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Sensing and detection of stressful conditions by plants

Ch. Aruna Kumari and Sameena Begum

Abstract

Plants must adapt to an environment that is constantly changing since they are exposed to it. Complex signaling pathways that all begin with stimulus perception tightly control their response. Here, we provide a summary of recent advancements in how various abiotic stresses are perceived. Much less is known about how stress signaling controls plant growth and vice versa than is known about how plants protect themselves from cellular damage brought on by stress. To build stress-resistant and high-yielding crops, it will be essential to comprehend this regulatory network in order to rebalance the relationship between growth and stress resistance.

Keywords: Plant, stress, response, signaling, environment

Introduction

When the environment is unfavorable for growth, plants are said to be under stress. In addition to being a fundamental scientific subject, how unfavorable conditions affect plant growth is crucial for agriculture and food security. Key agricultural crops were predicted to experience an overall yield loss of about 70% due to adverse conditions, meaning that the average production was only about 30% of the genetic yield potential (Shinozaki *et al.*, 2015; Zurbriggen *et al.*, 2010) [47, 67]. Abiotic stress can significantly lower plant growth, productivity, and even survival when it results from environmental deficiencies or excesses in water, salt, light, temperature, and nutrients. Abiotic stress inhibits plant growth since, by definition, stressed plants do not have the best environmental conditions for cellular expansion and division. For instance, water is required for cell turgor, which is the pressure that a contained liquid exerts on the cell wall and causes it to expand; similarly, cold stress slows plant development because enzyme and other protein activity is reduced in colder temperatures. However, slower plant growth under stress is not just a result of the unfavorable surroundings. Additionally, stressed plants deliberately restrict their growth in an effort to adapt to the stressful environment. Abiotic stressors are experienced by primary sensory processes that convert environmental factors like temperature, water availability, and ion concentration into biological signals. It is necessary for a real primary abiotic stress sensor to detect stress by detecting unfavorable environmental conditions and to activate a cellular signaling pathway to coordinate adaptation responses. We go over the developments and suggested sensing mechanisms for the key abiotic stress conditions that have been reported recently: drought, salinity, flooding, nutrient and heavy metal stress. Genetic engineering has been used by scientists in an attempt to reduce the detrimental effects of stress on agricultural output, but with mixed results. Despite the identification of numerous genes involved in plant abiotic stress signaling and response, developing crops with improved stress resistance is still difficult (Tardieu, 2012; Zhu, 2016) [52, 66]. Only one transgenic maize cultivar with a stress resistance trait (drought resistance) has been commercialized thus far among the major crops (Castiglioni *et al.*, 2008) [1]. Abiotic stressors alter the physiological and molecular makeup of plants in numerous ways. While the particular modules for sensing. Here, we discuss the key elements of abiotic stress signalling and how they relate to the pathways that control growth.

Drought

Lowered photosynthetic rates, stomatal closure, decreased turgor pressure, altered leaf gas composition, and reduced turgor pressure are only a few of the complex array of plant responses brought on by drought that affect plant development and agricultural productivity (Farooq *et al.*, 2012) [12]. Since a lack of water causes osmotic stress in plants, the first sign of water availability is probably a drop in osmotic potential. As a result, osmosensors are another name for drought sensors. Although numerous fundamental sensing mechanisms have been

postulated, it is difficult to uncover true sensors of water deficit due to the intricacy of plant responses to water-limiting conditions. In an experiment to investigate the inflow of Ca^{2+} in response to sorbitol, *Arabidopsis* seedlings expressing aequorin served as the first putative osmosensor. As a result, the *reduced hyperosmolarity-induced* $[\text{Ca}^{2+}]_i$ *increase1* was isolated (Yuan *et al.*, 2014) [62]. When exposed to sorbitol, this mutant demonstrated a reduction in Ca^{2+} buildup, but not in response to H_2O_2 or ABA. *Osc1* seedlings raised under osmotic stress showed enhanced sensitivity to osmotic stress as evidenced by a decrease in main root length and leaf area. A hyper osmolality-gated calcium channel called OSCA1 is present at the plasma membrane (Yuan *et al.*, 2014) [62]. Within seconds of the perception of the stress situation, high extracellular osmotic potential or plasma membrane tension brought on by a water deficit are likely to cause the pore to open and permit Ca^{2+} inflow (Liu *et al.*, 2018) [31]. Given the modest phenotypic variations in *osca1* mutants under hyperosmotic growth circumstances, it seems likely that plants have several redundant osmosensors. Phylogenetic study revealed that *Arabidopsis* has 15 homologs of OSCA1, indicating that a redundant family of calcium channels may be involved in the sense of hyperosmotic situations (Liu *et al.*, 2018) [31]. In reaction to mannitol, a related study determined that CALCIUM PERMEABLE STRESS-GATED CATION CHANNEL1 (*AtCSC1A/ AtOSCA1.2*) is a hyperosmotic stress-induced Ca^{2+} channel (Hou *et al.*, 2014). OSCA1 and CSC1A share a lot of sequence similarities. The drought-responsive protein Early Responsive to Dehydration4 also possesses a transmembrane domain that is homologous to the Domain of Unknown Function221 (DUF221) domain (ERD4; Ganie *et al.*, 2017) [16]. The precise role of CSC1A/OSCA1.2 in plants, however, as well as its subcellular localization, are yet unknown. Other sensory systems that resemble the two-component phosphorelay system (TCS) found in bacteria and yeast has been studied in the quest for osmosensors (Singh *et al.*, 2015) [48]. A kinase with an extracellular stress sensor is present in the TCS, which causes the His to be auto phosphorylated. The kinase then phosphorylates the matching Response Regulator protein, starting the signaling cascade. There have been identified typical bacterial TCSs for detecting changes in osmotic pressure (Yuan *et al.*, 2017) [63]. TCSs have also been reported in *Arabidopsis* and rice, however neither plant has shown any direct phosphorylation activity in response to osmotic or drought stress. It is less likely that AHK1 is an osmosensor even though ARABIDOPSIS HIS KINASE1 (AHK1) does appear to play a role in transcriptional regulation in response to drought because no reduction in ABA levels or defects in stomatal closure, two crucial drought responses, have been seen in the *ahk1* mutant (Sussmilch *et al.*, 2017) [51]. The reduction of turgor pressure, a sign of osmotic stress and drought in cells, can lead to plasmolysis and the separation of the plasma membrane from the cell wall under extreme, protracted drought circumstances. Several receptor-like kinases (RLKs) that keep an eye on the health of the cell wall are present in the plasma membrane. As a result, higher phosphorylation of downstream target proteins results from the separation of the plasma membrane from the cell wall (Feng *et al.*, 2016) [14]. Over 600 RLKs are encoded by the *Arabidopsis* genome, 17 of which are members of the *Catharanthus roseus* RLK family. In this family, FERONIA (FER) activity is induced by salt stress, which also induces osmotic stress and, ultimately,

plasmolysis. According to Feng *et al.* (2018) [13], CrRLKs are classified as cell wall integrity sensors rather than particular osmo- or sodium sensors. It is, however, likely that this is the outcome of disrupted pectin filament organization, monitored by FER, rather than direct sensing of turgor or plasmolysis.

Salt Stress

One of the main abiotic risks to agriculture is salinization of the soil. Similar to a drought, it initially reduces water intake, results in osmotic stress, and subsequently ion buildup results in ionic stress (Munns and Tester, 2008) [36]. As a result, reduced turgor pressure, reduced photosynthesis, and developmental changes (Julkowska and Testerink, 2015) [27]. Plants may sense both the osmotic and ionic component of salt stress, with greater spikes for salt stress than for osmotic stress at an identical degree of osmolarity, as first discovered through quantification of intracellular Ca^{2+} spikes (Donaldson *et al.*, 2004; Tracy *et al.*, 2008) [10, 54]. While processes similar to those described above for water deficiency might be used to sense the osmotic changes happening during salt stress, a different salt-sensing mechanism would be needed to sense the ionic component. The exclusion of Na^+ by the SALT OVERLY SENSITIVE (SOS) pathway depends mostly on Ca^{2+} signalling. The SOS_3 and SCaBP8 Ca^{2+} sensors, the SOS_2 and SOS_2 -LIKE PROTEIN KINASE5 (PKB_5) protein kinases, and the SOS_1 Na^+/H^+ antiporter make up the pathway's key components (Quan *et al.*, 2007; Yang *et al.*, 2019) [39, 60]. Within 10 seconds of sodium administration, Ca^{2+} spikes are seen and activate SOS_3 and SCaBP8 , which in turn activate SOS_2 (Quan *et al.*, 2007) [39]. Additionally, Ca^{2+} separates SOS_2 from 14-3-3 proteins, which are SOS_2 inhibitors (Zhou *et al.*, 2014) [65]. The plasma membrane-localized SOS_1 is then phosphorylated by SOS_2 , preventing Na^+ from entering the cytoplasm. It is assumed that salt stress-specific Ca^{2+} increases are what trigger this activation (Halfter *et al.*, 2000) [21]. Within 20 seconds of applying salt, SOS_1 exchanger activity is seen (Qiu *et al.*, 2002; Martinez-Atienza *et al.*, 2007) [38, 34]. Most recently, the salt stress-sensing mechanism was deciphered using Ca^{2+} spikes brought on by ionic stress (Jiang *et al.*, 2019) [26]. This allowed for the discovery of the monocation-induced $[\text{Ca}^{2+}]_i$ *increase1* (*moca1*) mutant. While spikes started by reactive oxygen species (ROS), cold stress, osmotic stress, or multivalent cations were unaffected, this mutant lacks the Ca^{2+} spike started by monovalent cations (Na^+ , as well as Li^+ , and K^+). Additionally, the SOS pathway's downstream signalling was compromised in the *moca1* mutant. The function of MOCA1-dependent Ca^{2+} signaling in response to these cations is unclear given that *moca1*'s tolerance to KCl or LiCl was unaffected by these cations. Furthermore, it is still unclear how this monovalent cation sensor starts responding in a way that is unique to Na^+ . A glucuronosyl transferase called MOCA1 converts inositol phosphorylceramide into glycosylinositol phosphorylceramide by adding a negatively charged GlcA. (GIPC; Rennie *et al.*, 2014) [40]. Increased IPC:GIPC ratio is brought on by MOCA1 mutations in the lipid microdomains of the plasma membrane (Rennie *et al.*, 2014; Jiang *et al.*, 2019) [40, 26]. In accordance with the robust Na^+ -binding abilities of GIPCs previously mentioned, *moca1* membranes have fewer binding sites for monovalent cations than the wild type because inositol phosphorylceramide does not contain the negatively charged head (Markham *et al.*, 2006) [33]. The function of MOCA1-dependent Ca^{2+} signalling

in response to these cations is unclear given that mocal's tolerance to KCl or LiCl was unaffected by these cations. Furthermore, it is still unclear how this monovalent cation sensor starts responding in a way that is unique to Na⁺. GIPCs are also present in fungi and protozoa, in addition to plants, however it is unknown if these lipids serve a universal purpose in cation sensing. As long as the related Ca²⁺ channel is undiscovered, the precise mechanism of the GIPC-mediated Ca²⁺ inflow is unclear and will remain elusive (Steinhorst and Kudla, 2019) [50]. In addition to sensing monovalent cations in general, plants may also detect the cation Na⁺. This is shown when roots develop in a different direction during halotropism, a procedure used to prevent exposure to excessive sodium concentrations (Galvan-Ampudia *et al.*, 2013) [15]. Other ions do not exhibit halotropism, which has been demonstrated to be mechanistically distinct from hydrotropism (Dietrich *et al.*, 2017; Deolu-Ajayi *et al.*, 2019) [9, 8]. Since the *sos1* mutant, which has a greater intracellular Na⁺ concentration (Shi *et al.*, 2002) [46], has an improved halotropic response, the Na⁺-specific sensor that causes this response has not yet been identified, but it is expected to sense the intracellular Na⁺ concentration (Galvan Ampudia *et al.*, 2013) [15].

Flooding

Flooding is another extreme situation for plants, even though all of the aforementioned stress scenarios have water depletion in common. Flooding has different impacts depending on how murky the water is, but in general it inhibits gas exchange and lessens photosynthesis. These restrictions gradually produce oxygen deprivation (hypoxia), which inhibits respiration and consequently results in an unbalanced energy supply. Since ethylene is a gaseous hormone and is not soluble in water, limiting gas exchange initially causes rapid buildup of the hormone in cell membranes. The transcription factors ETHYLENE-INSENSITIVE3 (EIN3) and ETHYLENE-INSENSITIVE3-LIKE1 are stabilized when it binds to the ethylene receptors in this location (EIL1). These control the gene expression responsible for a range of adaptive responses, such as the growth of adventitious roots, leaf hyponasty, and long shoots (reviewed by Sasidharan and Voeselek, 2015) [44]. The lack of oxidation at the N terminus of group VII ethylene response factor proteins signals hypoxia (ERFs; Gibbs *et al.*, 2011; Licausi *et al.*, 2011) [19, 30]. This system is comparable to oxygen sensing mediated by hypoxia-induced factor (HIF-1a) in metazoans (reviewed by Kaelin and Ratcliffe, 2008) [28]. Rapid ROS and bursts of nitric oxide (NO) are caused by hypoxia (reviewed by Sasidharan *et al.*, 2018) [43]. An N-terminal MCGAAIL sequence, which is highly conserved in other angiosperms, is present in all Arabidopsis ERFVIIIs. The destabilizing Cys at the N terminus is made visible when the Met from this conserved sequence is removed via MET AMINO-PEPTIDASE (MetAP) (Graciet *et al.*, 2010) [20]. Plant Cys Oxidases (PCOs) oxidise Cys during normoxia to produce Cys sulphuric acid, which is then targeted for degradation by Proteolysis 1/6 (PRT1/6; Garzón *et al.*, 2007) [17] by ARG-TRNA Protein Transferase 1/2 (ATE1/2; White *et al.*, 2017) [57]. ERFVIIIs stabilize in the absence of NO/O₂, following which they go into the nucleus and control hypoxia-responsive components (Gasch *et al.*, 2016) [18]. Within 30 minutes, these transcriptional alterations can be measured (Van Dongen *et al.*, 2009) [55]. O₂ acts as PCO1/2's direct

ligand during this activity, making these oxidases the plant's O₂ sensors (Weits *et al.*, 2014; White *et al.*, 2017) [56, 57]. It has also been shown that NO mediates the proteolysis of ERFVIIIs, but this action appears to be unrelated to PCO-mediated oxidation (Gibbs *et al.*, 2011) [19]. The ethylene signaling system and hypoxia sensing have recently been shown to interact (Hartman *et al.*, 2019) [22]. Initial fast ethylene signaling during submersion boosts PHYTOGLOBIN1, a NO-scavenging protein. As a result, ERFVII proteolysis is decreased, and the plant's survival and response to hypoxia are primed. Surprisingly, PIN2 is localised asymmetrically in roots, which causes them to grow agravitropically in the presence of hypoxia. This, it is hypothesized, enables roots to escape low-oxygen soil regions. However, roots exhibit a greater bending phenotype in an ERFVII quintuple knockout mutant (Eysholdt-Derzso and Sauter, 2017) [11]. It is postulated that root bending is not necessary for survival in wild-type plants since genes activated by ERFVIIIs are crucial for hypoxia tolerance. In the absence of all known sensors, this agravitropic expansion raises the possibility of the presence of an additional oxygen perception mechanism.

Nutrient Stress

Environmental factors such as abiotic stress and soil nutrient deficiency inhibit plant growth, productivity, and quality. Low phosphorus (P) availability is one of the most prevalent soil-related abiotic stresses in natural and agricultural ecosystems, limiting crop output across more than 70% of the world's arable land. The major tactic to sustain crop yields is the use of significant amounts of fertilizers, which helps to offset the low availability of inorganic P in the soil. The chemical underpinnings of the low-P stress response have been thoroughly investigated, but the processes governing epigenetic regulation are still unknown. In two soybean genotypes with various P efficiencies, Chu *et al.* (2020) [6] examined changes in DNA methylation, gene expression, and siRNA abundance in response to low-P stress. Both genotypes had greater DNA methylation levels during low-P stress, and it was discovered that transcriptional changes in specific genes were connected to methylation modifications. For potatoes, a lack of P is another constraining element. When P accumulates to high amounts (500 M), it can become hazardous. Plant morphology, mineral allocation, and metabolites were studied in the study by Chea and colleagues (2021) [3] under P deficiency and toxicity; the study also assessed the capacity of rhizobacteria to increase plant biomass and P intake. Under P deprivation, changed mineral concentration and allocation were seen coupled with a decrease in plant height and biomass. The buildup of proline was proof that P toxicity and insufficiency had caused stress. In their study of nutritional stress, Hornyák and colleagues (2020) [24] examined a number of embryological (such as matured ovules, embryo sacs, and pollen viability) and yield characteristics. The embryo sacs in flowers that were developed in vitro with drastically reduced nutrition content dramatically degenerated. In planta, it was discovered that lowering floral competition was the most effective way to boost output by raising the frequency of formed embryo sacs and the typical number of mature seeds. Increased production of SA and jasmonic acid (JA), which support more effective pollinator attraction, may cause these effects. Crop performance is impacted by high bicarbonate concentrations

in calcareous soils with high pH. (e.g., Fe deficiency). Tolerance depends on having the ability to mobilize weakly soluble Fe. A comparative transcriptome analysis of two *Arabidopsis thaliana* genotypes (carbonate-tolerant and -sensitive) conducted in the study of Pérez-Martín *et al.* (2021)^[37] showed that bicarbonate rapidly triggers Fe deficiency-related genes in the susceptible genotype. The tolerant line, on the other hand, had differential gene expression for starch breakdown, sulphur deprivation, and the jasmonate and salicylate pathways, indicating that carbonate-tolerant plants do not detect Fe depletion quickly. A macronutrient that is critical for plant growth, development, and stress response is potassium (K⁺). Yang and colleagues (2021)^[61] examined the root transcriptome following low-K⁺ therapy to better understand how cotton reacts to K⁺ deprivation (0.03 mM in hydroponic cultivation). The findings revealed several genes that need to be further defined and identified as being linked to tolerance to low K⁺. Plants can be significantly impacted by suboptimal growing circumstances, which can also raise the sustainable use of non-renewable inputs. In two types of lettuce that differ in the accumulation of secondary metabolites, Miras-Moreno and colleagues (2020)^[35] looked into the effects of sub-optimal availability of macrocations and various light intensities. Treatments altered several stress-related metabolites (such polyamines), indicating that effects on sustainable low-input agricultural systems should be assessed by taking into account both advantageous and unfavorable metabolic effects in addition to yield and socioeconomic indicators.

Heavy Metal Stress

Plant morphological, physiological, biochemical, and molecular functions are impaired by heavy metal exposure. Plant growth and yield are significantly impacted by environmental Pb and Cd. In contrast, plants obtain Zn from the soil for essential purposes. According to Shafiq and co-authors (2020)^[45] Zn makes Pb and Cd easier to accumulate and move in the aerial regions of maize plants. Other divalent metals cannot be absorbed or transported due to the interaction of Zn, Pb, and Cd. This work warns against overusing Zn fertilizers in metal-contaminated soils by highlighting how DNA methylation and histone acetylation affect metal stress resistance. Since cerium dioxide (CeO₂) nanoparticles are rarely immobilized in the environment, they are pollutants of emerging concern. CeO₂ nanoparticles (CNPs) were shown to have an impact on the uptake of metals in the study by Skiba *et al.* (2020)^[49]. The roots contain less Cu, Zn, Mn, Fe, and Mg in particular, but a reversal pattern was shown for Ca. This study is highly suited for examining the interactions caused by CNPs, which modify factors involved in photosynthesis in pea. The acetylation pathway of oxalate degradation, which controls how different higher plants react to biotic and abiotic stressors, is where acyl activating enzyme 3 (AAE3) is involved. The function of Glycine soja AAE3 (GsAAE3) in Cd and Al sensitivity was studied by Xian and colleagues (2020)^[59]. In *A. thaliana* and soybean hairy roots, overexpression of GsAAE3 increases Cd and Al tolerances, which is correlated with a reduction in oxalate buildup. Collectively, the data show that the GsAAE3-encoded protein is crucial for dealing with Cd and Al stressors. Al can be quite poisonous, especially in acidic soils. To reduce this stress and enhance the quality of plants, it is essential to understand the mechanisms underlying a

plant's reaction to Al stress. Rosa-Santos and colleagues (2020)^[41] collected 372 million paired-end RNA sequencing reads from the roots of CTC-2 and RB855453, two dissimilar cultivars, in order to determine the genes implicated in sugarcane response to Al stress. Most of the genes had elevated expression in the tolerant cultivar CTC-2 and down regulated expression in RB855453 (sensitive cultivar). Future genetic and genomic studies of sugarcane can start with the findings and recommendations of this study. The transcriptome research demonstrates that sugarcane tolerance to Al may be attributed to the development of lateral roots, activation of redox enzymes, and an effective detoxification mechanism. Heavy metal-polluted soils cause oxidative stress in plants growing there, which results in symptoms of toxicity as chlorosis and growth loss. Plants produce a variety of antioxidant compounds, including polyphenols and flavonoids, to combat oxidative stress. Salinitro *et al.* (2020)^[42] goal was to investigate how these molecules accumulated in response to rising Cd, Cr, Cu, Ni, Pb, and Zn concentrations and determine whether they might be used to measure metal-related stress in *Polygonum aviculare* and *Senecio vulgaris*. The results of this study confirmed that there was a direct link between the level of metal stress and the production of phenolic compounds with antioxidant activity, as 82% of the samples showed a good correlation between the level of polyphenols, flavonoids, and antioxidant activity and the metal concentration in plant shoots.

Stress defense signaling pathways

Stress Sensing and Early Signaling

Plants are quite sensitive to harsh situations since they are sessile. Despite the significance of stress sensing, we know very little about the molecular mechanisms that underlie it. In general, any early changes that occur in a cellular component in response to stress can act as a stress-sensing mechanism provided that the changes are detected and magnified by the cell's molecular machinery (Zhu, 2016)^[66]. For instance, turgor pressure, plasma membrane curvature, and cellular osmotic potential all change as a result of drought-induced hyperosmotic stress. In order to detect osmotic stress in plants, plasma membrane-localized mechano sensors or cytoplasm-localized sensors have been proposed (Christmann *et al.*, 2013; Zhu, 2016)^[5, 66]. Similar to this, as cell expansion-driven development necessitates ongoing cell wall modification, stress sensing by detection of stress-triggered cell wall modifications may be related to growth regulation. In this situation, receptor-like kinases (RLKs), which are highly amplified in the majority of plant genomes, may be used to sense diverse changes in the plant cell wall brought on by stress. Stress sensing and signaling most likely occur in waves, which could account for the many waves of transcriptome modifications that have been seen (Kollist *et al.*, 2019)^[29]. Inter organ signals might also be important. As mentioned before, a reduction in the rate of leaf elongation due by osmotic stress can be seen within seconds (Chazen and Neumann, 1994)^[2]. From roots to shoots, the earliest consequences of hyperosmotic stress may be communicated via hydraulic signals (Malone, 1993; Wildon *et al.*, 1992)^[32, 58]. Through a genetic screen, the hyperosmolality-gated calcium channel OSCA1 hyper osmolality-induced [Ca²⁺]_i increase was discovered (Yuan *et al.*, 2014)^[62]. Despite the mutant plants showing no obvious growth abnormalities under stress, loss-of-function mutations in

OSCA1 result in decreased cytosolic calcium transients and defective stomatal closure in response to hyperosmotic treatment (Yuan *et al.*, 2014) [62]. Jiang *et al.* identified the plasma membrane's glycosyl inositol phosphorylceramide (GIPC) sphingolipids as the sodium ion sensor using a similar screening system because loss-of-function mutations in the glucuronosyltransferase MOCA1 (monocation-induced [Ca²⁺]_i increase 1) result in decreased growth under salt stress and loss of calcium spikes (Jiang *et al.*, 2019) [26]. It is still unknown what OSCA1 and MOCA1's downstream effectors are. When a plant cell detects a stress, second messengers like calcium, reactive oxygen species (ROS), phospholipids, and nitric oxide (NO), as well as various protein kinases, relay and amplify the signal. The amount, frequency, and subcellular localization of stress-related increases in cytosolic calcium concentration (abbreviated [Ca²⁺]_i) are all variable. Within 15 seconds of receiving an osmotic stress treatment, guard cells from the Arabidopsis plant show calcium transients (Yuan *et al.*, 2014) [62]. Calcium-binding proteins can then detect calcium signals and pass the signal to an interacting protein kinase or a kinase that is directly fused to them, such as the calcium-dependent protein kinases, in most cases (CDPKs or CPKs). In plants, ROS can be generated by a variety of organelles, including as chloroplasts, mitochondria, and peroxisomes, as well as by Rboh NADPH oxidases that are found in the plasma membrane. Particularly, respiratory burst oxidase homologs D and F (RbohD and RbohF)-produced apoplastic ROS may trigger certain calcium and electrical signals and facilitate quick systemic communication in response to stress (Choi *et al.*, 2016) [4]. Arabidopsis was found to disseminate this type of signal at about 8.4 cm per minute. The synthesis of phosphatidic acid (PA), which is catalyzed by phospholipase Ds (PLDs) and can play either a positive or negative function depending on the stress condition, is also made easier by various abiotic stresses (Hong *et al.*, 2016; Testerink and Munnik, 2011) [23, 53]. Drought-induced PA synthesis in the guard cell is necessary for RbohD/F-mediated ROS buildup and stomatal closure. Different families of kinases, such as those in the MAPK (mitogen-activated protein kinase) module, the SNF1-related protein kinases (SnRKs), CDPKs, and RLKs, are also involved in stress signalling in plants (de Zelicourt *et al.*, 2016) [7]. For example, within 2 minutes of exposure to drought, salt, or low temperature stressors, MPK3, MPK4, and MPK6 can all be activated (Zhao *et al.*, 2017) [64].

Conclusion

Abiotic stressors will, regrettably, continue to be a constant threat to agriculture and the environment. Numerous, largely negative factors have an impact on plant and crop productivity, which lowers food supply and raises production costs. Even in a scenario of looming climate change, there remain hurdles to producing more due to the limited amount of arable land now available, the rising global population, and declining water resources. To better understand abiotic stress responses, discover stress protection networks, and create environmentally stable crops that are more productive and adaptable to environmental changes, increasing knowledge of plant biology and crop improvement are critical milestones. The contributions in this Special Issue focused on a variety of abiotic stress responses and demonstrate the scientific community's rising interest in finding effective remedies.

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