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Stress mechanisms and adaptations in plants

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Abstract

In natural conditions, plants are exposed to abiotic and biotic stresses. Abiotic stresses includes water stress, temperature stress, salinity stress, heavy metal stress and photo-oxidative stress while biotic stresses caused by biological factors like pests, pathogens or herbivore attack. These stresses affect the plant growth and development at the morphological, physiological, biochemical and molecular levels which either directly or indirectly affect the crop productivity. Plants possess various tolerance mechanisms that alter various gene expressions to bring about specific response to the stress. Additionally, researchers also used mitigation strategies like exogenous application phytohormones and alteration of plant genome by introducing stress tolerant genes which help the plants to cope with the stresses. In this review, we aim to discuss the various abiotic and biotic stresses, plant tolerance mechanism, mitigation of stress through phytohormones, various molecular approaches and cross tolerance between abiotic and biotic stresses.

Keywords: Abiotic stress, biotic stress, molecular approaches, phytohormones, and stress tolerance

Introduction

The term “stress” has been defined precisely in mechanics; however, in the case of biology it has been given widely different meanings. Probably due to an extension of the physical meaning, many of these definitions converge in attributing “stress” to any environmental factor “unfavourable” for the living organism under consideration (Levitt 1980) [24]. Plants are frequently exposed to different types of stress under natural conditions. Stress may be defined as any abiotic or biotic constraint that limits the rate of photosynthesis and reduces the plants’ ability to convert energy into biomass, or broadly it may be any external factor that exerts a deleterious influence on the plant. Stress is mostly measured in relation to plant survival, crop yield, growth (biomass accumulation) or the primary assimilation processes (CO_2 and mineral uptake), which are related to overall growth and development. Stress can be divided into two broad categories – abiotic and biotic stress. Abiotic stress may be any physical or chemical factor that the environment may impose on the plant. Abiotic stress includes water stress, decreased availability of essential nutrients from the soil (or conversely the build up of toxic ions during salt stress), extremes of temperature or excess light especially when photosynthesis is restricted (Hasanuzzaman *et al.* 2013; Akter *et al.* 2014; Vardhini and Anjum 2015; Ghasemi *et al.* 2018; Sytar *et al.* 2019) [15, 1, 42, 11, 40]. Biotic stress may be a biological factor (pest, pathogen or herbivore attack) to which a plant may be exposed during its life time (Taiz and Zeiger 2009; Zhu 2016) [41, 50].

At the morphological, biochemical, physiological, and molecular levels, abiotic environmental factors influence plant growth and development. As a result, plant responses to stress must be tailored to these circumstances. In general, abiotic stress responses in plants include inhibition of germination, reduction of growth, premature senescence and reduction in productivity. At physiological level, there is a reduction in water uptake, alteration in transpiration rate and respiration rate, reduced photosynthesis, decrease in nitrogen assimilation and metabolic toxicity. At the biochemical and molecular level, plants under stress show altered gene expression, reduced activity of vital enzymes, decreased protein synthesis, disorganization of membrane systems and breakdown of macromolecules (Rao *et al.* 2006) [33]. On the other hand biotic stress in plants caused by living organisms, such as viruses, bacteria, fungi, nematodes, insects, arachnids, and weeds, deprive their hosts of nutrients, which affects the plants’ vital physiological processes leading to reduced productivity (Amaral *et al.* 2021) [2].

In order to cope with the effects of stress, plants alter their physiology, metabolic mechanisms, gene expression and developmental activities. Therefore, plants possess unique mechanisms to tolerate various types of stress. However, the degree of tolerance varies from plant to plant.

Tolerance mechanisms start with stress perception followed by the formation of gene products that are involved in cellular protection and repair (Mo *et al.* 2021) [27]. It is expected that different perceiving mechanisms are involved. The most common model of perceiving external stimuli (stress) is that of a chemical ligand binding to a specific receptor. This model, however, is applicable only to chemical stress (e.g., heavy metal stress, nutrient depletion stress) and not to physical stress *i.e.* primary sensing of temperature stress (heat stress or chilling / freezing) does not involve any chemical ligand. The sugars synthesized during photosynthesis and carbon metabolism in source and sink tissues play an important role in perception and signaling, modulating growth, development, and stress responses. The signal transduction pathways that detect stress play a crucial role in the induction of stress tolerance in plants. In present review, we aim to focus on different types of stresses, tolerance mechanism in plants and mitigation strategies.

Water stress: This may arise either due to an excess of water (flooding) or water deficit (drought). Excess water can cause plant cells to swell and burst; whereas, water deficit can lead to desiccation. Flooding leads to reduced O_2 supply to the roots (hypoxia) followed by acidification of the cytoplasm, which in turn results in diminished protein synthesis, mitochondrial degradation, inhibition of cell division and elongation, disrupted ion transport and death of the root meristem. Hypoxia condition activates the O_2 sensing machinery in plants which regulates a subset of genes involved in metabolic adaptations to hypoxia, including proteins involved in ROS homeostasis and acclimation, to guide the molecular response to low O_2. (Pucciariello and Perata 2021) [32].

However, scarcity of water is the most important factor that limits crop growth worldwide. Water stress has several effects on plant growth, one of these is a limitation in leaf expansion which adversely affects water availability. Leaf area is an important because photosynthesis is usually proportional to it. Typically, as the water content of the plant decreases, its cells shrink and the cell walls relax. This decrease in cell volume results in lowering of the turgor pressure in the cells. The plasma membrane becomes thicker and more compressed because now it covers a smaller area than before. As reduction in turgor is the earliest significant biophysical effect of water stress, turgor-dependent activities such as leaf expansion and root elongation are the most sensitive to water deficits. Water stress can result in a dramatic increase in the vapour pressure gradient between the leaf and the surrounding air. Consequently, the rate of transpiration increases. An increase in the vapour pressure gradient also enhances drying of the soil. In addition, abscisic acid (ABA), a plant stress hormone, induces the closure of leaf stomata, thereby reducing water loss through transpiration, and decreasing the rate of photosynthesis (Waseem *et al.* 2011) [45]. Plants under water stress use a variety of strategies to reduce transpiration loss, including leaf rolling, root to shoot ratio dynamics, root length increment, accumulation of compatible solutes, increased transpiration efficiency, osmotic and hormonal regulation, and delayed senescence (Seleiman *et al.* 2021) [36].

Early responses of plants to drought stress usually help the plant to survive for some time. The acclimation of the plant to drought is indicated by the accumulation of certain new metabolites associated with the structural capabilities to improve plant functioning under drought stress. The main aspects of plant responses to water involve the maintenance of homeostasis (ionic balance and osmotic adjustment), ABA accumulation or by an increase of antioxidative mechanisms (Stikic *et al.* 2014) [37].

Salt stress: Salinity is one of the most serious factors limiting the productivity of agricultural crops, with adverse effects on germination, plant vigour and crop yield. Salinization affects many irrigated areas mainly due to the use of brackish water (Munns and Tester 2008) [29]. The basis for salinity is evaporation of water in a pure state leaving salts and other substances behind. High salinity affects plants in several ways: water stress, ion toxicity, nutritional disorders, oxidative stress, alter the metabolic processes, membrane disorganization and reduction of cell division (Zhu 2007) [49]. In response to salinity stress, the production of reactive oxygen species (ROS), such as singlet oxygen, superoxide, hydroxyl radical and hydrogen peroxide is enhanced. Salinity-induced ROS formation can lead to oxidative damages in various cellular components such as proteins, lipids, and DNA, interrupting vital cellular functions of plants (Gupta *et al.* 2014) [13]. Together, these effects reduce plant growth, development and survival.

During the onset and advancement of salt stress within a plant, all the major processes such as photosynthesis, protein synthesis and lipid metabolism are affected. During initial exposure to salinity, plants experience water stress, which in turn reduces leaf expansion. The osmotic effects of salinity stress have been observed immediately after salt application and these continue during the duration of exposure, resulting in inhibited cell expansion and cell division, as well as stomatal closure. Salt stress increases the intracellular osmotic pressure and can cause the accumulation of sodium to toxic levels. Thus, in response to salt stress signals, plants adapt via various mechanisms, including regulating ion homeostasis, activating the osmotic stress pathway, mediating plant hormone signaling, and regulating cytoskeleton dynamics and the cell wall composition (Zhao *et al.* 2021) [48]. 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. Thus, inhibition of plant growth due to salinity is the result of osmotic and ionic effects and the different plant species have developed different mechanisms to cope with these effects (Munns 2002) [28]. The osmotic adjustment, i.e., reduction of cellular osmotic potential by net solute accumulation has been considered an important mechanism for salt and drought tolerance in plants. This reduction in osmotic potential in salt stressed plants can be a result of inorganic ion (Na^+, Cl^-, and K^+) and compatible organic solute (soluble carbohydrates, amino acids, proline, betaines, etc) accumulations. Salinity can have effects similar to water stress on plant growth, except for the addition of ion cytotoxicity, which appears with salt excess in soil (Oliveira *et al.* 2013) [31].

Temperature stress: Plants exhibit a wide range of sensitivities to extremes of temperature. Some are killed or injured by moderate chilling temperatures while others can survive. Each plant has its unique set of temperature requirement for growth and development. There is an optimum temperature at which each plant grows and develops most efficiently.

Low temperature can affect the amount and rate of uptake of water and nutrients; under extremely cold conditions, the cell liquids can freeze, causing plant death because of desiccation and starvation. The major adverse effect of cold stress in plants has been seen in terms of plasma membrane damage which affects all physiological activities of plants. Plants exposed to cold stress show various phenotypic symptoms that include reduced leaf expansion, wilting, chlorosis and eventually necrosis (Bhattacharya 2022) [4]. Cold stress generally results in poor germination, stunted seedlings, yellowing of leaves, withering and reduced tillering. In cereals, the effects of cold stress at the reproductive stage delay heading and result in pollen sterility, which is thought to be one of the key factors responsible for the reduction in grain yield (Suzuki *et al.* 2008) [38].

At temperature -3 to -5ºC ice formation starts in the intercellular spaces. Plants synthesize specialized proteins for the development of freezing tolerance and several distinct proteins accumulate during acclimation to cold (Guy 1999) [14]. These are called antifreeze proteins, they bind to the surface of ice crystals to prevent or slow further crystal growth. Another group of proteins associated with osmotic stress are also up-regulated during cold stress. This group includes proteins involved in the synthesis of osmolytes, proteins for membrane stabilization, and the late embryogenesis abundant (LEA) proteins. Because the formation of extracellular ice crystals generates significant osmotic stress inside cells, coping with freezing stress also requires the means to cope with osmotic stress. Sugars and some of the cold-induced proteins have cryoprotective effects; they stabilize proteins and membranes during dehydration induced by low temperature (Zandalinas *et al.* 2022) [47].

High temperature stress induces morphological, anatomical as well as physiological and biochemical changes in plants (Waraich *et al.* 2012) [44]. Direct injuries due to high temperature include protein denaturation and aggregation and increased fluidity of membrane lipids while indirect heat injuries include inactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, and loss of membrane integrity. Heat stress also affects organization of microtubules and formation of microtubule asters in mitotic cells (Medina *et al.* 2021) [25]. High temperature during seed germination may slow down or totally inhibit germination, depending upon the plant species and intensity of the stress. At later stages temperature may affect vital physiological processes adversely and also modulate levels of hormones and primary & secondary metabolites (Hemantaranjan *et al.* 2014) [17].

Plants have evolved various mechanisms for flourishing under higher prevailing temperatures. They include short term avoidance/acclimation mechanism or long term evolutionary adaptations. Some major tolerance mechanisms, including ion transporters, LEA proteins, osmoprotectants, antioxidant defence and factors involved in signaling cascades and transcriptional control are essentially significant to counteract the stress effects (Wang *et al.* 2004, Rodriguez *et al.* 2005) [43, 35]. All plants when exposed to rapid increases in external temperatures, generally 5-10ºC above normal growth temperatures for a period of few minutes to a few hours exhibit synthesis of an elite set of proteins called heat shock proteins (HSPs).These HSPs are involved in cellular repair, cleanup and protection during the stress and recovery from it (Rao *et al.* 2006) [33].

Heavy metal stress: Among the naturally occurring elements, 53 are considered to be heavy metals and a few of them have got some biological significance for plants. However, the heavy metals like cadmium, if present in elevated levels in agricultural soils, are easily assimilated by plants and induce serious visible and metabolic perturbations e.g. leaf roll, chlorosis, growth reduction in root and shoot, browning of leaf tips, decrease in nutrient uptake, altered nitrogen metabolism, inhibition of stomatal opening, disruption of membrane composition and fluidity, decreased photosynthetic rate and disruption of ATPase activity. In addition to these hazards Cd hinders the development of chloroplasts and also affects the activities of two main photosynthetic enzymes Rubisco and phosphoenol pyruvate carboxylase (Hayat *et al.* 2010) [16]. Plants have developed several mechanisms that control and respond to the uptake and accumulation of heavy metals. The important heavy metal tolerance mechanism includes immobilization of metals by mycorrhizal association, metal binding to wall and reduced transport across the cell membrane, active efflux of metals, compartmentalization, chelation and sequestration of heavy metals by particular ligands (Emamverdian *et al.* 2015; Feng *et al.* 2021) [9, 10]. Antioxidative systems are also involved in heavy metal tolerance.

Photo oxidative stress or photo inhibition: Light stress is one of the important environmental constraints that limit the efficiency of photosynthesis and plant productivity (Yavari *et al.* 2021) [46]. Excessive excitation of chlorophylls can result in the formation of singlet oxygen ($^1O_2$). Injury caused by singlet oxygen derived from over excitation of chlorophyll is referred to as photo inhibition. The high turnover rate of D_1 protein of photosystem II shows its constant exposure to photo inhibitory damage. High energy triplet state of chlorophyll molecule is also a cause of free radical injury to membrane lipids. Carotenoids function as quenchers of chlorophyll photo sensitization by accepting excitation energy from chlorophyll. Excess excitation energy is also dissipated as heat through the xanthophyll cycle by non-photochemical quenching (Jones *et al.* 2013) [20].

Biotic Stress: Biotic stress causes damage to plants via living organisms, including fungi, bacteria and insects. Fungi cause more diseases in plants than any other biotic stress factor. More than 8,000 fungal species are known to cause plant diseases, while only about 14 bacterial genera cause various diseases in plants. Viruses also cause biotic stress to plants. Not many plant pathogenic viruses exist, but they are serious enough to cause nearly as much crop damage worldwide as fungi (Hopkins and Huner 2008) [18]. Microorganisms can cause plant wilt, leaf spots, root rot, or seed damage. Insects can cause severe physical damage to plants, including leaves, stem, bark and flowers. Insects can also act as a vector of viruses and bacteria from infected plants to healthy plants.

Plants use antimicrobial secondary metabolites as constitutive defenses against disease-causing microorganisms. When the plants detect invading pathogens, they induce additional defense mechanisms like the hypersensitive response, strengthening of the cell wall and synthesis of pathogenesis-related proteins such as chitinases, nucleases and proteases. Most plants have a range of local and systemic stress responses that are invoked by herbivory, predation and wounding; many of these reactions have features in common with abiotic stress responses, such as reactive oxygen species (ROS) production and accumulation of phenolics, tannins and phytoalexins.

Mitigation of stress through phytohormones: To overcome the yield losses due to abiotic stress, plants need to possess mechanisms of avoidance and tolerance to stress. Growth hormones, including abscisic acid and gibberellic acid play an important role in plant responses to biotic and abiotic stress (Lee and Park 2010) [23]. Seed priming with the phytohormones is an effective approach to mitigate the abiotic stress in plants (Rhaman *et al.* 2021) [34]. Some reports indicate that exogenous application of ABA confers heat tolerance in crops. ABA may impart thermotolerance by raising the levels of other molecules like nitric oxide (NO) (Ding *et al.* 2010) [8]. Salicylic acid (SA) is also closely related with abiotic stress responses as well as plant responses to pathogen infection. SA has been reported to induce stress tolerance and improve plant growth under salt and osmotic stress (Krantev *et al.* 2006) [22]. SA has been identified as a signaling component in numerous plant responses to stress, including UV-B, exposure to ozone and pathogen attack. SA is also involved in activation of the stress induced antioxidant system when plants are exposed to stress. Accumulation of polyamines, and particularly putrescine is stimulated in response to potassium deficiency, osmotic stress, low pH, nutrient deficiency or light. Putrescine accumulation during environmental stress is correlated with increased arginine decarboxylase (ADC) or ornithine decarboxylase (ODC) activity (Minocha *et al.* 2014) [26]. Jasmonic acid (JA) is also known to promote thermotolerance in various crops (Chen *et al.* 2006) [6].

Molecular approaches: Plant adaptation to environmental stress is controlled by a cascade of molecular networks. The application of genomic technologies has made remarkable success in understanding abiotic stress tolerance at genome level with potential to modify plants' tolerance for increasing yield under stressful conditions (Bohnert *et al.* 2006) [5]. In contrast to traditional breeding and marker-assisted selection programs, the direct introduction of a small number of genes by genetic engineering has proved to be a rapid approach to improve plant stress tolerance. The list of genes whose transcription is upregulated in response to stress is rapidly increasing. Functions for some of these polypeptides are close to being identified and their likely role in stress physiology is being determined. The understanding of mechanisms that regulate gene expression and the ability to transfer genes from other organisms into plants will expand the way in which plants can be utilized. The exploitation of cloned genes to alter the function of gene products in transgenic plants provides novel opportunities to assess their biological role in a stress response (Joseph and Jini 2011) [21]. The molecular analysis of stress responses has arrived at a stage where research can build upon a large collection of characterized genes. Identification of quantitative trait loci for abiotic stress resistance may well be an effective analytical tool. This approach is promising, considering that saturated DNA marker maps are now available for both genetic model plants and crop plants. The use of novel approaches combining genetic, physiological and molecular techniques should provide excellent results in the near future.

Cross-Tolerance between Abiotic and Biotic Stress: Many stress combinations lead to phenotypic damage and the expression of defense is affected according to the type of abiotic stress and the pathogens involved. Overall, the complex response of the plant stems from the interplay of specific signaling pathways involved in abiotic and biotic stress. The combination of both types of stress leads to an increased accumulation of a large number of signaling compounds that, in an ideal case, will be expressed as cross-tolerance. Plants perceive the information signal of each stress and consequently activate specific molecules. Only some of them, which are common to both stressors, will participate in the defense response to the specific stress combination and thus contribute to protect the plant and enhance its resistance (Atkinson *et al.* 2013) [3]. Various novel approaches can help plants to resist combinatorial stress. The 'Omics' technology is one of these approaches. Transcriptomics, proteomics and metabolomics have revealed plant responses under stress, their underlying mechanisms and these point to potential target genes, proteins or metabolites for inducing tolerance thereby improving plant responses. Recent reports indicate the use of 'Omics' for characterization of abiotic and biotic stress combinations (Suzuki *et al.* 2014) [39]. Although complete genome sequences are available for an increasing number of crop and model plants, in comparison, protein and metabolite databases are still incomplete, hence complicating the task of integrating all the observations. Additionally, different plant species or even cultivars may behave differently, plant responses are often organ-dependent, and results obtained with whole plants may be misleading. Another approach consists of molecular engineering of specific genes and their introduction into crop plants. The resistance of potato to biotic and abiotic stress was increased by modifying a gene coding for a small antimicrobial peptide and introducing into it (Goyal *et al.* 2013) [12]. The manipulation of common regulators is also a promising approach. Boosting the accumulation of flavonoid biosynthesis mitigates the negative effects of abiotic and biotic stress (Nakabayashi *et al.* 2014) [30]. Polyamines have long been known to mediate resistance to pathogens but they are also involved in abiotic stress resistance. Genetic manipulation of polyamine accumulation could lead to multi stress tolerance (Hussain *et al.* 2011) [19]. A further possibility to promote cross-tolerance is the exploitation of priming. Some chemicals (like SA and JA) have been shown to prime plants for both biotic and abiotic stress under laboratory conditions (Conarth *et al.* 2006) [7], and their application might allow a better management of multiple stress under field conditions.

Conclusion

Stress caused by biotic and abiotic factors alter plant metabolism leading to negative effects on growth, development and productivity of plants. If the stress becomes harsh or continues for a longer period, it may lead to unbearable metabolic burden on cells leading to reduced growth and in extreme cases even to plant death. To combat these stress, plants exhibit several mechanisms which make them withstand it with the formation of new molecules and various mechanisms. Additionally, a combination of abiotic and biotic stress caused a positive effect on plant performance by reducing the susceptibility to biotic stress. Such an interaction between both types of stress points to a crosstalk between their respective signaling pathways. The ultimate goal in every case is to maintain or even enhance plant performance, yield and productivity under adverse conditions. Moreover, the effects of abiotic stress are likely to get intensified due to climate change so adaptation and mitigation strategies need to be managed efficiently in order to counter their adverse effects.

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