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Regulation of Gene Expression in Response to Abiotic Stress in Plants

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1. Introduction

The multiple adverse conditions but not necessarily lethal, that occur sporadically as either permanently in a location that plants grow are known as "stress." Stress is usually defined as an external factor that carries a disadvantageous influence on the plant, limiting their development and their chances of survival. The concept of stress is intimately related to stress tolerance, which is the plant's ability to confront an unfavorable environment. Stress is, in most definitions, considered as a significant deviation from the optimal conditions for life, and induces to changes and responses in all functional levels of the organism, which are reversible in principle, but may become permanent.

The dynamics of stress include loss of stability, a destructive component, as well as the promotion of resistance and recovery. According to the dynamic concept of stress, the organism under stress through a series of characteristic phases. *Alarm phase:* the start of the disturbance, which is followed by loss of stability of structures and functions that maintain the vital activities. A very rapid intensification of the stressor results in an acute collapse of cellular integrity, before defensive measures become effective. The alarm phase begins with a stress reaction in which the catabolism predominates over anabolism. If the intensity of the stressor does not change the restitution in the form of repair processes such as protein synthesis or synthesis of protective substances, will be quickly initiated. This situation leads to a *resistance phase*, in which, under continuous stress, the resistance increases (hardening). Due to the improved stability, normalization occurs even under continuous stress (adaptation). The resistance may remain high for some time after the disturbance occurred. If the state of stress is too lengthy or if the intensity of the stress factor increases, a state of exhaustion can occur at the *final stage*, leaving the plant susceptible to infections that occur as a consequence of reduced host defenses and leading to premature collapse or still a chronic damage may occur, leading to plant death. However, if the action of the stressor is only temporary, functional status is restored to its original level. If necessary, any injury caused can be repaired during the restitution (Larcher, 1995).

The characteristics of the state of stress are manifestations nonspecific, which represent firstly an expression of the severity of a disturbance. A process can be considered nonspecific if it can not be characterized as a pattern, whatever the nature of the stressor.

Examples of non-specific indications of the state of stress are: increased respiration, inhibition of photosynthesis, reduction in dry matter production, growth disorders, low fertility, premature senescence, leaf chlorosis, anatomical alterations and decreased intracellular energy availability or increased energy consumption due to repair synthesis. The cell responses to stress include changes in cell cycle and division, changes in the system of vacuolization, and changes in cell wall architecture. All this contributes to accentuate tolerance of cells to stress. Biochemically, plants alter metabolism in several manners, to accommodate environmental stress (Hirt & Shinozaki, 2004).

Currently, all plant life is being threatened by rapid environmental changes. The gases associates to global warming as CO_2 and methane have a enormous impact on global environmental conditions, resulting in extreme changes in temperatures and weather patterns in many regions of the world (Hirt & Shinozaki, 2004). In contrast to animals, plants are sessile organisms and can not escape from environmental changes. The greenhouse effect also affects the ozone layer causing the levels of ultraviolet (UV) are much larger to reach the ground (Hirt & Shinozaki, 2004). Besides resulting in an increase in the registers of the occurrence of diseases in humans such as skin cancer. The greenhouse effect also affects the ozone layer causing the levels of ultraviolet (UV) are much larger to reach the ground. Another concern is the intense use of chemical fertilizers and artificial irrigation in agriculture. In many areas of the world, these practices have increased soil salinity. Under these conditions, resistance to abiotic stress corresponds to a more required to be found in several plant species (Hirt & Shinozaki, 2004). In short, the factors discussed above, together with the increasing use of agricultural land cultivated is one of the biggest challenges for the future humanity with regard to agriculture and conservation of genetic diversity in plant species.

2. Water stress

Water has a key role in all physiological processes of plants, comprising between 80 and 95% of the biomass of herbaceous plants. If water becomes insufficient to meet the needs of a particular plant, this will present a water deficit. The water deficit or drought is not caused only by lack of water but also the environment in low temperature or salinity. These different tensions negatively affect plant productivity (Hirt & Shinozaki, 2004).

Plants developed different mechanisms to adapt their growth in conditions where water is limited. These adjustments depend on the severity and duration of drought, as well as the development phase and morphology and anatomy of plants. The cellular response includes the action of solute transporters such as aquaporin, activators of transcription, some enzymes, reactive oxygen species and protective proteins. Two main strategies can be taken to defend the damage caused by dehydration: synthesis of molecules of protection to prevent damage and a repair mechanism based on rehydration in order to neutralize the damage. In the classic signaling pathways, environmental stimuli are captured by receptor molecules (Hirt & Shinozaki, 2004).

The main response that distinguishes tolerant plants of sensitive plants to drought stress is the marked intracellular accumulation of osmotically active solutes in tolerant plants. This mechanism, known as osmotic adjustment, is the ability of many species adjusts their cells by decreasing the osmotic potential and water potential in response to drought or salinity without a decrease in cell turgor.

In plants, dehydration activates a protective response to prevent or repair cell damage. The plant hormone, abscisic acid (ABA) has a central role in this process. The ABA is considered a "stress hormone" because plants respond to environmental challenges such as water and salt stress with changes in the availability of ABA, as well as being an endogenous signal required for adequate development. Dehydration in plants leads to increased levels of ABA, which in turn induces the expression of several genes involved in defense against the effects of water deficit. High levels of ABA cause complete closure of stomata and alteration of gene expression. Stomatal closure reduces water loss through transpiration (Hirt & Shinozaki, 2004). The ABA signaling is composed of multiple cellular events, including the regulation of turgor and differential gene expression.

Plants have developed several mechanisms to adapt their growth to the availability of water. The movement of water molecules is determined by water potential gradient across the plasma membrane, which in turn is influenced by the concentration of solute molecules inside and outside the plant cell. Fluctuations in water availability and flows of transmembrane extracellular solute disrupt cellular structures, altering the composition of the cytoplasm and modulate cell function (Hirt & Shinozaki, 2004).

One effect of the signal transduction cascade of dehydration is the activation of transcription factors, which each activates a set of target genes, including those necessary for the synthesis of protective molecules. Transcription factors that are activated by dehydration are differentially expressed in tissues. Dehydration causes high level of expression of many genes, among which the most prominent are the so called late embryogenesis abundant genes (LEA) (Hirt & Shinozaki, 2004). The last step in the signaling cascade in response to dehydration is the activation of genes responsible for synthesis of compounds that serve to protect cellular structures against the deleterious effects of dehydration. Plants that are able to survive in drought conditions have taken a variety of different strategies. There are three important mechanisms to allow the plants to resist dehydration: the accumulation of solutes, elimination of reactive oxygen species and synthesis of proteins with protective functions (Hirt & Shinozaki, 2004).

In many species, dehydration leads to the accumulation of a variety of compatible solutes. Compatible solutes are soluble molecules of low molecular weight that are not toxic and do not interfere with cellular metabolism. The chemical nature of solutes differ among plant species. They include betaines, including glycine betaine, amino acids (especially proline) and sugars such as mannitol, sorbitol, sucrose or trehalose. These compounds help to maintain turgor during dehydration, increasing the number of particles in solution. Furthermore, can modulate membrane fluidity and protein by keeping it hydrated, allowing the stabilization of its structure (Hoekstra et al., 2001).

One consequence of dehydration is an increase in the concentration of reactive oxygen intermediates (ROI) (Mittler, 2002). ROI cause irreversible damage to membranes, proteins, DNA and RNA. However, a low concentration of ROI is vital to the plant cells, they are essential components in defense signaling to stress. When the ROI concentration increases because of dehydration, prevention of damage to competitors is essential for survival. The accumulation of ROI is largely controlled by intrinsic antioxidant systems that include the enzymatic action of superoxide dismutase, peroxidases and catalases.

The analysis of differential gene expression and analysis of global patterns of gene expression using macro and microarray approaches have identified a broad spectrum of transcripts whose expression is modified in response to dehydration (Fowler & Thomashow, 2002; Kreps et al., 2002; Seki et al., 2002). These studies have provided a fairly comprehensive overview of the types of transcripts modulated by dehydration plant. They showed that at least hundreds of genes are affected by dehydration.

3. Oxidative stress

For plants, as for all aerobic organisms, oxygen is required for normal growth and development, but continuous exposure to oxygen can result in cellular damage and ultimately death. This is because molecular oxygen is continually reduced within cells by various forms of reactive oxygen species (ROS), especially the free radical superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2), which react with many cellular components resulting in acute or chronic damage resulting in cell death (Scandalios, 2002). Oxidative stress results from disequilibrium in the generation and removal of ROS within cells. In plant cells, ROS are generated in large quantities by both constitutive and inducible pathways, but in normal situations, the cellular redox balance is maintained through the action of a great variety of antioxidant mechanisms that evolved to remove ROS.

The calcium ions may also be related to oxidative stress and the antioxidant system in plants. Oxidative stress, many enzymes are involved in the mechanisms of protecting the protoplasm and cell integrity. This defense includes antioxidant enzymes able to remove or neutralize free radicals and intermediate compounds that enable their production. Among these enzymes, highlight the peroxidase (POX), catalase (CAT) and superoxide dismutase (SOD). The mechanisms of elimination of reactive oxygen involving SOD, whose synthesis is induced probably by increased production of O_2^-. In the process, SOD converts O_2^- to hydrogen peroxide (H_2O_2) and then peroxidase and catalase removes hydrogen peroxide formed. Hydrogen peroxide and superoxide radicals can exert deleterious effects in cells, acting on lipid peroxidation of membranes, as well as damaging their DNA.

Several environmental stresses and endogenous stimuli can disrupt the redox balance by increasing ROS production or reduced antioxidant activity, with continued oxidative stress. In response toto increased ROS is induced the expression of genes encoding antioxidant proteins and the genes that encode proteins involved in a variety of cellular processes of rescue. ROS are produced during photosynthesis and respiration, as a byproduct of metabolism, or by specific enzymes. Cells are equipped with a variety of effective antioxidant mechanisms to eliminate ROS. Transcriptome analyses indicate that the expression of many genes is regulated by ROS. These antioxidants include genes that encode the rescue of cell defense proteins and signaling proteins. ROS can lead to programmed cell death, stomatal closure, and gravitropism (Hirt & Shinozaki, 2004).

Oxygen is normally reduced by four electrons to produce water, a reaction catalyzed by cytochrome oxidase complex and the electron transport chain of mitochondria. It is relatively unstable and can be converted back to molecular form of oxygen or H_2O_2, either spontaneously or through a reaction catalyzed by the enzyme superoxide dismutase (SOD). H_2O_2 in particular, acts as a signaling molecule with regulated synthesis, specific effects and presents a series of removal mechanisms (Hirt & Shinozaki, 2004).

The evolution of photosynthesis and aerobic metabolism led to the development of processes of generation of ROS in chloroplasts, mitochondria and peroxisomes. It seems likely that the antioxidant mechanisms have evolved to combat the negative effects of these ROS (Scandalios, 2002). As environmental pressures increase the generation of ROS, would have been the evolutionary pressure for selection of ROS signaling mechanisms inducing genes encoding antioxidant proteins and cellular defense. This role of "defense" of ROS and these proteins may be one reason that leads to induction of cellular defense, where many genes show a common response to various environmental stresses and oxidative stress, allowing for acclimatization and tolerance (Bowler & Fluhr, 2000). Functions of protection against ROS may also have been responsible for the evolution of enzymes such as NADPH oxidase, where the reaction seems to be the key ROS generation, in which the enzyme activity can be regulated by environmental stresses. Thus, abiotic stress not only increases the generation of ROS through non-specific mechanisms, but also trigger the signaling of defense mechanisms that start with the induction of ROS production, continue with the induction of defense responses and end with removal of ROS to restore the redox status and cell survival.

Oxidative stress causes the intracellular environment becomes more electropositive, which may induce a change in the redox environment and thus interfere with signaling pathways. ROS are generated both electron transport and enzymatic sources. The generation of ROS occurs through the process of electron transport in chloroplasts and mitochondria. H_2O_2 is generated by various enzymatic reactions, from specific enzymes such as NADPH oxidase (Hirt & Shinozaki, 2004). Plant cells are rich in antioxidants, where the activity and location of these can affect the concentration of H_2O_2.

Gene expression in response to oxidative stress may be coordinated through the interaction of transcription factors (TF) with cis-elements common to the entity regulatory regions of these genes. Certainly, the increase of ROS in cellular compartments such as mitochondria or chloroplasts results in new profiles of transcription (Hirt & Shinozaki, 2004).

4. Flooding stress

The temporary or continuous flooding of the soil resulting from high rainfall, intensive practice of large-scale irrigation farms or soils with inadequate drainage (Kozlowski, 1997). In normal drainage, the soil contains air-filled pores that contain content similar to oxygen from the atmosphere (20%) (Pezeshki, 1994). Excess water replaces the air in these pores, extremely restricting the flow of oxygen in the soil, creating a condition of hypoxia (low O_2 availability) or, in more severe cases, anoxia (lack of O_2) (Peng et al., 2005). The gas diffusion becomes extremely slow in soils saturated with water, about 10,000 times slower than in air (Armstrong, 1979).

Under natural conditions, the flooding changes numerous physical and chemical properties of soil through processes of biological reduction, resulting from depletion of available oxygen (O_2), increasing the availability of P, Mn and Fe, and decreased availability of Zn and Cu and the formation of hydrogen sulfide and organic acids (Camargo et al., 1999). This soil is also characterized by accumulating a larger amount of CO_2 (Jackson, 2004) and stimulate organic matter decomposition (Kozlowski, 1997; Pezeshki, 2001; Probert & Keating, 2000). The phytotoxic compounds that accumulate in flooded soils can be produced

both by plant roots (ethanol and acetaldehyde) and the metabolism of anaerobic microorganisms (methane, ethane, unsaturated acids, aldehydes, ketones), and ethylene may be produced by by plants and microorganisms (Kozlowski, 1997).

Flooding can devastate vegetation species poorly adapted to this kind of stress (Jackson, 2004). The stress tolerance of hypoxia or anoxia can vary in hours, days or weeks depending on the species, the organs directly affected the stage of development and external conditions (Vartapetian & Jackson, 1997). The duration and severity of flooding may be influenced not only by the rate of influx of water, but also by the rate of water flow around the root zone and the absorption capacity of soil water (Jackson, 2004).

One major effect of flooding is the privation of O_2 in the root zone, attributed to the slow gas diffusion in soil saturated with water and O_2 consumption by microorganisms (Folzer et al., 2005). Higher plants are aerobic and O_2 supplies depend on the environment to support respiration and several other reactions of oxidation and oxygenation of vital (Vartapetian & Jackson, 1997). The O_2 as participate of aerobic respiration final electron acceptor in oxidative phosphorylation, generation of ATP and regeneration of NAD^+, and in several crucial biosynthetic pathways as the synthesis of chlorophyll, fatty acids and sterols (Dennis et al., 2000). Under hypoxia, glycolysis and fermentation can exceed the aerobic metabolism and become the only way to produce energy (Sousa & Sodek, 2002). The main products of fermentation in plant tissues are lactate, ethanol and alanine derived from pyruvate, the end product of glycolysis (Drew, 1997). Evidence suggests that cytosolic acidosis causes lactic fermentation and therefore the maintenance of cytosolic pH is important for the survival of plants under waterlogged conditions (Dennis et al., 2000).

The initial responses of many plants to flooding correspond to wilt and to stomatal closure, starting from one or two days of exposure of roots to this stress, accompanied by decreases in photosynthetic rate (Chen et al., 2002). These changes promote a decline in growth of stems and roots and can damage the roots and death of many species of plants (Kozlowski, 1997). The saturation of the soil causes significant decreases in total plant biomass and biomass allocation to roots and changes in biomass allocation pattern in many woody species and herbaceous (Pezeshki, 2001; Rubio et al., 1995).

The plant damage induced by hypoxia, have been attributed to physiological dysfunction, which include the change in the relationship between carbohydrates, minerals, water and hormones, as well as the reduction or alteration of several metabolic pathways (Kennedy et al., 1992). Initially, the plant under stress by hypoxia shows decreases in the rate of CO_2 uptake by leaves (Kozlowski, 1997). Some authors suggest that stomatal closure may be associated with a decrease in hydraulic conductivity of roots (Davies & Flore, 1986; Kozlowski, 1997), as well as the transmission of hormonal signals from roots to shoots. Among the hormones involved in signal transmission are the ABA and cytokinin (Else et al., 1996). During stages of prolonged flooding, the progressive decrease in photosynthetic rate is attributed to changes in enzyme carboxyl groups and loss of chlorophyll (Drew, 1997; Kozlowski, 1997). The decrease in activity of ribulose -1,5-bisphosphate carboxylase-oxygenase (RUBISCO), the enzyme responsible for assimilation of CO_2 in the biochemical phase of photosynthesis, contributing to losses in photosynthetic capacity (Pezeshki, 1994).

It is known that water temperature, light, O_2 and nutrient availability are the main abiotic factors that control the growth of woody plants (Kozlowski, 1997). The excess or shortage of

any of these factors, such as water, causes significant deviations in the optimum conditions for growth for a given species, generating a stress condition. Such a condition, depending on the level of specialization of the organism, the amplitude and duration of stress, may be reversible or become permanent (Lichtenthaler, 1996). Excess water in the root zone of terrestrial plants may be injurious or even lethal because it blocks the transfer of O_2 and other gases between soil and atmosphere (Drew, 1997). The responses of plants to flooding vary according to several factors, among which may include the species, genotype and age of the plant, the properties of water and duration of flooding (Kozlowski, 1997).

Plant growth and primary productivity of ecosystems are ultimately dependent on photosynthesis (Pereira et al., 2001). Either environmental stressor that, somehow, can interfere with the photosynthetic rate, will affect the net gain of dry matter and, therefore, growth (Pereira, 1995). Growth and development of most vascular plant species are restricted by flooding, particularly when they are completely submerged and may result in death (Jackson & Colmer, 2005). Generally, waterlogged soils affect the growth of aerial part of many woody species, suppressing the formation of new leaves, retarding the expansion of leaves and internodes that formed before flooding and reduce growth of stem diameter of species not tolerant to flooding, causing senescence and premature leaf abscission (Kozlowski, 1997). The plant response to flooding during the growing phase, including injury, inhibiting seed germination, of vegetative and reproductive growth and changes in plant anatomy (Kozlowski, 1997).

Morphological changes, such as the formation of hypertrophied lenticels, aerenchyma and adventitious roots, observed during O_2 deficiency in the soil are key to increasing the availability of O_2 in the tissues of plants. The lenticels participate in the uptake and diffusion of O_2 to the root system and the liberation of potentially toxic volatile products such as ethanol, acetaldehyde and ethylene (Medri, 1998). The best strategy of flooding tolerance is the supply of internal aeration, increased with the formation of hypertrophied lenticels, which are the main points of entry of O_2 in the plants, associated with the appearance of intercellular air spaces (White & Ganf, 2002). According Topa & McLeod (1986), the increase of these air spaces allows for an efficient entry of O_2 causing the lenticels assume the role of gas exchange in hypoxic conditions. The formation of hypertrophic lenticels occurs in submerged portions of stems and roots of various woody angiosperms and gymnosperms (Kozlowski, 1997), and involves both increased activity felogênica as the elongation of cortical cells (Klok et al., 2002). In addition, participating in the uptake and diffusion of O_2 to the root system and release potentially toxic volatile products such as ethanol, acetaldehyde and ethylene (Medri, 1998).

It can be observed the formation of aerenchyma in stems and roots of aquatic species tolerant to flooding, which usually occurs by cell separation during development (esquizogeny) or by lysis of cortical cells and cell death (lysogeny) (He et al., 1994; Drew, 1997). The point of view adaptive aerenchyma provides a low resistance to diffusion of air inside the submerged tissue, promoting survival of plants to flooding (Drew, 1997). The formation of aerenchyma, recorded during the stress by O_2 deficiency in soil is associated with the accumulation of ethylene. Roots under flooded soil containing high concentrations of ethylene, compared with roots in normal, and its precursor (acid-1-aminocyclopropane-1-carboxylic acid - ACC), and high activity of ACC synthase and ACC oxidase (He et al., 1994; He et al., 1996). Ethylene induces the activity of different enzymes such as cellulases, and

hydrolases xyloglucanases, enzymes, cell wall loosening related to the formation of aerenchyma (He et al., 1994; Drew, 1997).

In the submerged portion of the plant there is a dead roots and the production of adventitious roots on the root system portions of the original stem. These roots induced by flooding, are usually thickened and exhibit more intercellular spaces of the roots growing in well drained soils (Hook et al., 1971). The induction of adventitious roots has been reported in a wide variety of plant species tolerant and non-tolerant, but usually occurs in species tolerant to flooding (Kozlowski & Pallardy, 1997). According Kozlowski (1997), the adventitious roots are produced from the original roots and submerged portions of stems. According to the author in terms of flooding the induction of adventitious root formation can be reported in both angiosperms and gymnosperms in tolerant and non tolerant to this type of stress (Kozlowski, 1997). For Chen et al. (2002), the adventitious roots are important in plants with high root hypoxia, since they are responsible for obtaining O_2 needed for their development. The increased number of adventitious roots can be accompanied by an increment of damage and death of the original roots (Chen et al., 2002). Among the root adaptations to flooding can also cite the development of aerenchyma, induced by increasing endogenous levels of ethylene (Mckersie, 2001). This tissue serves as an air transport system in aquatic plants and can develop into plants that grow in hydromorphic soils. The intercellular spaces are developed primarily by disintegration of cells due to an increase in cellulase activity, or by increasing the intercellular spaces when there is lack of O_2 and hence increase in ethylene production (Fahn, 1982). In some plants, such stress induces abnormal formation of the wood and increase the proportion of parenchymatous tissues of xylem and phloem (Kozlowski, 1997).

Flooding can also cause a decline in the growth of petioles and leaf stomatal conductance (Domingo et al., 2002). Moreover, the saturation of the soil (i) interfere in the allocation of photoassimilates in woody and herbaceous plants, root can decrease metabolism and oxygen demand (Chen et al., 2002); (ii) inhibits the initiation of flower buds and the increase in fruit species not tolerant to flooding; (iii) induces abscission of flowers and fruits; (iv) reduces the quality of fruits due to the reduction of size, changing its appearance and interfering in its chemical composition (Kozlowski, 1997).

Other responses of plants to flooding include: (i) decreased permeability of the root and the absorption of water and mineral nutrients, the death and suppression of root metabolism; (ii) the epinasty, leaf chlorosis and necrosis, and (iii) decrease in fruit production. On the other hand, several morpho-physiological responses are driven by differential expression of a large number of genes induced by conditions of hypoxia or anoxia (Vartapetian & Jackson, 1997; Kozlowski, 1997; Holmberg & Büllow, 1998; Vantoai et al., 1994; Klok et al., 2002).

The decreased availability of O_2 also affects different processes of plant genetics (Blom & Voesenek, 1996; Kozlowski, 2002; Drew, 1997). Saab & Sachs (1995) observed in maize under conditions of flooding, the 1005 induction of the gene that encodes a homologue of the xyloglucan endotransglicosilase (x and t), an enzyme potentially involved in cell wall loosening (Peschke & Sachs, 1994). This gene, which is among the first to be induced by flooding, does not encode enzymes of glucose metabolism. Believed to be associated with the onset of the structural changes induced by flooding (Saab & Sachs 1995), because the substrate of XET and t are the xyloglucans that are part of the cell wall structure. Saab &

Sachs (1996) found that gene induction in regions of primary root and mesocotyl exhibiting signs of development of aerenchyma in flooded soil, suggesting an association between this enzyme and the structural changes induced by this type of stress.

The plants survive under conditions of anoxia, replacing the aerobic metabolism by anaerobic (Drew, 1997). However, before the metabolic adjustments are made, the stress can be perceived and signaled to induce the appropriate cellular and molecular responses (Dat et al., 2004). Studies on plants under conditions of O_2 deficiency in the soil have focused the role of calcium (Ca^{2+}) as a marker (Subbaiah et al. 1998; Subbaiah et al., 2000). Molecular processes are modulated by Ca^{2+} via high-affinity proteins such as calmodulin (CaM) and its isoforms in plants (Zielinski, 1998). The complex active Ca^{2+}-CaM can regulate the activity of many target molecules associated with plant responses to stress (Snedden & Fromm, 2001). Many CaM have been identified in herbaceous plants, but for woody plants have been little information. Folzer et al. (2005) were the first to identify a family of CaM in woody plant, *Quercus petraco* Liebl., demonstrating that the isolated isoforms exhibit organ-specific distribution and differential expression in the plant when the plant is subjected to flooding of the soil, suggesting that each isoform plays a role and specific activation or modulation of target enzymes directly associated with the stress response (Subbaiah et al., 2000).

Changes in gene expression in plants, induced by lack of O_2 in the soil, levels occur in transcriptional, translational and post-translational (Sachs et al., 1980). These changes result in immediate suppression of protein synthesis pre-existing, with simultaneous selective synthesis of transition of polypeptides (TPs, 33 kDa) and, after prolonged exposure to this condition of the plant, selective synthesis of anaerobic proteins (ANPs) (Sachs et al., 1980). The ANPs have been extensively studied, among which the enzymes are involved in sucrose consumption, glycolysis and fermentation in ethanol, lactate and alanine (Drew, 1997; Vartapetian & Jackson, 1997; Dennis et al., 2000). On the other hand, little is known about the genes or TPs rapid induction (1-2 h of anoxia). According to Dennis et al. (2000), the first stage (0-4 h) of the responses of plants to O_2 deficiency was the rapid induction or activation of markers of transduction components that promote the second stage (4-24 h) metabolic and structural adaptations, including the induction of genes required to maintain a continuous production of energy. In the third stage (24-48 h), critical to the survival of O_2 tension, there is the formation of aerenchyma in the roots; genes activated by the stage 1 and or 2 and accumulation of the hormone ethylene (Drew, 1997). Thus the TPs are associated with the initial signal, which would allow the plant to survive anoxia.

Flooding decreases the absorption of N, P and K and, in some species, this type of stress alters the partition of carbohydrates for the production of xylem cells and the cell wall thickening (Kozlowski, 1997). The decrease of macronutrients and decrease of nutrients found in the leaves of plants not tolerant to flooding can be attributed to mortality of roots, decrease of mycorrhizae, root metabolism, transpiration and water conductivity (Domingo et al., 2002). The mechanisms presented by plants tolerant to water stress over which survive periods of flooding are complex (Pezeshki, 2001).

The physical properties of water affect the leaf gas exchange when soils are submerged in water (Vartapetian & Jackson). The primary adaptation of plants to flooding of the substrate is the ability to absorb air O_2 into tissues, increasing its concentration in these tissues and favor the formation of hypertrophic lenticels, aerenchyma and adventitious roots

(Kozlowski, 1997). The transport of O_2 is necessary for the maintenance of aerobic respiration mainly in roots that are under hypoxia or anoxia (Pezeshki, 2001).

Under stress conditions, if the carbon assimilation is dependent on stomatal closure, the internal concentration of CO_2 in the leaf (Ci) may be low, resulting in limitations of photosynthetic activity (Ashraf, 2003). In a relatively long period of time, the non-stomatal limitations of photosynthesis are strongly associated with changes in the Calvin cycle enzymes and degradation of photosynthetic pigments, which, in turn, are directly related to the decrease in efficiency carboxylic acid and the quantum yield apparent photosynthesis (α) of plants under flooding (Pezeshki, 1994). In addition, the flooding stress promotes the reduction of plant transpiration rates, resulting from changes in stomatal conductance, because in this situation, the route may be of little use apoplastic hydraulic resistance and hence increased (Steudle & Peterson, 1998; Jones, 1998).

5. Salt stress

Soil salinity is a major abiotic stress that adversely affects crop productivity. The saline soil is characterized by toxic levels of chlorides and sulphates of sodium. The problem of soil salinity is enhanced by irrigation, improper drainage, sea water in coastal areas, and the accumulation of salt in arid and semi-arid. Considerable efforts have been invested to unravel the mechanisms of salt tolerance in plants. The success of breeding programs aimed at improving crop productivity is limited by lack of understanding of the molecular basis of salt tolerance (Hirt & Shinozaki, 2004). Excessive soil salinity could slow the differentiation of primary xylem and secondary xylem development. The salt stress can also bring down the rate of multiplication and cell elongation, limiting the length of the leaf and, consequently, plant growth.

Sodium (Na) is an essential micronutrient for some plants, but most crops are sensitive to this element. The salinity is detrimental to plant growth because it causes nutritional restrictions, reducing the absorption of phosphorus, potassium nitrate and calcium, increases the cytotoxicity of ions and results in an osmotic stress. Under salinity, excess Na + ions, these interfere with the function of protein hydration. The ionic toxicity, osmotic stress and nutritional problems under conditions of salinity can lead to tolerance mechanisms to salt, which can be grouped into: (i) cellular homeostasis (including ion homeostasis and osmotic adjustment), (ii) control of damage caused by stress (repair and detoxification), (iii) metabolic imbalances, which result in oxidative stress (Zhu, 2001b) and (iv) growth regulation. The cellular ionic homeostasis under salinity is achieved through the following strategies: (i) exclusion of Na^+ cell plasma membrane, (ii) use of Na^+ for osmotic adjustment to the partitioning of Na^+ in the vacuole. Thus, regulation of ion transport systems is essential for plant tolerance to salt. The cytoplasmic ion homeostasis, by excluding Na + from the excess cytoplasm may require the plant to synthesize compatible osmolytes to reduce the osmotic potential, which is necessary for the absorption of water under saline stress (Hirt & Shinozaki, 2004).

Excess Na^+ and Cl^- can lead to conformational changes in the structure of proteins and/or changes in the electrical potential of the plasma membrane, while the osmotic stress leads to loss of turgor and cell volume changes. Thus, the excess of ions (Na^+ and Cl^-) and osmotic stress induce changes in turgor can act as inputs to salt stress signaling. The loss of turgor

caused by osmotic stress leads to the synthesis and accumulation of ABA, which in turn regulates part of the cellular response to osmotic stress under salinity. ABA regulates the water balance of the cell by regulating stomatal and genes involved in biosynthesis of osmolytes as conferring tolerance to dehydration through LEA genes (Zhu, 2002).

Under high Na^+ concentration, it can enter cells through non-specific ion channels, causing membrane depolarization. A change in the polarization of the membrane can also indicate salt stress, known to activate Ca^{2+} channels (Sanders et al., 1999). The loss of turgor leads to a change in cell volume and retraction of the plasma membrane of the cell wall. Sodium is essential for a few C4 plants that import of pyruvate by mesophyll chloroplasts of the cotransporter Na^+/pyruvate.

Cytosolic Ca^{2+} oscillations occur within 50-10 seconds of salt stress. The three major families of proteins sensitive to signs of Ca^{2+} in plants are (Harmon et al. 2000): (i) calmodulin (CAM), which have no enzymatic activity, but they do signal transduction for protein interaction CAM, (ii) calcium dependent protein kinases (CDPKs), and (iii) SOS3 and SOS3 proteins with affinity for calcium (SCaBPs) (Guo et al 2001). Genes involved in the biosynthesis of osmoprotetores are regulated under drought and salt stress (Zhu 2002). The cytosolic signals induced by stress caused by excess calcium are perceived by the calcium-sensing protein, SOS3. The SOS3 activates SOS2, a protein kinase to be/thr. Salinity induces the biosynthesis and accumulation of the stress hormone in plants, the ABA (Jia et al 2002) and also induces accumulation of ROS (Hernandez et al., 2001). The ROS-mediated signaling under salt stress, occurs through the mitogen-activated protein kinases (MAPKs) (Pei et al. 2000).

The salt stress induces a decrease in the ratio of K^+/Na^+, and thus an enemy of cellular biochemical processes. In addition, the K^+ provides osmotic potential required for water uptake by plant cells. Thus, the K^+ uptake is crucial for maintaining cell turgor and the biochemical processes under salinity. In plants, Na^+ competes with K^+ uptake under salinity conditions (Hirt & Shinozaki, 2004).

6. Cold stress

One of the most severe environmental challenges for plants is the low temperature. The photoinhibition induced by low temperature process is completely reversible and may represent a strategy for protecting the damage caused by light energy absorbed and not used. When the photoinhibition is reversible, it can be considered as a protective and regulatory process. The photoinhibition is more pronounced at low temperatures.

The initial signaling events in response to cold hardening include changes in the membrane and cytoskeleton of cells, which is followed by increased levels of extra-and intracellular Ca^{2+-} and activation of protein kinase cascades, leading to the activation of transcription factors.

Different plant species vary greatly as to the ability to tolerate cold stress. The low temperature not only affects plant growth and distribution, but also causes serious damage to many plants. Tropical species sensitive to this kind of stress can be damaged even at temperatures significantly higher than the freezing temperature of the tissues. Injuries are caused by a deficiency of metabolic processes, changes in membrane properties, changes in

protein structure and interactions of macromolecules as well as inhibition of enzymatic reactions. Tolerant plants are able to survive freezing at temperatures slightly below zero, but are severely damaged after ice formation in tissues. On the other hand, frost-tolerant plants are able to survive to varying levels of low temperatures; the actual degree of cold tolerance depends on species, developmental stage and duration of stress.

The exposure of plants to temperatures below freezing results in formation of extracellular ice, water loss and cellular dehydration. Therefore, the cold tolerance is strongly correlated with tolerance to dehydration (eg, caused by drought or high salinity). The dehydration freezing-induced can cause various disturbances in membrane structure. Although the cellular dehydration induced by freezing is the central cause of the damage caused by such stress, additional factors also contribute to damage to the plants. The growth of ice crystals can cause mechanical damage to cells and tissues and low temperatures can cause dehydration, protein denaturation and disruption of macromolecular complexes. Common responses in various types of stress are the production of reactive oxygen species (ROS), which can cause damage to different macromolecules in cells. Low temperatures can cause excessive production of ROS and therefore tolerance to cold also correlates with effective systems for elimination of ROS in response to oxidative stress (Hirt & Shinozaki, 2004).

Temperate plants respond to low temperature, turning a cold acclimation that confers tolerance to freezing temperatures. This acclimation process is accompanied by changes in expression of several genes in response to stress as well as in controlling the synthesis of proteins and metabolites that protect cellular structures from the adverse effects of freezing and cold-induced cellular dehydration. Changes in gene expression in response to cold are controlled by a set of transcription factors responsive to stimuli of low temperature (Hirt & Shinozaki, 2004). Changes in temperature can induce a signal transduction cascade by activating the expression of target genes in response to cold. In plants, CBF1 is a transcriptional regulator for cold-responsive genes. One of the major classes of plasma membrane receptors consists of the receptor protein kinases. The plasma membrane fluidity is directly affected by changes in temperature and therefore may be involved in detecting low temperature (Hirt & Shinozaki, 2004).

In winter the acclimation process in woody plants usually occurs in two steps. Initially, the reduction of the photoperiod occur for a critical value there is a pause in growth, development of dormancy and leads to a moderate increase in freezing tolerance. The second phase of acclimation is triggered by a subsequent exposure to low temperatures (Hirt & Shinozaki, 2004).

The extreme cold leads to an acclimation response that requires the synergistic action of two factors. The perception of the photoperiod, presumably involves the phytochrome A (Phya) (Olsen et al., 1999), which is the critical component for acclimatization (Li et al., 2003). In many annual and herbaceous plants in winter, the temperature is the only one capable of unleashing the full acclimatization, regardless of photoperiod. However, recent studies have indicated that phytochrome-mediated processes may also have an important role in the process of acclimation in herbaceous plants (Kim et al., 2002). Furthermore, photosynthesis is controlled by acclimation, because this process requires energy supplied by photosynthesis (Wanner & Junttila, 1999). The close association with other stress freezing results in water deficit, such as drought or high salinity. There is a temporary increase in the

level of ABA during cold acclimation. This hormone in the acclimation process, by applying in plants leads to an increased tolerance to freezing.

Cold adaptation is a polygenic characteristic controlled by several genes. The control of expression of these genes leads to a series of physiological, cellular and molecular changes, including changes in membrane lipid composition, accumulation of compatible solutes, changes in levels of hormones and antioxidants, and synthesis of new proteins (Xin & Browse, 2000). Genes expressed in response to cold are divided into two distinct main categories: (i) genes that encode enzymes or structural components of cells and believed to be involved in the direct protection of cells against damage caused by freezing (Thomashow, 1999) and (ii) genes that encode transcription factors and other regulatory proteins, it is believed that regulate the responses to low temperatures, or transcriptionally postranscriptionally (Viswanathan & Zhu, 2002). The cold response genes appear to exhibit a complex temporal pattern of expression controls involving both transcriptional and post-transcriptional (Hughes & Dunn, 1996). The cold response genes appear to exhibit a complex temporal pattern of expression controls involving both transcriptional and post-transcriptional (Zhu, 2001a). The genes that encode transcription factors, such as CBF, DREB, ABF, AREB, are involved in gene regulation in response to cold. The activity of these TFs is modulated by cold temperatures. Temperature variations can be recognized in any part of cell, but the cellular components that are most directly affected by changes in temperature are the membranes and proteins.

Calcium is also acting as a second messenger in signal transduction in response to cold. A transient increase in levels of cytosolic Ca^{2+} has been shown in response to cold. The levels of $Ca2^{+-}$ Cytosolic change in response to a variety of different stimuli than the cold, such as light, growth regulators, wind and touch (Gilroy & Trewavas, 1994).

7. Heat stress

Response to heat stress occurs in organisms as diverse as bacteria, fungi, plants and animals, and is characterized by the sudden increase in body temperature and the synthesis of a set of proteins called heat shock proteins (HSPs). HSPs include several families of evolutionarily conserved proteins such as hsp100, hsp90, hsp70, HSP60 and small HSPs (sHSPs). A common response to heat stress is the thermotolerance. How thermotolerant cells express high levels of HSPs, these proteins have been associated with the development of thermotolerance. A common feature of the response to heat stress is that an initial exposure to mild heat stress provides resistance against a subsequent lethal dose of the usual heat stress. This phenomenon is known as acquired thermotolerance (Hirt & Shinozaki, 2004).

High level of temperature leads to extensive denaturation and aggregation of cellular proteins, which, if not controlled, can lead to cell death. Through its activity HSPs help cells deal with damage induced by heat. During stress, the function of these proteins is to prevent aggregation and promote proper renaturation of denatured proteins, they also play important roles in normal conditions. The main role of HSPs under normal conditions is to assist in synthesis, transport and proper folding of target proteins (Hirt & Shinozaki, 2004).

In nature, temperature changes may occur more quickly than other stress-causing factors. Plants due to their inability to translocation are subject to large fluctuations in both diurnal

and seasonal temperature, and must therefore adapt to heat stress quickly and efficiently. The response to heat stress is characterized by inhibition of transcription and translation, increased expression of HSPs and induction of thermotolerance. If stress is severe, the signaling pathways leading to cell death by apoptosis are also activated. As molecular chaperones, HSPs provide protection for cells against the harmful effects of heat stress and improve survival. The higher expression of HSPs is regulated by transcription factors heat shock (HSFS). Although knowledge about the expression and function of HSPs has already been acquired, understanding the regulation of these mechanisms is still limited (Hirt & Shinozaki, 2004).

One striking feature of plants is that they contain a highly complex multigene family that encodes HSFS and HSPs. The HSF gene in plants is composed of a conserved DNA molecule, an oligomerization domain and an activation domain. The HSFS of higher eukaryotes are converted from a monomer of a trimeric form in response to stress. The trimeric active form binds to DNA and activates transcription factors. Although all HSPs function as molecular chaperones, each family of HSPs has a unique mechanism of action. The relative importance in stress tolerance of the different families of HSPs varies from one organism to another (Hirt & Shinozaki, 2004).

The hsp100 family of proteins present in prokaryotes and eukaryotes, with sizes ranging from 75 to 100 kDa. Hsp100 proteins are divided into two main classes: 1 class represented by proteins that contain two ATP binding sites, and the 2 class that contains proteins with only one ATP binding site (Miernyk, 1999). An important feature of the hsp100 protein is its ability to promote dissociation of protein aggregates in a manner dependent on ATP, as opposed primarily to prevent the unfolding and aggregation of proteins, as is attributed to other chaperones (Parsell et al., 1994). Hsp100 proteins have been identified in several plant species, and its expression analysis revealed that both are induced by stress (Agarwal et al., 2001).

The molecular chaperone Hsp90 is essential for eukaryotic cells, with key functions in signal transduction, cell cycle control, degradation and transport of proteins. Hsp90 genes are found in the inner compartments of plastids, mitochondria and endoplasmic reticulum (ER). The occurrence of multiple proteins hsp90 in the cytoplasm and other family members in different subcellular compartments suggests a number of specific functions for these proteins. While hsp90 is an abundant protein in normal conditions, its highest expression is observed in response to high temperatures, suggesting a protective role for them in conditions of heat stress (Krishna & Gloor, 2001).

Hsp70 family members are found in the cytosol of eukaryotes, and within the mitochondria, ER and plastids of eukaryotic cells (Lin et al., 2001). In higher eukaryotes, including plants, some hsp70 is constitutively expressed (Hsc70), while others are induced by stress (Hartl & Hayer-Hartl, 2002). The structure of hsp70 is composed of an NH_2-ATPase domain of approximately 45 kDa domain and a COOH-terminal peptide bond of approximately 25 kDa. In higher eukaryotes, the functions of hsp70 co-occur and post-translationally. HSP70 family members can be expressed in response to stress from heat or cold, on maturity and seed germination.

SHSPs are a group of proteins ranging in size from 15-42 kDa that can be synthesized in prokaryotic and eukaryotic cells in response to thermal stress. The patterns of expression and function of sHSPs suggest that its synthesis is correlated with thermotolerance. The

functions of sHSPs extend beyond those associated with protection against heat stress; they are also synthesized under normal conditions in specific stages of development such as germination, embryogenesis, pollen development and maturation of fruits (Sun et al., 2002).

The chaperonins comprise a diverse family of molecular chaperones that are present in the cytoplasm, in plastids and mitochondria of eukaryotes. They occur in two distinct subgroups, type I and type II (Hirt & Shinozaki, 2004). The chaperonins type I are located in the chloroplast and mitochondria and are expressed as chaperonins 60 (Cpn60). The plastidic Cpn60 is composed of two types of subunit, α and β.

During the prolonged thermal stress in plants, sHSPs aggregates produce orderly cytoplasmic complex of 40 mm in diameter. The heat stress granules (HSGS) are unique and are synthesized in all plant species. The HSGS comprise mainly sHSPs cytosolic of classes I and II. The HSGS represent the local storage and protection for cleaning of mRNPs, which are released after removal of stress (Nover et al., 1989). During heat stress in the long term, the sHSP protein complexes are stored temporarily in HSGS (Löw et al., 2000).

High temperature exposure is often accompanied by high light exposure, it is important also to consider how high intensity lighting leads to plant stress. The strong radiation introduces a number of the leaf photochemical energy greater than the ability to use this energy in photosynthesis, overloading the photosynthetic processes and, ultimately, resulting not only in a quantum low utilization, but also on a low efficiency assimilatory (photoinhibition). High light intensity can, under aerobic conditions, catalyze the generation of oxygen species on highly damaging to cellular integrity and functionality. The photosynthetic capacity is impaired, with effects on plant growth and productivity.

The term photoinhibition is often used generically by reference to events of photoprotection and photodamage. Photoinhibitory process often comes down to photodamage, a drop in quantum efficiency caused by damage to the photosynthetic apparatus. Recovery from photoinhibition requires the presence of low-intensity light. In general, photoinhibition causes a decrease in the efficiency of photosynthetic O_2 release and induces changes in photochemical reactions associated with chlorophyll *a*. Plants sensitive to photoinhibition, biochemical and physiological changes occur that result in loss of membrane integrity (the lamellae of thylakoids) chloroplastidics, including its lipid and protein domains. The photoinhibition is a process dependent on temperature and light, resulting in the decreased efficiency of utilization of energy of photons captured in photochemical reactions in photosystems I and II.

When subjected to high light conditions, many higher plants, especially those of tropical origin, suffer from inhibition of photosynthesis due to the inability of tissues chlorophyll dissipate excess radiant energy, resulting in photoinhibition. Photoinhibitory process may be reversible or not. Only characterizes the occurrence of photoinhibition occurs when a prolonged downturn in the quantum efficiency of PSII. The reaction center of PSII is the primary target of photoinhibitory process, where certain subunits of proteins are quickly broken. The photosynthetic damage can be repaired by its own mechanisms, intrinsic to each species according to their degree of sensitivity to cooling temperatures. The resilience of the damage photoinhibitory, even for those species less sensitive, is greater the lower the extent of damage.

Two types of photoinhibition are identified: (a) dynamic photoinhibition, which occurs under moderate excess of light, is caused by deviation of absorbed light energy in the direction of heat dissipation, which leads to a decrease in quantum efficiency, but this decrease is temporary quantum efficiency and can return to its initial value higher; (b) chronic photoinhibition, which results from exposure to high levels of excess light, which damage the photosynthetic system and decrease the quantum efficiency and maximum photosynthetic rate, as opposed to dynamic photoinhibition, such effects are relatively long duration, persisting for weeks or months.

Extremely high temperatures can occur in soils exposed to the sun without vegetal cover, or even rock formations. Species closely related to the same genus may differ in relation to this ability, and even different organs and tissues of the same individual have different capacities of resistance to high irradiance. Typical differences in resistance, related to the conditions of the distribution and the geographical origin of the species are developed in the course of evolution.

The successful establishment of plants under conditions of high irradiance stress depends, in fact, the ability of different species to capture and use in an efficient, light. The less efficient for the capture of radiation by the pigment complex, the plant is more resistant compared to the strong radiation. As a first measure of protection, the inputs of radiation is deviated directly from photosystem via fluorescence and, especially, in the form of heat. Another protective mechanism by which energy can be diverted in a cyclic process is the metabolism of glycolate, or plants MAC, reassimilation internal CO_2, when the stomata are permanently closed due to drought.

Three types of resistance to high irradiance can be highlighted: (i) sensitive species: species which include all species that suffer injuries at 30-40 ° C or a maximum of 45 ° C (algae, lichens and most terrestrial species); (ii) relatively resistant eukaryotic organisms: dry sunny spots are usually able to acquire a rustification in relation to high irradiance, including plants that can survive in temperatures of 50-60 ° C for at least 30 minuntes; however, the range between 60-70 °C is the typical temperature limit for the survival of highly differentiated cells and organisms; (iii) prokaryotic organisms tolerant to high irradiance, some thermophilic prokaryotic organisms (cyanobacteria, bacteria and archaea hyperthermophiles) can withstand extremely high temperatures. All these organisms have cell membranes, proteins and nucleic acids highly resistant.

An extremely high temperature can destroy the photosynthetic pigments and thylakoid structures (photodestruction). The photodestruction is responsible for the decline in photosynthetic capacity of leaves senescence. The effect of heat depends on its duration; it follows the rule of the dose, which indicates that little heat for a long period causes so much injury as an intense heat for a short period. Photosynthesis and respiration are inhibited at high temperatures, but the photosynthetic rates fall before respiratory rates. Photosynthesis at elevated temperatures can not replace the carbon used as a substrate for respiration. As a result, the carbohydrate reserves decrease and lose the fruit sugars. Heat stress can alter the rate of metabolic reactions that consume or produce protons, it can affect the activity of proton pumping ATPases. This would cause an acidification of the cytosol, which would cause additional metabolic disturbances during stress.

8. Stress by heavy metals

Heavy metals are defined as metals with a density greater than 5 g cm^{-3}. However, only a limited number of these elements is soluble under physiological conditions and therefore may become available to living cells. Among them, the factors used for the metabolism of plants as micronutrients or trace elements (Fe, Mo, Mn, Zn, Ni, Cu, V, Co, W, Cr) and become toxic when in excess, as well as other biological functions not known and high toxicity, as As, Hg, Ag, Sb, Cd, Pb and U (Hirt & Shinozaki, 2004).

Regulatory limits for heavy metals in the environment are defined by national legislation. The concentrations of heavy metals in soils are regional differences and could exceed regulatory limits in 10 to 50 times (Haag-Kerwer et al., 1999). The soil covering the rocks of ore naturally contains heavy metals in amounts that are toxic to most species of plants. In such places, specialized plant communities called "chemotypes" evolved offering opportunities to investigate traces of resistance to heavy metals. There is a growing concern about the increased release of heavy metals in the environment. The sources of heavy metals include traffic, garbage and sewage sludge. Emissions of dust, aerosols, ashes and metal processing industries lead the spread of heavy metals in rural areas. In agricultural soils, pollution by heavy metals is a growing problem because of soil contamination with municipal sewage sludge and intensive use of phosphate fertilizers containing cadmium as a contaminant.

The long-term biological and retention of heavy metals in soil favor its accumulation in the food chain with potentially negative effects on human health. The bioavailability of heavy metals in plants is specific and depends on the demand for specific metals as micronutrients and plant capacity to actively regulate the mobilization of metals by exuding organic acids or protons in the rhizosphere. In addition, soil properties influence the chemical mobility of metals, thus regulating its release to the soil solution. The ability of plants to extract metals from the soil, the internal allocation of the metal in the plant cell and detoxification mechanisms are areas of research that has attracted increasing attention (Hirt & Shinozaki, 2004).

The absorption of heavy metals in plant cells is modulated by biotrophic interactions and the inherent characteristics of plants, such as its ability to retain heavy metals in the roots, for example, by binding to cell wall components. A common response to exposure to heavy metals is a significant reduction in plant growth (Sanita di Toppi & Gabrielli, 1999). Normal growth is the result of cell division, elongation and differentiation also including programmed cell death in certain tissues such as xylem. The excess of heavy metals affects root functions on various levels and causes the accumulation of abscisic acid (ABA). In the whole plant, roots are the main site access for heavy metals. In general, a large fraction of cadmium (Cd) or copper (Cu) is retained by the roots and only a relatively small amount (about 10%) are transported to the shoot (Liao et al., 2000). The cytokinins act as antagonists to Cd, indicating that the internal hormonal status can critically affect plant tolerance to heavy metals.

Cu is a micronutrient essential for the catalytic activity of many enzymes. His capture and transport are regulated and mediated by specific transporters and escorts. The Cu serves as an intermediary for the flag receiving the hormone ethylene. Excess Cu is detected by binding to transcription factors, thus activating an arsenal of defense against abiotic stresses,

including increased expression of metallothioneins, phytochelatins and antioxidants which help to remove the Cu "free" and to restore homeostasis ionic and cellular redox. These free metals are potentially dangerous, and therefore its uptake and cellular concentration must be regulated. The Cu has a high affinity for peptide, carboxylic and phenolic groups. Therefore, Cu is usually present in living cells. It is believed that the superoxide dismutase (SOD), which contain Cu / Zn, Fe or Mn in its reaction center, play a dual role in preventing metal toxicity on the one hand, they clean the O_2^- radical, thus maintaining lower concentrations of reactive oxygen species and on the other, they seem to be involved in preventing the accumulation of free metal (Hirt & Shinozaki, 2004).

Differently from Cu, no specific uptake system for Cd is known. Once accumulated in the body, trigger discharges of Cd in the activation of signaling pathways as well as a sequence of biochemical reactions and morpho-physiological changes that can cause programmed cell death in various tissues and organs (Souza et al., 2010). According to these authors, cell death induced by Cd can present apoptotic features such as chromatin condensation, nuclear DNA cleavage oligonucleossomos and formation of apoptotic bodies. Cd enters cells through transporters with broad specificity for metals, and probably also through calcium channels. It is toxic due to its high reactivity with sulfur and compounds derived from this type of stress causes depletion of antioxidant systems and stimulates the production of H_2O_2 by enzymes. The CD has more affinity with thiol groups of other metal micronutrients (Schützendübel & Polle, 2002). This feature is probably also the main basis for its toxicity. Cadmium inhibits HS-structural, redox regulated enzymes in living organisms (Hall, 2002). CDs can also be linked to other functional groups containing nitrogen or oxygen.

Exposure to Cd leads to oxidative damage as lipid peroxidation and protein carbonylation (Romero-Pueras et al., 2002). The excess of Cd in plant tissue can stimulate the formation of free radicals and reactive oxygen species (ROS), causing severe oxidative stress (Souza et al., 2010), in addition, the Cd disturbs the cellular redox balance. One of the most important answers to the CD, and also for other heavy metals, is an initial transient depletion of GSH, which is probably due to an increased demand for this precursor for the synthesis of PC (Schützendübel et al., 2001). Cd suppresses cell expansion. In shoots, Cd inhibits the proton pump responsible for maintenance of turgor (Aidid & Okamoto, 1992). This is likely to occur in other parts of the plant as well. Moreover, the roots exposed to Cd increased the production of ethylene, a hormone that inhibits cell expansion. The Cd also leads to significant accumulation of H_2O_2 which causes hardening of the cell wall (Ros Barcelo, 1997). Therefore, inhibition of root growth is probably a pleiotropic effect caused by direct inhibition of enzymes important for Cd interference in cell signaling.

Cu and Cd activate the formation of phytochelatins (PCs) and metallothioneins (MT), both compounds with functions sequestration of heavy metals (Cobbett & Goldsbrough, 2002). MTs are a family of small proteins. The promoter regions of MT transport elements MRE (metal responsive elements: GCGCGCA), leading to the accumulation of MT because of exposure to heavy metals (Cobbett & Goldsbrough, 2002). PCs are produced enzymatically from the tri-peptide precursor GSH (glycine cysteinyl γ-glutamyl). In response to heavy metals γECS (synthase γ-glutamyl transferase cisteinyl) and is transcriptionally activated (Noctor et al., 1998) and is transcriptionally activated (Lee & Korban, 2002) leading to accumulation of PC (Rauser, 1999). MTs may contribute to control the concentration of metals "free" and reactive oxygen species can activate the defenses.

Cd induces the biosynthesis of ABA and ethylene in the roots (Chen, et al., 2001). These are signs that lead to stress responses in the shoot. Ethylene inhibits the growth of cells and plays a role in cell signaling. In situations of stress by excess Cd, the absorption of water in the roots is disturbed, the hydraulic conductivity decreases and thus the water supply to the shoot decreases (Marchiol et al., 1996). The transport of Cd to the shoot is driven by perspiration and can be reduced through the application of ABA (Salt et al., 1995). The excess of Cu leads to a decline in the efficiency of water use and an accumulation of proline (Vinit-Dunant et al., 2002). The biosynthesis of proline was also found in plants stressed with Cd (Talanova et al., 2000).

9. Mechanical Stress

Plants respond to various mechanical disturbances, such as weight changes, snow, ice, wind and rain. Thygmotropism directional growth is determined by a stimulus and describes phenomena such as the ability of roots to grow around objects in the soil (Porter et al., 2009). The change in physiology, morphology and composition of plants resulting from prolonged stimulation by mechanical disturbances is referred to as thygmomorphogenesis. The most common morphological changes associated with thigmomorphogenesis is the development of compact plants decreased due to stretching, bending and friction caused by the shoot in the wind, animals or other plant parts. However, it is possible to observe significant differences in responses thigmomorphogenetics between and within species, with an indication of genetic diversity in the regulation of this phenomenon (Porter et al., 2009).

These thigmomorphogenetics changes may lead to increases in the width of the plants and decreased sensitivity to these various stresses. The most pronounced effects found in conditions of high rates of turbulent wind or water flow (Onguso et al., 2006). Plants react to mechanical stress according to species, cultivar, habit and growth. The morphological responses to mechanical stress are characterized by: decreasing the ratio between growth and stem diameter growth and decrease or increase in stem diameter. The responses also include increased production of xylem and flexed at the point decreases leaf area.

10. Conclusion

The evolution of knowledge about the mechanisms of stress tolerance in various species, through the study of functional genomes and proteomes, has provided valuable information for the development of genotypes that can tolerate periods of stress without productivity is substantially impaired. The dissemination of new molecular techniques such as DNA microarrays, which allow simultaneous analysis of thousands of genes and implicate metabolic pathways activated or deactivated under specific conditions, will promote the viewing of hundreds of interactions that occur in the context transcriptional and proteomic analysis in response to stress events. Confirmation of such changes by real-time PCR then allows the precise quantification of mRNA levels of genes of interest under different conditions. These techniques allow the design strategies aimed at increasing tolerance to environmental stress conditions. These strategies have been through traditional breeding methods, facilitated by the use of molecular markers linked to individual genes or linked to quantitative trait locus (QTL) of importance, or through the use of genetic engineering. Genes identified by tolerance mechanisms have shown potential to be used in studies of plant transformation.

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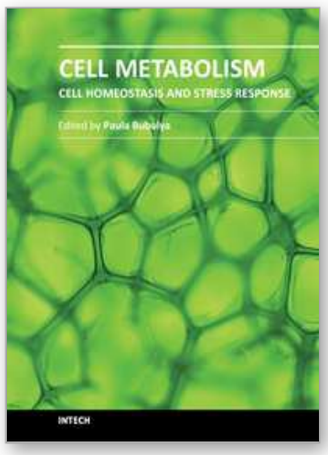

Cell Metabolism - Cell Homeostasis and Stress Response
Edited by Dr. Paula Bubulya

ISBN 978-953-307-978-3
Hard cover, 208 pages
Publisher InTech
Published online 25, January, 2012
Published in print edition January, 2012

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