JS, Vadez V, et al. ,2014), sugarcane (*Saccharum officinarum*) (Augustine SM, Narayan JA, Syamaladevi DP, et al.,2015), soybean (*Glycine max*) (De Paiva Rolla AA, Carvalho JD, Fuganti-Pagliarini R, et al. ,2014) and wheat (*triticum aestivum*) (Riaz MW, Lu J, Shah L, et al. ,2021).

13.5. Drought stress responsive transcription factor family NAC

NAC gene family is the largest plant-specific TF family, whose name is derived from the association of three proteins forming a specific NAC domain from *Petunia* and *Arabidopsis,* i.e. NAM protein (no apical meristem), ATAF1/2 protein and CUC2 protein (cup shaped cotyledon) (Feng K, Hou XL, Xing GM, et al. ,2020). Purification and characterization of NAC TFs uncovered the highly conserved N-terminal DNA binding domain and a variable C-terminal domain meant for transcriptional regulation. DNA binding NAC domain contains a nucleolus localization signal and interacts with other similar domains or different domains to form a homodimer or heterodimer, respectively (Puranik S, Sahu PP, Srivastava PS, Prasad M. ,2012). NAC TFs interact with a CACG sequence known as NAC recognition sequence (NACRs) present in the promoter region of drought responsive ERD1 (RESPONSE TO DEHYDRATION1) genes. It has been found that SNAC1 TFs play a pivotal role in enhanced drought tolerance in rice *via* ABA independent regulation of downstream genes *OsPP18* and *aPP2C*. Enhanced expression of various NAC genes has been reported in rice in response to early stages of drought and salt stress (Hong Y, Zhang H, Huang L, et al. ,2016). Drought stress increased the transcriptome level of about 40 NAC genes of rice and 38 NAC genes of soybean (Le DT, Nishiyama RIE, Watanabe Y, et al. ,2011).

13.6. Drought stress responsive transcription factor family bZIP

Analysis of another TF family, bZIP (basic leucine zipper) revealed the presence of a conserved bZIP domain containing an N-terminal basic nuclear localization signal, a DNA binding region and a C-terminal leucine rich motif meant for dimerization. In addition to the regulation of plant growth and development, bZIP TFs play an essential role in the regulation of drought responsive genes (Llorca CM, Pots chin M, Zentgraf U., 2014). Isolation and characterization of various members of bZIP TFs have been reported in various eukaryotes. for example, 55 in grapevine (*Vitis vinifera*) (Liu J, Chen N, Chen F, et al. ,2014), 89 in barley (*Hordeum vulgare*) and rice (*Oryza sativa*) (Nijhawan A, Jain M, Tyagi AK, et al. ,2008; Pourabed E, Golmohamadi FG, Monfared PS, et al. ,2015), 96 in *Brachy podium distachyon* (Liu X, Chu Z. ,2015), 92 in sorghum (*Sorghum bicolor*) 131 in soybean (*Glycine max*) (Liao Y, Zou HF, Wei W, et al. ,2008; Llorca CM, Pots chin M, Zentgraf U. ,2014; Jia N, Patel DJ. ,2021) and 125 in maize (*Zea mays*). It has been reported that bZIP TF-mediated regulation of abiotic stress related genes occurs in ABA-dependent manner after recognizing the ABRE specific promoter region (Llorca CM, Pots chin M, Zentgraf U., 2014).

14. Role of CRISPR/Cas9 in stress tolerance

Clustered regularly interspaced short palindromic repeats (CRISPRs)/CRISPR-associated 9 (Cas9), a newly discovered targeted genome editing tool, is a prokaryotic molecular immunity system against viral pathogens (Borrelli VM, Brambilla V, Rogowsky P, et al. ,2018; Hanley-Bowdoin L, Bejarano ER, Robertson D, et al. ,2013; Hu JH, Miller SM, Geurts MH, et al. ,2018; Ji X, Zhang H, Zhang Y, et al.,2015; Jia N, Patel DJ.,2021). CRISPR and its associated complexes can be easily programmed to target any sequence of choice. This can be utilized and implemented for various crop improvement traits like drought stress resistance and other biotic stress tolerance and management within a short span of time (Cong Á, Ran FA, Cox D, et al. ,2013; Jaganathan D, Ramasamy K, Sellamuthu G, et al.,2018; Karkute SG, Singh AK, Gupta OP, et al. ,2017; Osakabe Y, Watanabe T, Sugano SS, et al.,2016; Wang L, Chen L, Li R, et al.,2017). Abiotic stress resistance has been achieved in plants by targeting and cleaving genes of interest using the CRISPR/Cas9 system. Also, the host genome can be modified in order to introduce resistance in plants for abiotic and biotic stresses. Thus, CRISPR/Cas9 is a powerful tool to provide resistance to multiple abiotic stresses in plants (Biswas D, Saha SC, Dey A. ,2021; Zhang D, Zhang Z, Unver T, et al. ,2020). It can be utilized and implemented for the amelioration of agriculturally important crop plants (Osakabe Y, Watanabe T, Sugano SS, et al. ,2016; Wang L, Chen L, Li R, et al. ,2017; Ma X, Zhu Q, Chen Y, et al. ,2016; Shan Q, Wang Y, Li J, et al.,2013; Shi J, Gao H, Wang H, et al.,2017).

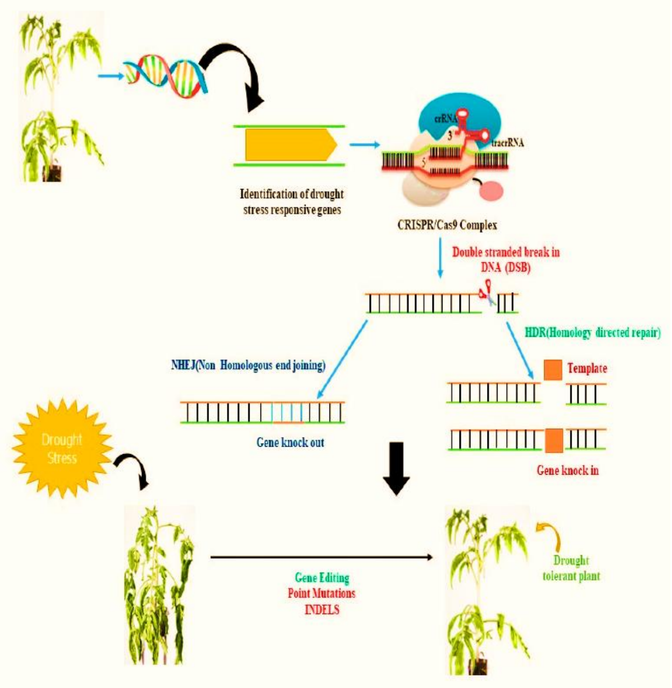

Figure 20: CRISPR/Cas9-mediated genetic manipulation can be used to enhance plant productivity under stress conditions. The Cas9 protein can be guided by a single guide RNA (sgRNA) to a specific genomic region of interest. The CRISPR/Cas9 system then identifies a G-rich protospacer adjacent motif (PAM) region at the proximal end of the target DNA and cleaves it, creating a blunt-ended double-stranded break (DSB). These DSBs can be repaired by the plant's endogenous repair system via non-homologous end joining (NHEJ) or homology-directed repair. CRISPR/Cas9 can induce mutations through insertions or deletions (INDELs), gene deletions, or multiplex gene knockout, providing a powerful tool for genetic manipulation in plants. *Sources: Rai, Gyanendra Kumar, Danish Mushtaq Khanday, Pradeep Kumar, Isha Magotra, Sadiya M. Choudhary, Rafia Kosser, Raviraj Kalunke, Maria Giordano, Giandomenico Corrado, Youssef Rouphael, and et al. 2023*.

The trends of application of the CRISPR/Cas9 technology for amelioration of crop plants in tropical climates within the last 5 years are phenomenal, and it betokens a rapid immensely colossal-scale application of it in addressing emerging challenges in engenderment of crops in tropical climates (Kamburova VS, Nikitina EV, Shermatov SE, Buriev ZT, et al. ,2017). This advanced CRISPR/Cas9 tool helped in precise and highly efficient gene editing even at a single base level. This in turn has brought about a revolution in crop improvement programs especially in abiotic stress tolerance (Lu Y, Zhu JK. ,2017; Zong Y, Wang Y, Li C, et al. ,2017). Further, such techniques have widened up the opportunities to discover new traits associated with different characters.

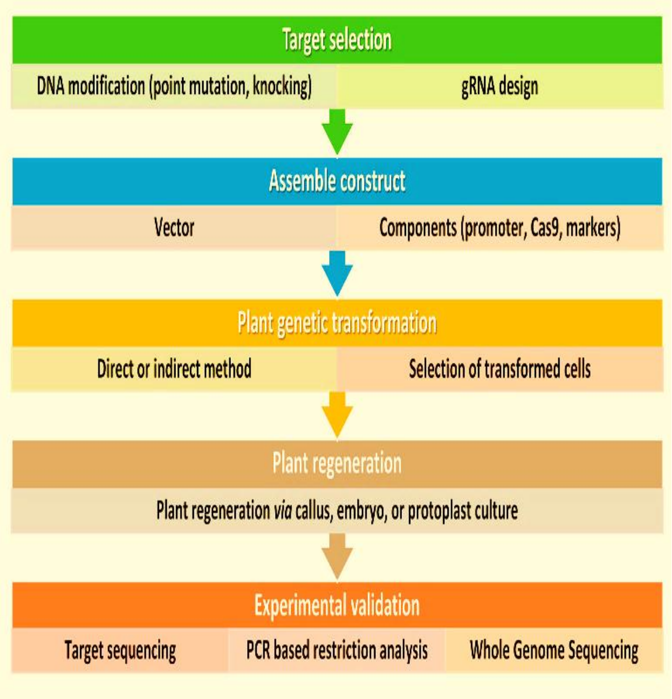

Figure 21: Simplified workflow for CRISPR/Cas9 genome editing in plants. This workflow outlines the key steps involved in using this technology for plant biotechnology. It is important to consider all factors before starting and to design and implement screening procedures also beyond the DNA analysis of the transformed plants. Step 1: Selection of target sequence. The first step in CRISPR/Cas9 genome editing is to select the target sequence. The aim is typically to generate point mutations or small insertions/deletions that result in gene knockout or loss of function. An accurate guide RNA (gRNA) design is carried out to maximize efficiency and minimize the risk of off-target mutations. Step 2: Vector design and assembly. Before constructing a vector, several factors should be considered, including the techniques used for plant genetic transformation and the aim of the study. Several vectors are available and can be tailored for a specific application. For instance, Cas9 and gRNA can be generated from the same vector or separate vectors, and, the Cas9 and gRNA expression can be driven by different promoters according to the plant species and aims. The most used proteins are based on the type IIA Cas9 from *Streptococcus pyogenes*. The native Cas9 coding sequence has been codon optimized for monocots or dicots. Step 3: DNA delivery. Delivering DNA into plant cells is performed using conventional methods in plant biotechnology, such as Agrobacterium-mediated transformation, biolistic microparticle bombardment, or protoplast transformation, followed by plant regeneration when necessary (Step 4). Step 5: Screening. The screening of plant DNA follows standard procedures and may include whole genome sequencing to check for off-target mutations, especially if back-crossing is not a viable option. *Sources: Rai, Gyanendra Kumar, Danish Mushtaq Khanday, Pradeep Kumar, Isha Magotra, Sadiya M. Choudhary, Rafia Kosser, Raviraj Kalunke, Maria Giordano, Giandomenico Corrado, Youssef Rouphael, and et al. 2023.*

Which could be used in targeted improvements in crops against different stresses (Dalla Costa L, Malnoy M, Gribaudo I. ,2017; Klap C, Yeshayahou E, Bolger AM, et al. ,2018). Various genes, transcriptional factors and networks have been identified in the last decade that play a pivotal role in biotic and abiotic stress tolerance (Cao D, Li Y, Liu B, et al. ,2018; Nasr Esfahani M, Inoue K, Chu HD, et al. ,2017). However, there has been a decrease in the genetic diversity of important and most cultivated crop plants because of the continuous and large use of a few 'best' cultivars, which has led to an increase in susceptibility towards various stresses (Flint-Garcia SA. ,2013).

Therefore, there is a need to develop more stress resilient crops with high yield potential under abiotic stress especially drought stress and salinity stress, which could be done by creating variation in gene pools where CRISPR/Cas9 based genome editing technology can play its role. So far, many crop traits have been modified by knocking out species' gene with the help of CRISPR/Cas9 resulting in improvements in abiotic and biotic stress management and yield (Oerke EC. ,2006; Ricroch A, Clairand P, Harwood W. ,2017). Mitogen-activated protein kinases (MAPKs) is an important group of signaling molecules in plants that play a vital role during drought stress, which helps in the regulation of transcription of many genes associated with drought stress. The *mitogen-activated protein kinases 3* (*slmapk3*) gene was knocked out using CRISPR/Cas9, assisting in understanding the mechanism associated with tolerance by tomato (*Solanum lycopersicum*) regulated by *SlMAPK3*. (Wang L, Chen L, Li R, et al. ,2017; Abdelrahman M, Al-Sadi AM, Pour-Aboughadareh A, et al. ,2018; Liu X, Wu S, Xu J, et al. ,2017).

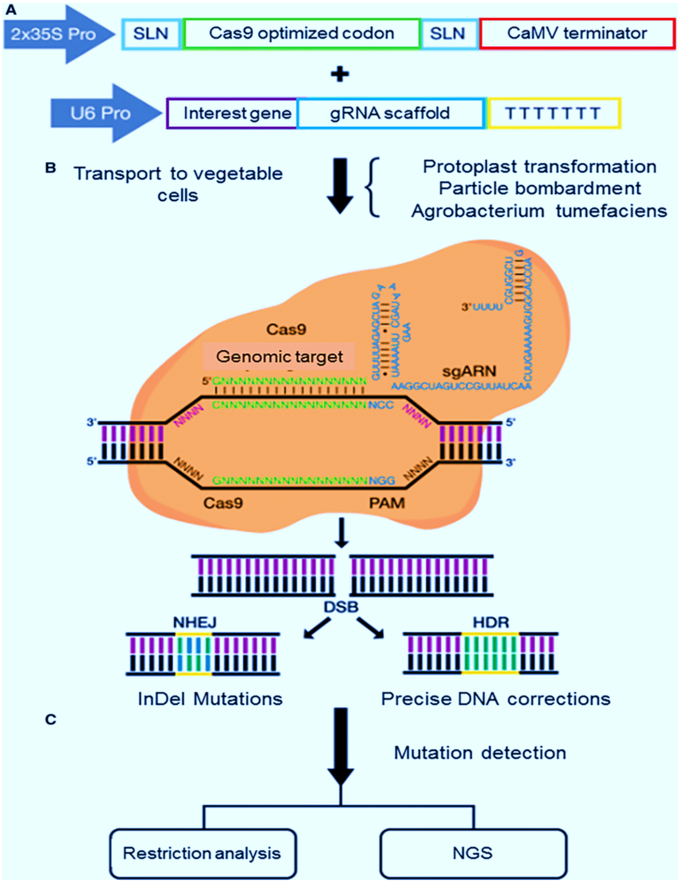

Figure 22: Mechanism of genome editing through CRISPR/Cas9 in plants. (A) The cassette expressing Cas9 is driven by the 35S promoter and the guiding RNA is usually driven by the U6 promoter. (B) The CRISPR/Cas9 system is introduced into plant cells by protoplast transformation, particle bombardment or Agrobacterium transformation. Once in the cells, the sgRNA directs the Cas9 to the target site of the genome. Cas9 recognizes the PAM sequence and performs the double DNA chain break. Through the NHEJ repair system, deletions or insertions of bases (InDel) are generated in the target site, on the other hand, by means of the HDR repair system, precise corrections can be made in the DNA or directed sequences can be inserted. (C) Finally, gene editing could be detected by restriction enzymes or by sequencing. Source Own elaboration based on Tang and Tang (2017)

Using CRISPR/Cas9 promotor region *auxin regulated gene involved in organ size ARGOS8* in *Zea mays* was replaced by *GOS2* promoter, which led to constitutive expression of *ARGOS8.* The new variant had increased yield under drought conditions compared to the wild type (Shi J, Gao H, Wang H, et al., 2017). Thus, genome editing tools like CRISPR/Cas9 can be utilized to improve the important crop traits and yield under drought conditions. Genes, regulatory sequences, transcriptional factors etc. are very important and suitable targets for genome editing tools like CRISPR/Cas9, helping in producing abiotic stress resilient and high yielding crops (Zhao Y, Zhang C, Liu W, et al. ,2016; Xie K, Yang Y . ,1983). Under drought conditions, a complex network of genes/transcriptional factors might be regulating simultaneously, which could affect the selection of novel targets. Still, there is a need for better progress in CRISPR/Cas9 application for the development of highly efficient and stress-tolerant crops.

15. Significance of stress on the productivity of horticultural crops

The significance of investigating the interplay between horticultural crops and their environment is increasingly acknowledged, particularly considering the prevailing climate change scenario. These crops have significant nutritional value and have the potential to serve as a primary source of food for developed and developing countries alike. Global horticulture crop production is largely controlled by abiotic stress factors such as temperature extremes, salt, drought, metal pollution, lack of oxygen, UV radiation, inadequate nutrients, and pesticides, which have a negative impact on plant development and production. Abiotic stress-induced changes in a plant's physiological, anatomical, biochemical, morphological, and molecular composition have been linked to these negative effects. There are various factors that affect how plants respond to abiotic stress, like the nature and intensity of the stress, environmental conditions, and growth phase of the plant, both living and non-living, under which it is cultivated. The interplay of these factors can impact the plant's capacity to adapt and manage stress, which can ultimately influence its development and yield. Some of the ways in which plants may respond to abiotic stress include reducing their growth rate, losing photosynthetic pigments or membrane integrity, or even shutting down their photosynthetic machinery. Therefore, it is imperative for the advancement of diverse horticultural methods to diligently investigate the intricate interplay between environmental stressors and the underlying morphological and physiological mechanisms that govern plant responses. Such scientific research endeavors are crucial to enhance our understanding of these complex relationships and developing effective strategies to mitigate the adverse effects of environmental pressures on horticultural crop productivity.

16. Conclusion

Abiotic stresses still pose a great threat to sustainable agriculture nowadays and in the near future, and with the advent of erratic weather conditions and extreme temperatures as a consequence of climate change, these abiotic stresses will become more lethal for crop growth and productivity. Adequate research has been conducted to unravel the physiological, biochemical, and molecular mechanisms underlying abiotic stress tolerance in crop plants. More focused research needs to be carried out to better comprehend plant responses to abiotic stresses. This is conceivable with the dawn of emerging scientific inventions in the field of plant biology, such as genome editing and the advancement in artificial intelligence, which aid the food requirements of the ever-increasing human population. Despite the toxicity conferred by heavy metals onto various parameters of plants in general, the introduction of metal-tolerant PGPR in polluted soils greatly diminishes the ruinous effects of metals, and enhances the growth and yield of wheat. The metal-tolerant bacteria, through biosorptive ability and capability to secrete EPS, can remove significant amounts of metal ions from the contaminated environment. The release of EPS by metal-tolerant strains also protects plants from other challenges, like pathogen attacks and desiccation. This consequently allows them to survive, and perform normal physiological and biochemical activities in stressed environments. Moreover, the secretion of MTs and melanin by viable cells under the influence of heavy metals could be considered another vital strategy evolved within bacterial strains to mitigate metal toxicity. Overall, the microbial management strategy to detoxify/remediate the contaminated environment through biosorption, secretion of MTs, melanin and EPS secretion makes metal-tolerant bacterial strains a promising and most suitable choice for heavy metal clean up from contaminated soils. The novel and fascinating traits of metal-tolerant bacteria could serve as an inexpensive yet environmentally viable approach in the metal clean-up program *vis-a-vis*, the growth and yield enhancement of wheat growing in metal-enriched soils.

17. Author Contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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20.Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

21. Publisher’s Note

22. Author Disclaimer

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during writing or editing of this manuscript.

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