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Abiotic Stress Effects on Plants under Climate Change

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Abstract

Abiotic stress is a stress that occurs as a result of damage done to plants by non-living and often tangible factors such as intense sunlight, wind etc. This naturally occurring stress is most detrimental to plant health when it influences the environment beyond its normal range of variation. Since abiotic stresses originate from surrounding environment therefore, these are more harmful for plants than animals as plants are dependent on environmental factors. Research has also shown that abiotic stressors are at their most harmful when they occur together, in combinations of abiotic stress factors. Extended exposure to extreme temperatures, high salinity, etc results in certain physiological and biochemical changes in plants that adversely affect the growth and productivity of crops worldwide. Plant biodiversity is determined by many things, and one of them is abiotic stress. If an environment is highly stressful, biodiversity tends to be low. If abiotic stress does not have a strong presence in an area, the biodiversity will be much higher. This means that species are more likely to become plants population threatened, endangered, and even extinct, when and where abiotic stress is especially harsh. Thus, abiotic stress leads to altered metabolism and damage to bio-molecules and is responsible for reduced yield in several major crops. In this review, we summarize recent progress on systematic analysis of plant responses to abiotic stress. Abiotic stresses are serious threats to agriculture and the environment which have been exacerbated in the current century by global warming and industrialization.

Keywords: Stress, abiotic stress, drought, temperature stress

1. Introduction

Abiotic stresses are serious threats to agriculture and the environment which have been exacerbated in the current century by global warming and industrialization. Today, in a world of 7 billion people, agriculture is facing great challenges to ensure a sufficient food supply while maintaining high productivity and quality standards. In addition to an ever increasing demographic demand, alterations in weather patterns due to changes in climate are impacting crop productivity globally. Unfavorable climate (resulting in abiotic stresses) not only causes changes in agro-ecological conditions, but indirectly affects growth and distribution of incomes, and thus increasing the demand for agricultural production (Fukuda, 2000).

Abiotic stress is defined as the negative impact of non-living factors on the living organisms in a specific environment (Pennell and Lamb, 1997). Abiotic stresses include drought, excess water, salinity, heat, cold, wounding, exposure to xenobiotics (now including chemical pollution) and UV radiation. Furthermore plants are also confronted by biotic stresses through microbial pathogens such as fungi,

nematodes and bacteria (Tippmann *et al.*, 2006). Some of the most serious effects of abiotic stresses occur in the arid and semiarid regions where rainfall, high evaporation low, native rocks, saline irrigation water, and poor water management all contribute in agricultural areas (Vahdati and Leslie, 2013). Stress research has traditionally focussed on single stress aspects. However, in their natural environment, plants have to adapt to numerous environmental stresses at the same time and different stresses can occur at different stages of the plant's life cycle. The adaptation to various stresses has led to the development of common stress transduction pathways and includes, among others, the increased synthesis of secondary metabolites, Ca²⁺ fluxes, an oxidative burst and an overlapping set of stress response genes (Cheong *et al.*, 2002; Roberts *et al.*, 2002). Abiotic stress leads to a series of morphological, physiological, biochemical and molecular changes in plants that adversely affect growth and productivity. Stresses also affect the biosynthesis, concentration, transport, and storage of primary and secondary metabolites. As a more comprehensive view of these processes evolves, applications to reducing plant stress are emerging (Vahdati and Leslie, 2013).



Abiotic stress comes in many forms. The most common of the stressors are the easiest for people to identify, but there are many other, less recognizable abiotic stress factors which affect environments constantly. The most basic stressors include: high winds, extreme temperatures, drought, flood, and other natural disasters, such as tornadoes and wildfires. The lesser-known stressors generally occur on a smaller scale and so are less noticeable, but they include: poor edaphic conditions like rock content and pH, high radiation, compaction, contamination, and other, highly specific conditions like rapid rehydration during seed germination (Jump et al., 2006).

2. Features of Salinity, Cold and Drought Stress

Salinity, cold and drought stress are all osmotic stresses: they cause a primary loss of cell water, and, therefore, a decrease of cell osmotic potential. However, the elicitor of cell water loss differs between stresses: i) salinity stress decreases cell water content due to the decrease of external water potential, caused by the increased ion concentration (mainly Na^+ and Cl^-), turning more difficult water uptake by roots and water translocation to metabolically active cells; ii) cold stress decreases cell water content due to the so-called physiological drought, *i.e.*, the inability to transport the water available at the soil to the living cells, mainly the ones of the leaf mesophyll; iii) the decrease of the cell water content under drought stress is due to water shortage in soil or/and in the atmosphere. Anyway, dehydration triggers the biosynthesis of the phytohormone abscisic acid (ABA) and it has been known for a long time that a significant set of genes, induced by drought, salt, and cold stresses, are also activated by ABA (Boudsocq and Lauriere, 2004).

Different combinations of biotic and abiotic stresses are presented in the form of a matrix to demonstrate potential interactions that can have important implications for agriculture. Different interactions are color coded to indicate potential negative [*i.e.* enhanced damage or lethality owing to the stress combination (purple)] or potential positive [*i.e.* cross-protection owing to the stress combination (green)] effects of the stress combination on plant health. However, the potential effects of stress combination could vary depending on the relative level of each of the different stresses combined (*e.g.* acute versus low) and the type of plant or pathogen involved. Data to generate the matrix was obtained.

3. Temperature

Temperature stress is becoming the major concern for plant scientists worldwide due to the changing climate. The difficulty of climate change is further added considering its precisely projecting potential agricultural impacts (Watanabe and Kume, 2009; Shah et al., 2011). Temperature stress has devastating effects on plant growth and metabolism, as these processes have optimum temperature limits in every plant species. Global climate change is making high temperature

(HT) a critical factor for plant growth and productivity; HT is now considered to be one of the major abiotic stresses for restricting crop production (Hasanuzzaman and Hossain, 2012).

The most observed effect of heat stress on plants is the retardation of growth. As heat stress often occurs simultaneously with drought stress, the combination of drought and heat stress induce more detrimental effect on growth and productivity of crops than when each stress was applied individually (Prasad et al., 2008). In higher plants, heat stress significantly alters cell division and cell elongation rates which affect the leaf size and weight. However, it was reported that heat stress resulted in significant increases in leaf numbers, particularly when reproductive development was arrested without any decrease in leaf photosynthetic rates (Prasad et al., 2006; Prasad et al., 2008). Exposure of plants to severe heat stress decreased the stem growth resulting in decreased plant height (Prasad et al., 2006; Rahman, 2004; Ahamed et al., 2010) reported that plant height of wheat plant ranges from 66.4–97.3 cm and 55.7–82.3 cm in normal and heat stress condition, respectively. While studying with *T. aestivum*, Ahamed et al., (2010). observed that sowing time mediated heat stress negatively influenced the plant height and number of tillers of 4 different genotypes. In a recent study, Al-Busaidi et al. (2012) observed that high atmospheric temperature causes significant water loss which negatively influenced the growth and biomass production in biofuel plant, *Jatropha curcas*. Parallel to shoot growth heat stress often decreases root growth, number of roots and root diameter (Porter and Gawith, 1999). Recently, Johkan et al. (2011) observed that the number of tillers in wheat plants decreased in response to HT, especially high night-time temperatures, however shoot elongation was promoted. Prasad et al. (2011) reported that high night temperature (31.9 °C/27.8 °C) decreased chlorophyll (Chl) content and photosynthetic rate by 8% and 22%, respectively, compared to optimum night temperature. In a recent study, Prasad et al. (2011) observed that spring wheat plants grown under HT (31/18 °C) showed a significant reduction in number of grains spike⁻¹ (50%), total dry weight (20%), grain yield (39%) and harvest index (24%) as compared to optimum temperature (24/14 °C).

High temperature decreased shoot dry weight, relative growth rate (RGR) and net assimilation rate (NAR) in maize, millet and sugarcane (Wahid, 2007; Ashraf and Hafeez, 2004). In their review, Wahid (2007) mentioned that HT can cause considerable pre- and post-harvest damages, including scorching of leaves and twigs, sunburns on leaves, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage. High temperature also alters the internal morphology (anatomy) of plants and these changes are generally similar to those under drought stress. Under HT stress, there is a general tendency towards reduced cell size, closure of stomata



and curtailed water loss, increased stomatal density and trichomatous densities, and larger xylem vessels in both roots and shoots (Wahid, 2007). According to Angadi and Cutforth (2000), temperatures below 10 °C result in slower and reduced growth and premature stem elongation in *B. napus*, *B. rapa* and *Raphanus sativus*. It is well reported that plants at their seedling stage are very much sensitive to cold stress. At early stage of plant growth, and various phenotypic symptoms in response to chilling stress are surface lesions, chlorosis, necrosis, desiccation, tissue break down and water soaked appearance of tissues, reduced leaf expansion, wilting (Solanke and Sharma, 2008; Jiang et al., 2002). Nahar et al. (2009) observed varieties of cold injury symptom is rice including stunted growth, yellowing of leaves, abnormal number of tiller, malformed grain, abnormal colors in grain.

4. Programmed Cell Death as a Response to High Light

4.1. UV and Drought Stress in Plants

Because of their sessile nature, plants are unable to avoid fluctuating environment conditions like high light, ultraviolet radiation, drought, salt stress, heat, cold or flooding. Upon certain threshold of these changes, plant cells can no longer maintain proper metabolic processes and programmed cell death (PCD) is induced.

There are two main categories of PCD in plants: developmentally- and environmentally-induced PCD. Example of developmentally- induced PCD is a formation of unisexual flowers in monoecious species (e.g. maize), bearing generative organs of both sexes on the same plant. Sex determination in these species involves the developmental arrest of one of the organ primordia-either the 2013 Wituszyńska and Karpiński; licensee InTech. This is an open access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. Female or male within a bisexual floral meristem (Dellaporta and Calderane, 1993). The production of complex leaf shapes also frequently employs PCD. Such remodeling of leaf blades occurs in *Monstera obliqua*, *Monstera deliciosa* or lace plant (Gunawardena et al., 2004). These species tend to induce death pathway in some patches of cells and thus form distinctive perforations within the leaf (Gunawardena, 2008).

Moreover, PCD during senescence helps to block spreading of diseases to still vital parts of the plant (Gan and Amasino, 1995). Under heat stress leaf temperature and stomatal conductance increased significantly, whereas under drought and drought + heat stress condition photosynthesis and stomatal conductance decreased and leaf temperature increased as compare to control.

5. High and Excess Light Stress

Light is an essential factor in the regulation of plant growth,

development and stress responses but it is also responsible for the production of reactive oxygen species leading to PCD. The cell death phenotype of many lesion mimic mutants of *Arabidopsis thaliana* and *Zea mays* is dependent on light (Jabs et al., 1996; Mach et al., 2001; Gray et al., 2002). Plant cells have been equipped with sophisticated light-perception mechanisms and signaling pathways that are very important for the plant defense. Three families of photoreceptors collecting different light qualities exist in plant cells: phytochromes (PHY), cryptochromes (CRY) and phototropins (PHOT).

In the last decade a significant progress has been made in improving light-induced oxidative stress tolerance in plants. Various components of anti-oxidative system involved in ROS scavenging have been up- or down-regulated to develop transgenic lines with altered antioxidants levels. Over-expression of enzymes involved in AsA biosynthesis has been shown to confer oxidative stress tolerance in tomato plants (Zhang et al., 2011). Increased AsA content has been also demonstrated to enhance high light stress tolerance in *Arabidopsis* (Wang et al., 2010). Higher concentration of GSH has proven to protect potato plants against oxidative damage (Eltayeb et al., 2010). Moreover, reduced level of light-mediated cellular damage has been observed in transgenic tobacco plants over-expressing chloroplast-localized Cu/Zn-SOD (Gupta et al., 1993) and thylakoid membrane-bound APX (Yabuta et al., 2002). MDHAR over-expression in *Arabidopsis* has been demonstrated to enhance the tolerance towards photo-oxidative stresses (Li et al., 2010). Moreover, some studies have reported that combined expression of antioxidant enzymes in transgenic plants acts synergistically on stress tolerance, e.g. simultaneous over-expression of Cu/Zn-SOD and APX in tobacco chloroplasts enhances the resistance to the photo-oxidative stress in comparison to their single over-expression (Tang et al., 2006).

6. UV Radiation Stress

Being exposed to sunlight, plants need to deal with the damaging effect of ultraviolet (UV) radiation which reduces the genome stability, impeding their growth and productivity. These effects result from damage to cell components including not only nucleic acids, but also proteins and membrane lipids. Upon UV exposure, strongly mutagenic cross-linked forms of DNA can be produced (Britt, 1999). In order to minimize effects of UV radiation, plants accumulate UV-absorbing secondary metabolites, perform the monomerization of UV-induced pyrimidine dimers (DNA repair) and neutralize generated ROS (Molinier et al., 2005; Kunz et al., 2006). UV radiation consists of UV-C (below 280 nm), UV-B (280–320 nm) and UV-A (320–390). Although UV-C is not physiologically relevant to plants since it is efficiently blocked by the stratosphere, the UV-C-triggered cell damage is comparable to induced with UV-B radiation, which reaches Earth's surface (Danon and Gallosis, 1998). Therefore, UV-C radiation has been widely



used to study DNA damage and repair mechanisms upon UV stress (Sinha et al., 2002). UV has been demonstrated to trigger apoptosis in animals (Babu et al., 2003) and apoptosis-like changes in *Arabidopsis*, including DNA laddering, changes in nucleus morphology (crescent shape) and its fragmentation (Danon and Gallosis, 1998). It has been also proven to induce oxidative burst in plant cells (Babu et al., 2003), considered as the main cause of cell death, which aims at the limitation of damage spreading. Light is necessary for UV-C-triggered cell death and caspase-like proteases participating in this process since caspase-inhibitors are able to block the onset of DNA fragmentation (Essemine et al., 2010, Zhang et al., 2009). Recent study performed on *Arabidopsis* protoplasts has shown that during the early stage of UV stress, a burst of ROS in chloroplasts and adjacent mitochondria is detected. Mitochondria dysfunction has been also observed, manifested by changes in their distribution, mobility and the loss in mitochondrial trans-membrane potential. Moreover, the pre-incubation with antioxidant molecule - ascorbic acid or inhibitor of photosynthetic electron transport - DCMU decreases the ROS production and retards PCD. These results prove that mitochondria and ROS act as mediators in the UV-C-induced cell death (Gao et al., 2008) and that AsA can be considered as an important antioxidant during this process (Gao and Zhang, 2008), which is consistent with what has been reported in various types of PCD. It has been also shown that *Arabidopsis* proteins AtDAD1 and AtDAD2 (defender against apoptotic death), localized in the endoplasmic reticulum membrane can suppress DNA fragmentation, indicating an involvement of the ER in UV-C-triggered PCD pathway (Essemine et al., 2010). The microarray approach has identified numerous genes responsible for ROS scavenging, signalling, transcription regulation and involved in DNA replication or conformation changes that have been deregulated after exposure to UV-C radiation (Molinier et al., 2005). Metacaspase-8 (AtMC8) has been proven to be strongly up-regulated by UV-C. Over-expression of AtMC8 in *Arabidopsis* has resulted in more severe cell death, while knocking-out AtMC8 has reduced the UV-C-triggered PCD, which suggests that metacaspase-8 is a part of PCD pathway activated by UV radiation (He et al., 2008). The activation of PCD program upon UV helps plants in eliminating damaged cells to control cell quality and quantity after the trauma.

7. Drought Stress-soil Water Deficit

Drought is one of the most unfavorable environmental factors that affects growth and development of plants and consequently limits plant productivity. Plants have developed specific acclimation and adaptation mechanisms to survive the soil water deficit. In response to drought, plants can exhibit either escape (ability to complete the life cycle before severe stress) or resistance mechanisms. Resistance mechanisms include drought avoidance and drought tolerance. The latter depends on the cell turgor maintenance by accumulating

osmolytes and soluble sugars (Harb et al., 2010). There are several examples of molecules that help to maintain an osmotic balance under dehydration conditions: sugars, polyols and proline (Yoshida et al., 1997). Proline is accumulated in the cytoplasm and chloroplast stroma while other solutes (sugars, organic acids, potassium) are cumulated in the vacuole. When the cellular water content decreases, they stabilize cellular structures through hydrophilic interactions and hydrogen bonding (Verslues and Sharma, 2010).

In figure 1 it shows unique physiological characteristics of drought and heat stress combination. A combination of drought and heat stress is shown to be different from drought or heat stress by having a unique combination of physiological parameters.

Photosynthesis is one of major processes affected by water deficit since stomata closure causes reduced CO₂ diffusion to the chloroplast. As a result of the inhibition of photosynthesis and the predominance of photorespiration, ROS are generated (Noctor et al., 2002). It has been demonstrated that in drought-stressed plants, the ABA-controlled stomata closure is mediated by H₂O₂ (Pei et al., 2000). Under severe drought stress, some antioxidant enzymes have been shown to be highly induced (Dat et al., 2000). However, studies on many drought-stressed crop species showed an inconsistency in their expression since in some cases they have been induced, but in other repressed, suggesting that different ROS balance may be required during different response phases (Cruz and Carvalha, 2008). Recent studies have shown that the water deficit triggers PCD not only in green tissues but also in plant root tips. Apical meristem cells of primary roots undergoing PCD, demonstrate increased size of vacuole, degradation of organelles and the collapse of plasma membrane (Duan et al., 2010).

7.1. ROS - reactive oxygen species

During water deficit, ROS are responsible for the induction of leaf senescence, which is executed through the programmed cell death and plays an important role in the plant survival (Petrov et al., 2015). This is an active, genetically controlled process which is initiated to isolate and remove damaged tissues thereby ensuring the survival of the organism. It contributes to the nutrients remobilisation during stress and allows the rest of plant to benefit from them and stay alive. Plants can perceive biotic and abiotic stresses via specific receptors. The stress recognition is usually followed by production of messengers such as reactive oxygen species (ROS) or Inositol-1, 4, 5-triphosphate (IP₃), and modulation of intracellular calcium (Ca²⁺). Production of these early messengers can be receptor mediated, however, in many abiotic stresses (e.g. drought, cold, salt stress) membrane over-excitation can directly lead to ROS generation. The messengers also seem to influence each other, e.g., via IP₃ gated calcium channels. Receptors, ROS or Ca²⁺ dependent signals initiate specific phosphorylation cascades (e.g. mitogen



activated protein kinases - MAPK, calcium dependent protein kinases - CDPK) and finally interact with the promotor regions of transcription factors (TF) and response genes. The regulation of gene transcription can additionally depend on the activity of plants hormones and other regulatory molecules (e.g. Absciscic acid - ABA, salicylic acid - SA, Jasmonic acid - JA, ethylene - ET). The plant hormones can also influence the ROS and Ca^{2+} levels and initiate a second round of signaling.

8. Wind Stress

It is commonly thought that wind must play a part in the formation of this peculiar forest; to date there is no consensus about how wind influences elfin forest stature. Some authors have viewed elfin stature as the result of severe mechanical stress (Beard, 1949; Howard, 1968). Others have suggested that elf-in stature can be attributed to wind-induced water or nutrient stress (Schimper, 1903; Shreve, 1914; Seifrizz, 1953; Odum, 1970; Weaver et al., 1973; Leigh, 1975). The common feature of all these explanations is that they rest upon the assumption that elfin stature is a pathological condition.

Plants generally respond to environmental stress by adjusting their growth to reduce that stress (Levitt, 1972; Evans, 1972). For instance, Jacobs (1954) attached guy wires to young *Pinus radiata* D. Don on an Australian plantation to prevent their swaying in the wind. He then compared their growth to that of unguyed trees. The unguyed trees grew less in height and more in trunk diameter than the trees with the mechanical support of the guy wires.

Thigmomorpho-genetic response to mechanical stress, especially wind stress, has been observed in a wide variety of vascular plants (Jacobs, 1954; Whitehead, 1962; Larson, 1963; Neel and Harris, 1971; Jaffe, 1973, 1976, 1980; Grace and Russell, 1977; Ashby et al., 1979). In trees the most conspicuous thigmomorpho-genetic response is retarded stem elongation and increased radial growth (Jacobs, 1954; Larson, 1963, 1965; Neel and Harris, 1971; Ashby et al., 1979).

Grubb and Tanner (1976) and Grubb (1977) have suggested that wind-clipping is rare in tropical mountains, and that wind therefore has little influence upon the regulation of forest stature. However, growth responses such as those observed in *D. pittieri* might have major effects upon forest stature in windy locales. In general, ridges are windier than adjacent valleys and slopes (Geiger, 1961; Grace, 1977). Persistent strong winds are a commonly noted feature of the elfin forest environment (Shreve, 1914; Brown, 1919; Gleason and Cook, 1927; Seifrizz, 1923, 1943, 1953; Beard, 1955; Baynton, 1968; Lawton, 1980). If, in response to the mechanical stresses of wind, stem elongation is retarded, while radial growth continues apace, then trees of similar age should be shorter and have thicker stems on ridges. Presumably, short, thick trunks, branches and twigs would be less susceptible to wind-clipping. Therefore the absence of conspicuous wind-clipping is not necessarily a good indication that wind plays an

unimportant role in the regulation of forest stature.

9. Conclusion

Abiotic stresses will remain a challenge to the natural environment and agriculture. The early evolution of land plants took place under dry conditions with extremes of temperature and harsh sunlight, while crop domestication occurred later in more favorable environments. Subsequently, the selection of plants for productivity traits did not always result in crops that are productive under random stress factors, although the natural variations of crops are genetic reservoirs for abiotic stress adaptation.

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