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Abiotic stress tolerance in agriculture

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Abstract

Plants being sessile, are seriously affected by plethora of factors among which abiotic stresses notably drought, salinity and extreme temperature conditions are major constraint worldwide, reducing more than 50% yield in major crops. Stress conditions reduce plant growth by affecting various physiological and biochemical processes such as photosynthesis, respiration, translocation, ion uptake, sugar and nutrient metabolism, and also phytohormones. To overcome such situation, plants have developed innate adaptations to stress conditions with an array of biochemical and physiological interventions that involves the function of many stress-associated genes. Thus, understanding the physiological and biochemical responses to stresses is essential for a holistic perception of plant resistance mechanisms to overcome the conditions.

Keywords: abiotic, drought, salt, stress, plants, resistance

Introduction

Increasing crop production is now the highest agricultural priority worldwide because of burgeoning population. According to the United Nation's World Population Prospects report, the world population is currently increasing at an alarming rate of approximately seventy four million people per year and expected to reach more than 9 billion near 2050 (<http://www.un.org/esa/population/unpop.htm>), whereas, global food productivity is declining due to the negative effect of various environmental stress factors. It is estimated that global warming decreased the yield of major crops like maize, wheat and barley by ~40 million metric tons per year between 1981 and 2002 (<http://environmentalresearchweb.org/cws/article/news/27343>). Therefore, minimizing the losses in crop productivity is a matter of concern for all nations to feed the several billion people living on this planet. It is well documented that among abiotic stresses extreme temperatures (freezing, cold, heat), water availability (drought, flooding), and ion toxicity (salinity, heavy metals) are the major causes which adversely affect the plant growth and productivity worldwide (Pereira, 2016) [1]. Stress is quite unpredictable in its duration, occurrence, and intensity and thus maintaining the growth and survival is a herculean task in affected regions. Plants can perceive even a lowest environmental stress signal and reproductive stages are most sensitive to it. The duration and magnitude of stress determines the severity of symptoms while the physiological manifestations involve an increase in respiration, alterations in electron transport system, inhibition of photosynthesis, and reduction in biomass (Singhal *et al.* 2016) [2]. The cellular responses to stress include altered cell cycle, changes in the induction of vacuolization, and cell wall organization allowing to tolerate the stress (Zhu 2016) [3]. There are alterations in the anatomy, physiology, and energy consumption which increases due to a shift in cellular metabolism to maintain cellular homeostasis. Plants react to stress by either acclimatization i.e., adjusting to the new conditions and reaching a state of homeostasis or adaptations which involve permanent alterations introduced to resist stress. Acquired stress tolerance in plants is often a result of various stress- response mechanisms that act coordinately or synergistically to prevent cellular damage and to reestablish cellular homeostasis (Ha *et al.* 2012) [4]. The present review summarizes our current understanding of the possible mechanisms associated with various stress conditions. We also aim to highlight the roles of other key factors in abiotic stress signaling and their roles in shaping the outcome of stress adaptation reactions.

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Generic Stress Signaling Pathway

The stress is first perceived by the receptors present on the membrane of the plant cells (Fig. 1), the signal is then transduced downstream and this results in the generation of second messengers including calcium, reactive oxygen species (ROS) and inositol phosphates (Todaka *et al.* 2015) [5]. These second messengers, such as inositol phosphates, further modulate the intracellular calcium level. This perturbation in cytosolic Ca^{2+} level is sensed by calcium binding proteins, also known as Ca^{2+} sensors. These sensors apparently lack any enzymatic activity and change their conformation in a calcium dependent manner. These sensory proteins then interact with their respective interacting partners often initiating a

phosphorylation cascade and target the major stress responsive genes or the transcription factors controlling these genes (Nakashima *et al.* 2014) [6]. The products of these stress genes ultimately lead to plant adaptation and help the plant to survive and surpass the unfavorable conditions (Sewelam *et al.* 2014) [7] (Fig.1). Thus, plant responds to stresses as individual cells and synergistically as a whole organism. Stress induced changes in gene expression in turn may participate in the generation of hormones like ABA, salicylic acid and ethylene (Fahad *et al.* 2015) [8]. These molecules may amplify the initial signal and initiate a second round of signaling that may follow the same pathway or use altogether different components of signaling pathway.

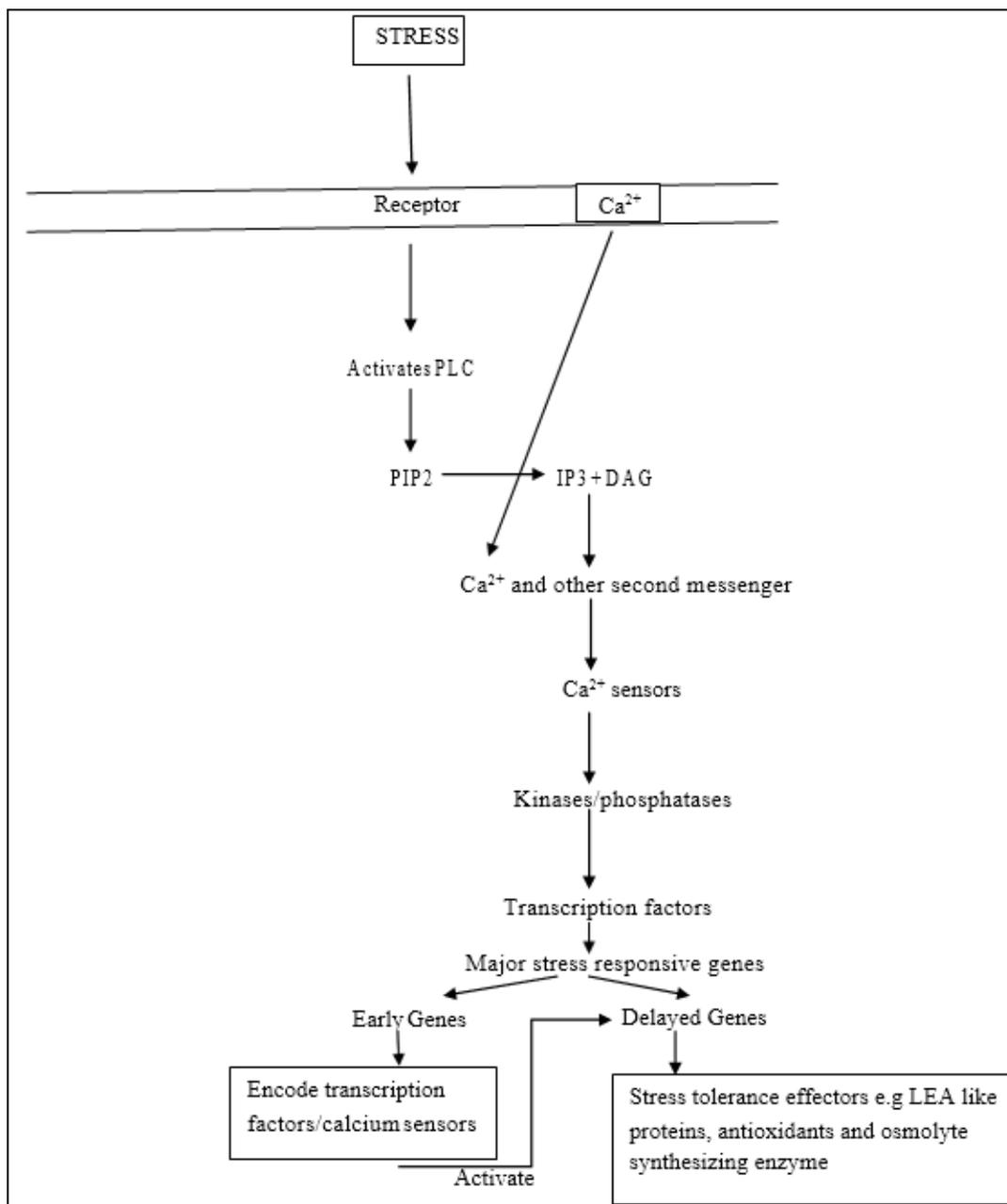


Fig 1: Signal transduction pathway

Plant Responses to Abiotic Stresses

When in adverse or limiting growth conditions, plants respond by activating tolerance mechanisms at multiple levels of organization (molecular, tissue, anatomical, and morphological), by adjusting the membrane system and the

cell wall architecture, by altering the cell cycle and rate of cell division, and by metabolic tuning (Mittler 2002) [9]. At a molecular level, many genes are induced or repressed by abiotic stress, involving a precise regulation of extensive stress-gene networks (Nguyen *et al.* 2018) [10]. Products of

those genes may function in stress response and tolerance at the cellular level. Proteins involved in biosynthesis of osmoprotectant compounds, detoxification enzyme systems, proteases, transporters, and chaperones are among the multiple protein functions triggered as a first line of direct protection from stress. In addition activation of regulatory proteins (*e.g.*, transcription factors, protein phosphatases, and kinases) and signaling molecules are essential in the concomitant regulation of signal transduction and stress-responsive gene expression.

Common Physiological and Biochemical Responses under stress conditions

Salinity, cold and drought stress are all osmotic stresses: they cause a primary loss of cell water, and, therefore, a decrease of cell osmotic potential (Pandey *et al.* 2015) ^[11]. However, the elicitor of cell water loss differs between stresses: i) salinity stress decreases cell water content due to the decrease of external water potential, caused by the increased ion concentration (mainly Na⁺ and Cl⁻), turning more difficult water uptake by roots and water translocation to metabolically active cells; ii) cold stress decreases cell water content due to the so-called physiological drought, *i.e.*, the inability to transport the water available at the soil to the living cells, mainly the ones of the leaf mesophyll; iii) the decrease of the cell water content under drought stress is due to water shortage in soil or/and in the atmosphere. Anyway, dehydration triggers the biosynthesis of the phytohormone abscisic acid (ABA) and it has been known for a long time that a significant set of genes, induced by drought, salt, and cold stresses, are also activated by ABA.

As a consequence of water loss and decreased cell volume, cell sap solute concentrations increase and thereby cell osmotic potential decreases. As cell turgor also decreases, an early effect common to these stresses is a sharp decrease in leaf expansion rate and overall plant growth rate. Furthermore, an additional active decrease of the cell sap osmotic potential is observed, as an attempt to keep cell hydration (Cramer *et al.* 2011) ^[12]. In fact, at the metabolic level, a common feature to these three stresses is the osmotic adjustment by synthesis of low molecular weight osmolytes mainly carbohydrates (Suprasanna *et al.* 2016) ^[13], betain (Giri 2011) ^[14] and proline (Slama *et al.* 2015) ^[15] that can counteract cellular dehydration and turgor loss. On the other hand, differences between these stresses do also exist. While drought stress is mainly osmotic, ion toxicity, namely Na⁺, is a distinctive feature of salinity stress. Cold stress, behinds physiological drought, has an impact on the rate of most biochemical reactions, including photosynthetic carbon metabolism reactions, as enzyme activities are extremely temperature-dependent (Zhu *et al.* 2016) ^[3]. Also water stress and salinity stress decrease photosynthesis, which create conditions to increased photoinhibition, particularly under high irradiances (Singh and Thakur 2018) ^[16].

The generation of reactive oxygen species (ROS) is one of the earliest biochemical defense response of plants to abiotic stresses. The ROS such as O²⁻, H₂O₂ and ·OH radicals, can directly attack membrane lipids and increase lipid peroxidation, leading damage to various organelles and ultimately death of plant (Choudhury *et al.* 2017) ^[17]. To

protect itself from oxidative damage, plants are armed with sophisticated antioxidant defense systems enzymatic and non-enzymatic antioxidants, which function as an extremely efficient cooperative system (Gill and Tuteja 2010) ^[18]. The major scavenging mechanisms include superoxide dismutase (SOD), enzymes and metabolites from the ascorbate-glutathione cycle, and catalase (CAT) (Lakshmi *et al.* 2017) ^[19]. They are located throughout the different compartments of the plant cell, with the exception of catalase that is exclusively located in peroxisomes. SOD is the front-line enzyme in ROS attack since it rapidly scavenges superoxide, one of the first ROS to be produced, dismutating it to oxygen and H₂O₂. However, this reaction only converts one ROS to another, and H₂O₂ also needs to be destroyed since it promptly attacks thiol proteins. The major enzymatic cellular scavengers of H₂O₂ are catalase and ascorbate peroxidase (APX). They have however different affinities for this ROS and seem to have different cellular roles in H₂O₂ scavenging. In fact CAT does not need a reductant to scavenge H₂O₂ making it reducing power-free, whereas APX needs a reductant, ascorbate. On the other hand, CAT has a lower affinity for H₂O₂ (mM range) than APX (mM range). All this gathered has led to the hypothesis that APX, an enzyme located in every cellular ROS producing compartment, might function as a fine regulator of intracellular ROS steady-state levels, possibly for signaling purposes, whereas CAT located exclusively in the peroxisomes, might function as a bulk remover of excess ROS production under stress conditions. Glutathione reductase (GR), the last enzyme of the ascorbate/glutathione cycle, has a major role in maintaining the intracellular glutathione pool in the reduced state (GSH) (Das and Roychoudhury 2014) ^[20]. GSH can function as an antioxidant either directly (non-enzymatically), like ascorbate, by scavenging singlet oxygen, superoxide or even hydroxyl radicals, or indirectly as a reducing agent that recycles ascorbic acid from its oxidized form to its reduced form by the enzyme dehydroascorbate reductase (Kasote *et al.* 2015) ^[21]. In the chloroplast, the Mehler reaction occurring during photosynthesis is an important alternative sink for electrons, but it produces superoxide as side effect (Ashraf and Harris 2013) ^[22]. This active oxygen species is however rapidly dismutated by a membrane bound superoxide dismutase (SOD), producing H₂O₂. H₂O₂ is then locally converted to water by ascorbate peroxidase (APX) (Kasote *et al.* 2015) ^[21]. This is called the Mehler-peroxidase reaction or the water-water cycle. One of the major advantages of the water-water cycle is the scavenging of superoxide and H₂O₂ at their production site, without further damage to the thylakoids or other cellular compartments (Fig. 2). Furthermore, the water-water cycle seems to be autonomous regarding its energy supply since it gets its reducing power directly from the photosynthetic apparatus (Ashraf and Harris 2013) ^[22]. H₂O₂ is a very stable ROS with the longest half-life (~1 ms) and is also the more diffusive so it can readily “escape” from the organelle where it was produced to the cytosol. It can also be directly produced in the cytosol by existing cytosolic SODs. However in the cytosol, H₂O₂ is readily scavenged by ascorbate through the ascorbate/glutathione cycle (Das and Roychoudhury 2014) ^[20].

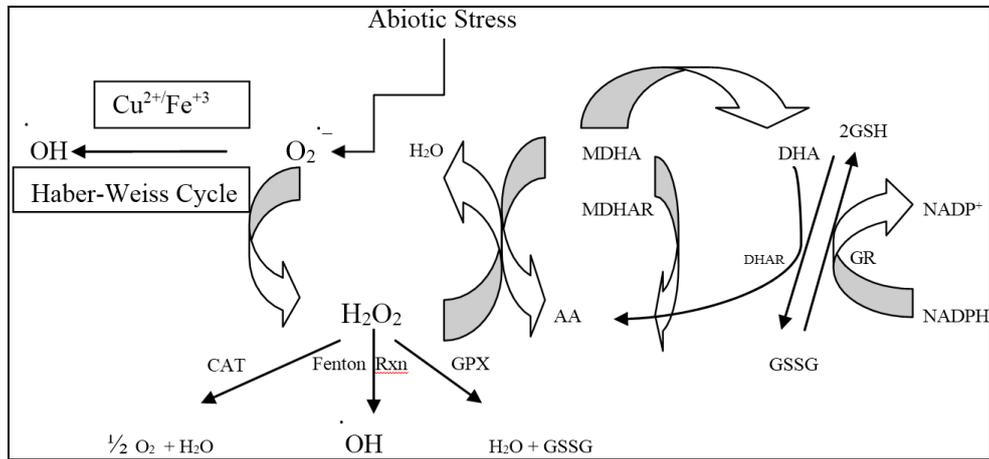


Fig 2: Reactive oxygen species production and scavenging mechanism

Molecular responses

Genes induced during stress conditions function not only in protecting cells from stress by producing important metabolic proteins, but also in regulating genes for signal transduction in the stress response (Arbona *et al.* 2017) [23]. The first group includes proteins that probably function in stress tolerance, such as chaperones or late embryogenesis abundant (LEA) proteins. The second group contains protein factors involved in further regulation of signal transduction and gene expression that probably function in stress response (Ulrike and Benjamin 2018) [24]. In some cases networks and cascades of expression are activated in response to a stress condition. The regulation of the expression of these networks is being studied during the last decades. Members of dehydration-responsive element-binding (DREB) or C-repeat binding factor (CBF), MYB, basic-leucine zipper (bZIP), and zinc-finger families have been well characterized with roles in the regulation of plant defense and stress responses. Most of these transcription factors (TFs) regulate their target gene expression through binding to the cognate cis-elements in the promoters of the stress-related genes (Joshi *et al.* 2016) [25]. More recently the WRKY transcription factors are becoming one of the best-characterized classes of plant transcription factors (Chen *et al.* 2011) [26]. Several WRKY proteins were shown to be involved in plant drought and salinity stress responses. For example, over expression of the *Oryza sativa* WRKY11 under the control of Heat Shock Protein 101 (HSP101) promoter led to enhanced drought tolerance (Lee *et al.* 2018) [27]. Recently, the over expression of TsNAC1 cloned from the halophyte *Thellungiella halophila* has been found to improve abiotic stress resistance, especially in salt stress tolerance, in both *T. halophila* and *Arabidopsis* (*Arabidopsis thaliana*). For an instance, OsNAC6 also showed high sequence similarity to the *Arabidopsis* stress-responsive NAC proteins ANAC019, ANAC055, and ANAC072 (RD26) (Todaka *et al.* 2015) [5].

Conclusion

Under the influence of changing environmental conditions, reduction in crop yield and production is a serious consequence that threatens global food security. Stress affects almost every plant process, from membrane conformation, chloroplast organization and enzyme activity, at a cellular level to molecular basis. To minimize the negative effects of enhanced stress, plants have various signalling pathways and respond by changing their growth pattern, up-regulation of antioxidants, accumulation of compatible solutes and by

producing stress proteins via over-expression of certain genes. Based upon the findings the research workers focus to develop stress resistant varieties so as to meet the needs of ever growing population.

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