RESEARCH REVIEW JOURNALS
Volume-02
Issue-12
December-2017

ISSN: 2455-3085 (Online)
RESEARCH REVIEW International Journal of Multidisciplinary
www.rrjournals.com

Plants Sensing and Responding to Stresses - A Review

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ARTICLE DETAILS

Article History
Published Online: 31 December 2017

Keywords
Environmental stresses, temperature, radiation,cellular response and signaling

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ABSTRACT

Plants are exposed to an ever-changing stresses environment which reduce and limit their growth and productivity. Two types of environmental stresses are encountered to plants which can be categorized as (1) Abiotic stress and (2) Biotic stress. The abiotic stress causes the loss of major crop plants worldwide and includes radiation, salinity, floods, drought, extremes in temperature, heavy metals, etc. On the other hand, attacks by various pathogens such as fungi, bacteria, oomycetes, nematodes and herbivores are included in biotic stresses. As plants are sessile in nature, they have no choice to escape from these environmental cues. Plants have developed various mechanisms in order to overcome these threats of biotic and abiotic stresses. They sense the external stress environment, get stimulated and then generate appropriate cellular responses. They do this by stimuli received from the sensors located on the cell surface or cytoplasm and transferred to the transcriptional machinery situated in the nucleus, with the help of various signal transduction pathways. This leads to differential transcriptional changes making the plant tolerant against the stress. The signaling pathways act as a connecting link and play an important role between sensing the stress environment and generating an appropriate biochemical and physiological response.

1. Introduction

Stress in plants refers to peripheral conditions that unfavorably affect growth, development and productivity of plants [1]. Stresses activate an extensive variety of plant responses like changed gene expression, cellular metabolism, changes in growth rates, crop yields, etc. A plant stress usually reflects some abrupt changes in environmental condition. However in stress tolerant plant species, exposure to a particular stress leads to acclimation to that explicit stress in a time time-dependent manner [1]. Plant stress can be divided into two primary categories namely abiotic stress and biotic stress. Abiotic stress imposed on plants by environment may be either physical or chemical, while as biotic stress exposed to the crop plants is a biological unit like diseases, insects, etc. [1]. Some stresses to the plants injured them as such that plants exhibit several metabolic dysfunctions [1]. The plants can be improved from injuries if the stress is mild or of short term as the effect is temporary while as severe stresses leads to death of crop plants by preventing flowering, seed formation and induce senescence [1]. Such plants will be considered to be stress vulnerable. However several plants like Ephemerals can escape the stress altogether [2].

Biotic stress in plants is caused by living organisms, particularly viruses, bacteria, fungi, insects, arachnids and weeds. The agents causing biotic stress directly divest their host of its nutrients and can lead to death of plants. Biotic stress can become major because of pre- and postharvest losses. Despite lacking the adaptive immune system plants can counteract biotic stresses by evolving themselves to certain sophisticated strategies. The defense mechanisms which act against these stresses are controlled genetically by plant's genetic code stored in them. The resistant genes against these biotic stresses present in plant genome are encoded in hundreds. The biotic stress is totally different from abiotic stress, which is imposed on plants by non-living factors such as salinity, sunlight, temperature, cold, floods and drought having negative impact on crop plants. It is the climate in which the crop lives that decides what type of biotic stress may be imposed on crop plants and also the ability of the crop species to resist that particular type of stress. Many biotic stresses affect photosynthesis, as chewing insects reduce leaf area and virus infections reduce the rate of photosynthesis per leaf area.

Abiotic stresses are perceived by primary sensory mechanisms that translate the physical and chemical environment, such as water availability, ion concentration, and temperature, into a biological signal. For example, heat perception in mammals is mediated by both the TRANSIENT RECEPTOR POTENTIAL (TRP) cationic channel family and the TWIK-RELATED POTASSIUM (TREK) channel family present in neurons. Increasing temperatures led to depolarization and increased action potential firing of corresponding neurons. Abiotic stresses such as drought (water stress), excessive watering (water logging), extreme temperatures (cold, frost and heat), salinity and mineral toxicity negatively impact growth, development, yield and seed quality of crop and other plants. In future it is predicted that fresh water scarcity will increase and ultimately intensity of abiotic stresses will increase. Hence there is an urgency to develop crop varieties that are resilient to abiotic stresses to ensure food security and safety in coming years. A plants first line of defense against abiotic stress is in its roots. The chances of surviving stressful conditions will be high if the soil holding the plant is healthy and biologically diverse. One of the primary responses to abiotic stress such as high salinity is the disruption of the Na^+/K^+ ratio in the cytoplasm of the plant cell. The phytohormone abscisic acid (ABA) plays an important role during plant adaptation to environmental stress such as high salinity, drought, low temperature or mechanical wounding [3].

2. Abiotic stresses

Plants are encountered by number of abiotic stresses which impact on the crop productivity worldwide. These abiotic stresses are interconnected with each other and may occur in form of osmotic stress, malfunction of ion distribution and plant cell homeostasis. The growth rate and productivity is affected by a response caused by group of genes by changing their expression patterns. So, the identification of responsive genes against abiotic stresses is necessary in order to understand the abiotic stress response mechanisms in crop plants. The abiotic stresses occurring in plants include.

1) Heat:- Increased temperatures lead to water loss due to increased evaporation. In addition, high temperatures inhibit proper protein folding and induce formation of protein aggregates at the cellular level. When plants encounter heat stress the percentage of seed germination, photosynthetic efficiency and yield declines. Under heat stress, during the reproductive growth period, the function of tapetal cells is lost, and the anther is dysplastic.
2) Drought:- Nowadays climate has changed all around the globe by continuously increase in temperature and atmospheric CO_2 levels. The distribution of rainfall is uneven due to the change in climate which acts as an important stress as drought. The soil water available to plants is steadily increased due severe drought conditions and cause death of plants prematurely. Drought induces a complex array of responses in plants, including stomatal closure, reduced turgor pressure, altered leaf gas composition, and reduced photosynthesis rates, leading to reduced growth and crop yield. Water deficit results in osmotic stress for plants, and thus water availability is likely first sensed as a decrease in osmotic potential. Therefore, drought sensors are also referred to as osmosensors. The complexity of plant responses to water-limiting conditions make it challenging to find true sensors of water deficit, although several primary sensing mechanisms have been proposed. After drought is imposed on crop plants growth arrest is the first response subjected on the plants. Plants reduce their growth of shoots under drought conditions and reduce their metabolic demands. After that protective compounds are synthesized by plants under drought by mobilizing metabolites required for their osmotic adjustment.
3) Cold: Low temperatures delay many developmental processes and vegetative growth in plants. Extremely low temperatures, i.e. freezing temperatures, result in the formation of ice crystals which can permanently damage cells if not dealt with appropriately. Cold stress as abiotic stress has proved to be the main abiotic stresses that decrease productivity of agricultural crops by affecting the quality of crops and their post-harvest life. Plants being immobile in nature are always busy to modify their mechanisms in order to prevent themselves from such stresses. In temperate conditions plants are encountered by chilling and freezing conditions that are very harmful to plants as stress. In order to adopt themselves, plants acquire chilling and freezing tolerance against such lethal cold stresses by a process called as acclimation. However many important crops are still incompetent to the process of cold acclimation. The abiotic stress caused by cold affect the cellular functions of plants in every aspect. Several signal transduction pathways are there by which these cold stresses are transduced like components of ROS, protein kinase, protein phosphate, ABA and Ca^{2+}, etc. and among these ABA proves to be best.
4) Salt: Soil salinization is one of the major abiotic threats for agriculture. Similar to drought, it quickly limits water uptake and causes osmotic stress, with later accumulation of ions leading to ionic stress. As a result, plant growth on saline soils is limited by reduced turgor pressure, reduced photosynthesis, and changes in development, which are required for survival. Soil salinity poses a global threat to world agriculture by reducing the yield of crops and ultimately the crop productivity in the salt affected areas. Salt stress reduces growth of crops and yield in many ways. Two primary effects are imposed on crop plants by salt stress; osmotic stress and ion toxicity. The osmotic pressure under salinity stress in the soil solution exceeds the osmotic pressure in plant cells due to the presence of more salt, and thus, limits the ability of plants to take up water and minerals like K^+ and Ca^{2+}. These primary effects of salinity stress causes some secondary effects like assimilate production, reduced cell expansion and membrane function as well as decreased cytosolic metabolism.
5) Toxin: The increased dependence of agriculture on chemical fertilizers and sewage waste water irrigation and rapid industrialization has added toxic metals to agriculture soils causing harmful effects on soil-plant environment system.
6) Flooding: While all of the abovementioned stress conditions share the characteristic of water depletion,

flooding presents another extreme condition for plants. The effects of flooding vary depending on the turbidity of the water, but generally it leads to inhibition of gas exchange and reduction of photosynthesis. These limitations gradually lead to oxygen depletion (hypoxia), which restricts respiration and therefore causes energy imbalance. Initially, limited gas exchange leads to rapid accumulation of the gaseous hormone ethylene, which is not soluble in water and therefore accumulates in the membranes of the cells. Here it binds to the ethylene receptors, resulting in the stabilization of transcription factors ETHYLENE-INSENSITIVE3 (EIN3) and ETHYLENE-INSENSITIVE3-LIKE1 (EIL1). These regulate gene expression responsive for various adaptive responses, including shoot elongation, leaf hyponasty, and adventitious root formation

3. Biotic Stresses

Plants struggle with many kinds of biotic stresses caused by different living organisms like fungi, virus, bacteria, nematodes, insects etc. These biotic stress agents cause various types of diseases, infections and damage to crop plants and ultimately affect the crop productivity. However, different mechanisms have been developed through research approaches to overcome biotic stresses. The biotic stresses in plants can be overcome by studying the genetic mechanism of the agents causing these stresses. Genetically modified plants have proven to be the great effort against biotic stresses in plants by developing resistant varieties of crop plants.

4. Polyamine: plant response to stresses

Plants being immobile in nature have to go through continuous fluctuations in the environment with appropriate physiological, developmental and biochemical changes [4]. More than 50% reduction in crop plants occur due to abiotic stresses worldwide which is the main cause of crop loss [5]. To counteract the stresses, plants are equipped with a large set of defense mechanisms [6]. Among the different classes of compatible solutes, polyamines stand as one of the most effective against extreme environmental stress. Polyamines are low molecular weight aliphatic nitrogen compounds positively charged at physiological pH [7]. Investigations into plant polyamines at a molecular level have led to isolation of a number of genes encoding polyamine biosynthetic enzymes from a variety of plant species [8]. In recent years, molecular and genomic studies with mutants and transgenic plants having no or altered activity of enzymes involved in the biosynthesis of polyamines have contributed to a better understanding of biological functions of polyamines in plants.

4.1 Polyamine and plant response to abiotic stresses

Stress derived changes in cellular polyamines provide clues on their possible implication in stress but do not provide evidence of their role in counteracting stress. The levels of endogenous polyamines can be increased by application of exogenous polyamines, which has been attempted before or during stress [9, 10]. Exogenous application of polyamines could preserve plant cell membrane integrity, minimize growth inhibition caused by stress, moderate expression of osmotically responsive genes and increase activities of antioxidant enzymes. In another approach treatment with biosynthesis inhibitors can reduce endogenous polyamine resulted in stress sensitive phenotypes. However this effect is reversed by the concomitant application of exogenous polyamine [9, 11]. Another genetic approach employed for analyzing biological functions of polyamine metabolism in stress response is the use mutant deficient in polyamine biosynthesis [12].

4.2 Polyamine and plant response to biotic stresses

Polyamine metabolism has long been known to distort in plant cells responding to insightful changes in plants interacting with fungal [13], viral pathogens [14] and mycorrhizae [15]. It is hard to identify the contribution of polyamine accumulation in infected organs as it is present both in plants and pathogenic fungi. The possibility of control of fungal plant diseases through specific inhibition of polyamine biosynthesis is most excited and for reaching development [16, 17].

5. Downstream Signaling

Following sensing of specific abiotic stress cues, there is substantial overlap in the downstream signaling molecules utilized. These include Ca^{2+}, ROS, and mitogen-activated protein kinases (MAPKs), as well as the phytohormones auxin, ABA, gibberelins, ethylene, and brassino steroids. Yet, plants are able to use these similar signaling components to induce stress-specific transcriptional and physiological responses.

Ca^{2+} Signaling

Calcium signaling plays a central role in abiotic stress signaling and is, among others, involved in the response to heat, cold, touch, salt, flooding, hypoxia, osmotic stress, and drought [18]. Ca^{2+} enters the cell via Ca^{2+}-permeable channels and then regulates downstream responses. These Ca^{2+} influxes contain a stress-specific fingerprint that varies in amplitude, timing, and frequency and could be formed by the activation of different Ca^{2+} channels by different stresses [19]. The patterns activate specific intracellular Ca^{2+} sensors, which in turn regulate specific downstream responses like stress-responsive gene expression and protein interactions, illustrated by the aforementioned activation of the SOS pathway [19,20,21]. Also, the location of the Ca^{2+} influx has been shown to be stress-specific. For example, ionic stress in the roots results in transient Ca^{2+} waves through the whole plant [22].

ROS and Calcium Interplay

ROS are formed in almost every plant compartment during numerous enzymatic reactions and have long been considered solely detrimental to plant life. On the other hand, the large array of antioxidant molecules and enzymes keep ROS levels in balance, rendering ROS excellent signaling molecules on the single-cell level as well as for cell-to-cell communication [23,24]. ROS signals are mainly produced at the cell wall and plasma membrane in response to stress conditions, and in chloroplasts due to damage to the photosynthetic apparatus. The proteins responsible for the largest production of ROS at the cell wall and plasma membrane are respiratory burst oxidase homologs (RBOHs), peroxidases, and to a lesser extent oxalate oxidases [25]. Recent reports have shown that ROS accumulation and calcium production each enhance induction of the other during abiotic stress conditions. Superoxide produced by RBOH protein D activates calcium channels, which in turn activate the vacuolar calcium channel TWO PORE CHANNEL1 (TPC1). TPC1 transports vacuolar-stored Ca^{2+} resulting in the activation of RBOH protein D [26]. This feedback loop is likely instrumental for propagation of the ROS and Ca^{2+} waves during salt stress and a proper acclimation response. Stress conditions including drought and high temperatures show similar calcium and ROS waves across the plasma membrane, but no in-depth mechanistic reports are present yet. The many different origins of ROS and the corresponding Ca^{2+} waves argue for a sophisticated signaling mechanism. Integrative studies could provide evidence for common ROS-calcium signaling pathways among different stress conditions.

Protein Kinases

MAPKs are a conserved protein family important for stress signaling and development [27,28]. MAPKs are activated in a phosphorylation cascade, which typically consists of three kinases, namely a MAPK kinase kinase (MAPKKK), a MAPK kinase (MAPKK), and a MAPK. In Arabidopsis, MAPKs are activated upon touch, cold, salt, drought, and wounding stress, for example [29], and regulate cellular responses such as gene expression [30]. Furthermore, MAPK pathways show cross talk with ethylene [31,32], ROS [33], and ABA signaling pathways [34]. An example of such cross talk is the regulation of ICE1, which is stabilized upon cold stress by phosphorylation at Ser-278 by OST1/SnRK2.6. However, in parallel, cold initiates a MAPK cascade via MPK3/6, which phosphorylates ICE1 at sites different from those targeted by OST1/SnRK2.6, marking ICE1 for degradation [35]. The exact reason for this interplay of stabilization and degradation is unknown, but it is hypothesized that this fine-tunes the stress responses. Like the other general stress responses, it is largely unknown how MAPK signaling cascades are able to initiate stress-specific responses [36].

6. Conclusion

It is expected that earth's temperature will increase by 3–5°C in the coming 50–100 years. As there is continuous increase in temperature and uneven rainfall the changes of flood and drought is always in consideration. The anthropogenic activities such as excessive fertilizers, inappropriate irrigation and exploitation of metal resources can lead to salt stress to a large extent. Under these circumstances, plants will probably encounter more frequently, concurrently both biotic and abiotic stresses. It is the duty of plant breeders to develop stress tolerant cultivars in order to secure food security and to ensure safety to the farmers. Molecular work is to be done at the genetic level to develop mechanisms in plants in order to prevent them from different types of stress conditions. Unless responsive mechanisms are not developed against biotic and abiotic stresses, the plants will continuously subjected to such stresses and ultimately will prove a great threat to world agriculture.

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