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EFFECTS OF THIRST ON PLANT HEALTH AND RECOVERY MECHANISMS

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ABSTRACT

Crop plants are exposed to several environmental stresses, all affecting plant growth and development, which consequently hamper crop productivity. Among all stresses drought is considered the single most devastating environmental stress. During germination phase, the water absorbed is required for several enzymatic reactions, for solubilization and transport of metabolites and as a reagent in the hydraulic digestion of proteins, carbohydrates and lipids from the tissue reserve of the seed towards the embryo. Drought stress negatively impacts growth, yield, membrane integrity, pigment content, osmotic adjustment, water relations and photosynthetic activity. It causes not only a significant damage to photosynthetic pigments, but also affects thylakoid membranes. The generation of reactive oxygen species (ROS) is one of the earliest biochemical responses of eukaryotic cells to biotic and abiotic stresses. Being highly reactive, ROS can seriously damage plants by increasing lipid peroxidation, protein degradation, DNA fragmentation and ultimately cell death. Escape from drought is attained when phenological growth is effectively coordinated with periods of water availability, where the growing season is shorter and terminal drought stress predominates. Drought avoiders maintain water status through stomatal closure to minimize transpirational water loss and maintains water uptake through an extensive and prolific root system, osmoregulation and anti-oxidant enzymes. Both conventional and molecular breeding have paved the way towards tolerance and plant scientists have developed new line of crop plants that can cope with water stressed environment without sacrificing yield.

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INTRODUCTION

Global climate change has endangered crop production that will ultimately lead to food and fiber insecurity. To support the growing human population, a potential solution is to make improvement in crop yield both in irrigated and non-irrigated lands and create novel varieties with enhanced tolerance to environmental stresses. Progress has been made in the identification and functional analyses of genes controlling yield and tolerance to environmental stresses. Crop plants are exposed to several environmental stresses, all affecting plant growth and development, which consequently hamper the productivity of crop plants (Seki *et al.* 2003; Farooq *et al.* 2009). Climate models have predicted increased severity and frequency of drought under the ongoing global climate change scenarios (IPCC 2007; Walter *et al.* 2011).

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Drought is considered the single most devastating environmental stress, which decreases crop productivity more than any other environmental stress (Lambers *et al.*, 2008). Global warming due to heat trapping gases increases potential evapotranspiration that is directly linked with surface heating. This will probably result in an increase in actual evaporation, or evapotranspiration in plants, only if adequate moisture is available (Trenberth *et al.*, 2013). A continuous shortfall in precipitation (meteorological drought) coupled with higher evapotranspiration demand leads to agricultural drought (Mishra and Cherkauer 2010). Agricultural drought is the lack of ample moisture required for normal plant growth and development to complete the life cycle (Manivannan *et al.* 2008). Drought severely affects plant growth and development with substantial reductions in crop growth rate and biomass accumulation. The main consequences of drought in crop plants are reduced rate of cell division and expansion, leaf size, stem elongation and root proliferation, and disturbed stomatal oscillations, plant water and nutrient relations with

diminished crop productivity, and water use efficiency (Li *et al.* 2009; Farooq *et al.* 2009). To cope with such challenges, understanding the morphological and physiological effects of drought on plants and their adaptations is crucial (Yamaguchi-Shinozaki and Shinozaki 2006).

Effects of drought on plants

i) Morphological effects

Impaired germination and poor seedling growth are the first and foremost effects of water stress (Harris *et al.*, 2002, Kaya *et al.*, 2006). Reduced cell growth due to loss of turgor pressure is one of the most important physiological effects of drought on plants (Taiz and Zeiger, 2006). During the germination phase, the water absorbed is required for several enzymatic reactions, for solubilization and transport of metabolites and as a reagent in the hydraulic digestion of proteins, carbohydrates and lipids from the tissue reserve of the seed towards the embryo (Woodstock, 1998; Carvalho and Nakagawa, 2000; Khajeh-Hosseini *et al.*, 2003). Low moisture levels in the germination environment induce protection mechanisms against drying or even prevent a stop in the developmental process (Bewley and Oliver, 1992). Severe water stress, however, results in a metabolic imbalance (Blackman *et al.*, 1992) and a reduction of metabolic activities (Vertucci, 1989). During water deficit cell elongation of higher plants is inhibited through the break of water flow from the xylem to the surrounding elongating cells (Nonami, 1998). For instance, water shortage at pre-anthesis reduces time to anthesis, while at post anthesis it shortens the grain-filling period in triticale genotypes (Estrada-Campuzano *et al.*, 2008). Water deficit accelerates abscisic acid (ABA) biosynthesis, which decreases stomatal conductance to minimize transpirational losses (Yamaguchi-Shinozaki and Shinozaki 2006).

Post-anthesis drought stress reduces number of tillers, spikes, number of grains, grain weight and ultimately grain yield in barley (*Hordeum vulgare*) regardless of stress severity (Samarah, 2005). Drought stress at flowering commonly results in pollen sterility by reducing assimilate flux to the developing ear below some threshold level indispensable to sustain optimal grain yield (Yadav *et al.*, 2004). Water stress reduces cotton (*Gossypium hirsutum*) yield, although intensity, duration and speed of development definitely has pivotal role in determining plant's response to stress. Lint yield absolutely reduces due to flower and boll abortion when drought is imposed at flowering stage (Pettigrew, 2004). Limited water supply triggers a signal to cause an early switching of plant development from the vegetative to reproductive phase (Desclaux and Roumet 1996). Under water stress, grain setting and kernel growth in cereals is diminished due to reduced rate of endosperm cell division coupled with eminent levels of abscisic acid (Morgan, 1990; Ober *et al.*, 1991).

Under limited supply, water-use efficiency of stressed wheat was greater than well-watered. This higher water-use efficiency was associated with stomatal closure and reduced transpiration (Abbate *et al.*, 2004). In pigeon pea, drought stress at the flowering stage reduced seed yield by 40–55% (Nam *et al.*, 2001). By contrast, in rice, water deficit during

the grain-filling period enhanced remobilization of pre-stored carbon reserves to grains that improved grain filling (Yang *et al.*, 2009). In wheat relative water content of leaves was higher during leaf development and lowered as the leaf matured. Obviously, water deficit stressed wheat and rice plants had lower relative water content than non-stressed ones. Disclosure of these plants to drought stress considerably lowered the leaf water potential, relative water content and transpiration rate, with a concomitant increase in leaf temperature (Siddique *et al.*, 2001). Drought impacts include growth, yield, membrane integrity, pigment content, osmotic adjustment water relations, and photosynthetic activity (Benjamin and Nielsen, 2006; Praba *et al.*, 2009). Acclimation of plants to water deficit is the result of different events, which lead to adaptive changes in plant growth and physio-biochemical processes, such as changes in plant structure, growth rate, tissue osmotic potential and antioxidant defenses (Yan *et al.*, 2007). Drought stress severely hampered the gas exchange parameters of crop plants and this could be due to decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence, oxidation of chloroplast lipids and changes in structure of pigments and proteins (Menconi *et al.*, 1995).

ii) Physiological effects

Even due to the lack of understanding of drought tolerance mechanisms, physiological and molecular studies have acknowledged several plant responses to drought stress (Bohnert *et al.*, 1995; Blum, 1996; Ingram and Bartel, 1996; Bray, 1997; Schroeder *et al.*, 2001; Luan, 2002). Many studies have shown the decreased photosynthetic activity under drought stress due to stomatal or non-stomatal mechanisms (Del Blanco *et al.*, 2000; Ahmadi, 2007; Samarah *et al.*, 2009). Stomata are the points of water loss and CO₂ absorption and stomatal closure is one of the early responses to drought stress which results in reduced rate of photosynthesis. Stomatal closure deprives the leaves of CO₂ and photosynthetic carbon assimilation is decreased in favor of photorespiration and the rate of photosynthesis in higher plants is also decreased (Lawlor and Cornic, 2002). Although, the question remains unsolved as to whether drought mainly limits photosynthesis through stomatal closure or through metabolic impairment (Tezara *et al.*, 1999; Lawson *et al.*, 2003). Stomatal factor is generally believed to be the main determinant of reduced photosynthesis under drought stress (Cornic, 2000). Environmental stresses have a direct impact on the photosynthetic apparatus, essentially by disrupting all major components of photosynthesis including the thylakoid electron transport, the carbon reduction cycle and the stomatal control of the CO₂ supply, together with an increased accumulation of carbohydrates, per-oxidative destruction of lipids and water imbalance (Allen and Ort, 2001; Leakey *et al.*, 2006).

Photosynthetic pigments are important to plants mainly for harvesting light and production of reducing powers. Both the chlorophyll a and b are prone to soil dehydration (Farooq *et al.*, 2009). Decreased or unchanged chlorophyll level during drought stress has been reported in many species, depending on the duration and severity of drought (Kpyoarissis *et al.*, 1995; Zhang and Kirkham, 1996). It is evident that stomata close progressively with increased drought stress. It is well known that leaf water status always interacts with stomatal

conductance and a good correlation between leaf water potential and stomatal conductance always exists, even under drought stress (Lawlor and Cornic, 2002). It is now clear that there is a drought-induced root-to-leaf signaling, which is promoted by soil drying through the transpiration stream, resulting in stomatal closure (Reddy, 2004). The "non-stomatal" mechanisms include changes in chlorophyll synthesis, functional and structural changes in chloroplasts, and disturbances in processes of accumulation, transport, and distribution of assimilates (Anjum *et al.*, 2011). Recently, molecular and biochemical studies have pointed out many of these ABA and stress-responsive genes and some transcription factors responsible for their induction in model plants as well as crop plants (Ingram and Bartel, 1996; Hasegawa *et al.*, 2000; Thomashow, 2001; Finkelstein *et al.*, 2002; Ozturk *et al.*, 2002; Shinozaki *et al.*, 2003; Yu and Setter, 2003; Buchanan *et al.*, 2005; Poroyko *et al.*, 2005).

Studies on expression pattern of stress-regulated genes, either by overexpressing these target genes directly or by regulating their transcription factors, results in improved tolerance to stresses (Xu *et al.*, 1996; Kasuga *et al.*, 1999; Haake *et al.*, 2002). Under limited water supply, drought stress generally reduces nutrient uptake and diminishes tissue concentrations in crop plants. During water stress inorganic nutrients absorption is reduced due to the intervention in nutrient uptake and the unloading mechanism, and reduced transpirational flow (Burman *et al.*, 2003). Translocation of assimilates from source to reproductive sinks is vital for seed development while seed setting and grain filling becomes limited by source or sink limitation (Lemoine *et al.*, 2013). Water stress normally fastens the allocation of dry matter to the roots, which can enhance water uptake (Leport *et al.*, 2006). Translocation of sucrose from source to sink tissues depends upon the contemporary rate of photosynthesis and the concentration of sucrose in the leaves (Komor, 2000). Drought stress increases activity of acid invertase that negatively affects the rate of photosynthesis, carbohydrate metabolism and level of sucrose in leaves (Kim *et al.*, 2000). Limited photosynthesis and sucrose accumulation in the leaves may hamper the rate of sucrose export to the sink organs and ultimately affect the reproductive development (Davidson *et al.*, 2011). The root is a major consumer of carbon fixed in photosynthesis and uses it for growth and maintenance, as well as dry matter production (Lambers *et al.*, 1996).

Drought stress causes not only a significant damage to photosynthetic pigments, but it also affects thylakoid membranes (Huseynova *et al.*, 2009; Anjum *et al.*, 2011). Thus, a reduction in photosynthetic capacity in plants exposed to drought stress is expected and reduction in chlorophyll content is a commonly observed fact under drought stress (Bijan-zadeh and Emam 2010; Mafakheri *et al.*, 2010; Din *et al.*, 2011). In contrast, Kulshretha *et al.* (1987) found no considerable effect of water stress on chlorophyll content in wheat while some reports show improved chlorophyll content under water stress (Estill *et al.*, 1991; Al-Hakimi and Hamada, 2001; Pirzad *et al.*, 2011). Plants accumulate different types of organic and inorganic solutes in the cytosol to lower osmotic potential thereby maintaining cell turgor (Rhodes and Samaras, 1994). Relative water content (RWC), leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy

temperature are important characteristics that influence plant water relations. Relative water content is considered a measure of plant water status, reflecting the metabolic activity in tissues and used as a most meaningful index for dehydration tolerance. RWC of leaves is higher in the initial stages of leaf development and declines as the dry matter accumulates and leaf matures. A decrease in the relative water content (RWC) in response to drought stress has been noted in wide variety of plants as reported by Nayyar and Gupta (2006) that when leaves are subjected to drought, leaves exhibit large reductions in RWC and water potential. Exposure of plants to drought stress substantially decreases the leaf water potential, relative water content and transpiration rate, with a concomitant increase in leaf temperature (Siddique *et al.*, 2001). When two poplar species were submitted to progressive drought stress, the decrease of RWC in the water-stressed cuttings was 23.3% in *Populus cathayana*, whereas it was 16% in *Populus kangdingensis*. RWC is affected by the interaction of severity, duration of the drought event and species (Yang and Miao, 2010).

iii) Biochemical effects

The generation of reactive oxygen species (ROS) is one of the earliest biochemical responses of eukaryotic cells to biotic and abiotic stresses. The production of ROS in plants, known as the oxidative burst, is an early event of plant defense response to water-stress and acts as a secondary messenger to trigger subsequent defense reaction in plants. ROS, which include oxygen ions, free radicals and peroxides, form as a natural byproduct of the normal metabolism of oxygen and have important role in cell signaling. However, during environmental stress such as drought, ROS levels increase dramatically resulting in oxidative damage to proteins, DNA and lipids (Apel and Hirt, 2004). Being highly reactive, ROS can seriously damage plants by increasing lipid peroxidation, protein degradation, DNA fragmentation and ultimately cell death. Drought induces oxidative stress in plants by generation of reactive oxygen species (ROS) (Farooq *et al.*, 2009). The ROS such as $O^{\cdot -}$, H_2O_2 and $\cdot OH$ radicals, can directly attack membrane lipids and increase lipid peroxidation (Mittler, 2002). Drought-induced overproduction of ROS increases the content of malondialdehyde (MDA). The content of MDA has been considered an indicator of oxidative damage (Moller *et al.*, 2007).

MDA is considered as a suitable marker for membrane lipid peroxidation. A decrease in membrane stability reflects the extent of lipid peroxidation caused by ROS. Furthermore, lipid peroxidation is an indicator of the prevalence of free radical reaction in tissues. Moreover, oxygen uptake loading on the tissues as both processes generate reactive oxygen species, particularly H_2O_2 that produced at very high rates by the glycolate oxidase reaction in the peroxisomes in photorespiration. Yang and Miao (2010) noted the increments of the MDA and H_2O_2 concentrations in the water-stressed cuttings were 88.9 and 99.7% in *P. cathayana*, respectively, whereas they were only 44 and 63.6% in *P. kangdingensis*. In pea (*Pisum sativum*) plants, levels of lipid peroxidation in leaves increased two to four fold with an increase in drought stress, and this was highly correlated with protein peroxidation (Moran *et al.*, 1994).

Mechanisms of drought tolerance

Drought tolerance is a complex phenomenon that involves morphological, physiological, biochemical and molecular changes at whole-plant, cell and tissue levels. Manifestation of these changes determines the ability of the plant to cope with limited moisture supply. An overview of various morphological mechanisms functioning under drought conditions is given below.

Escape

Generally drought stress at flowering is most critical that reduces yield and its contributing traits in plants. To cope with these situations, shortened life cycle and flowering time are important adaptations that make plant able to complete its life cycle before the onset of drought (Araus *et al.*, 2002). Escape from drought is attained when phenological growth is effectively coordinated with periods of water availability, where the growing season is shorter and terminal drought stress predominates (Araus *et al.*, 2002). Time of flowering is a major trait of a crop adaptation to the environment, predominantly when terminal drought and high temperatures prevail. Early maturing and short duration varieties have been developed because early maturity is a favorable trait that makes plant able to start flowering before the weather becomes drier (Kumar and Abbo, 2001). Conversely, the length of growing season is correlated with yield under favorable growing conditions, and shortened crop duration below the optimum would tax yield (Turner *et al.*, 2001).

Avoidance

Drought avoiders maintain water status through stomatal closure that minimize transpirational water loss and maintains water uptake through an extensive and prolific root system (Turner *et al.*, 2001; Kavar *et al.*, 2008). The root characters such as rooting length, density, biomass and depth are the main drought avoidance traits that contribute to final yield under deadly drought stress (Subbarao *et al.*, 1995; Turner *et al.*, 2001). A deep and thick rooting system is helpful for extracting water from extensive depths (Kavar *et al.*, 2008), waxy layer on leaves helps with maintenance of high tissue water potential, and is therefore considered as a desirable trait for drought tolerance (Gollan *et al.*, 1986; Ludlow and Muchow, 1990). In wheat waxiness on leaves increased water-use efficiency, but did not affect total water use or harvest index. Analysis of leaf temperature depicted that, compared with non-waxy leaves, waxy leaves were 0.7 °C cooler and had a lower rate of leaf senescence (Gollan *et al.*, 1986).

These authors suggested that a 0.5 °C reduction in leaf temperature for six hours per day was sufficient to extend the grain-filling period by more than three days. However, yield advantages are likely to be small as many varieties already show some degree of glaucousness. Under drought stress, the maintenance of leaf turgor may also be achieved by osmotic adjustment by the accumulation of proline, sucrose, soluble carbohydrates, glycinebetaine, and other solutes in cytoplasm improving water uptake from drying soil. Accumulation of such solutes under drought stress is the osmotic adjustment

which strongly depends on the rate of plant water stress. Wheat is marked by low level of these compatible solutes and the accumulation and mobilization of proline was observed to enhance tolerance to water stress (Nayyar and Walia, 2003). Of these solutes, proline is the most widely studied because of its considerable importance in the stress tolerance. Proline accumulation is the first response of plants exposed to water-deficit stress in order to reduce injury to cells. Progressive drought stress induced a considerable accumulation of proline in water stressed maize plants. Proline content increase as the drought stress progressed and reached a peak when recorded after 10 days after stress, and then decreased under severe water stress as observed after 15 days of stress (Anjum *et al.*, 2012). Decrease in water contents results in progressive increase of free proline in cotton cultivars as well as difference in the proline level between the cultivars (De Ronde *et al.*, 2000), increase in leaf proline contents were revealed to be positively associated with biomass recovery.

Tolerant genotypes accumulated more proline under water stress than the susceptible ones resulting in high biomass recovery and stability of seed cotton yield (Singh and Sahay, 1990). Osmoregulation prevents folded protein structures against denaturation, stabilizes cell membranes by increasing phospholipids, or serves as an energy and nitrogen source (Nayyar and Walia, 2004; Claussen, 2005). Proline is a reliable indicator for the evaluation of tolerance or sensitivity of plants to stress (Patel and Vora, 1985). Free proline under stress conditions accumulates which primarily is due to the stimulation of proline biosynthesis (Rhodes *et al.*, 1986). Proline can act as a signaling molecule to modulate mitochondrial functions, influence cell proliferation or cell death and trigger specific gene expression, which can be essential for plant recovery from stress (Szabados and Savoure', 2010). Accumulation of proline under stress in many plant species has been correlated with stress tolerance, and its concentration has been shown to be generally higher in stress-tolerant than in stress-sensitive plants. It influences protein solvation and preserves the quaternary structure of complex proteins, maintains membrane integrity under dehydration stress and reduces oxidation of lipid membranes or photo-inhibition (Demiral and Turkan, 2004). Furthermore, it also contributes to stabilizing sub-cellular structures, scavenging free radicals, and buffering cellular redox potential.

In general, antioxidant enzymes content of leaves increased with the decline in irrigation water, suggesting that the production of antioxidant enzymes is probably a common response of plants under drought conditions. The activities of antioxidant enzymes are generally increased during abiotic stress conditions and correlate with enhanced cellular protection. There is a defensive system in plants, that is to say, plants have an internal protective enzyme-catalyzed clean up system, which is fine and elaborate enough to avoid injuries of active oxygen, thus guaranteeing normal cellular function (Horváth *et al.*, 2007). The balance between ROS production and activities of antioxidative enzyme determines whether oxidative signaling and/or damage will occur (Moller *et al.*, 2007). To minimize the affections of oxidative stress, plants have evolved a complex enzymatic and non-enzymatic antioxidant system, such as low-molecular mass antioxidants (glutathione, ascorbate, carotenoids) and ROS-scavenging

enzymes (superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX) (Apel and Hirt, 2004). Non-enzymatic antioxidants cooperate to maintain the integrity of the photosynthetic membranes under oxidative stress. The enzymatic components may directly scavenge ROS or may act by producing a non-enzymatic antioxidant (Yang *et al.*, 2009). Oxidative damage due to different abiotic stresses is the common phenomenon in plants that results from the generation of reactive oxygen species i.e superoxide anion (O_2^-), hydroxyl radicals (OH), hydrogen peroxide (H_2O_2), alkoxy radicals (RO) and singlet oxygen (O^1_2) (Munné-Bosch and Penuelas, 2003). Active oxygen species may react with proteins, lipids and deoxyribonucleic acid, causing oxidative damage and impairing the normal functions of cells (Foyer and Fletcher, 2001). Active oxygen species are produced in different cell compartments, of these, chloroplasts are a major place because of the excited pigments in thylakoid membranes may interact with O_2 to form strong oxidants such as O^2 or O^1_2 (Niyogi, 1999; Reddy *et al.*, 2004). Further downstream reactions produce other reactive oxygen species such as H_2O_2 and OH. The interaction of O_2 with reduced components of the electron transport chain in mitochondria can lead to reactive oxygen species formation and peroxisomes produce H_2O_2 when glycolate is oxidized into glyoxylic acid during photorespiration (Fazeli *et al.*, 2007). During stressful and normal conditions several apoplastic enzymes may also generate active oxygen species, as they also act as strong messengers. Other oxidases, responsible for the two-electron transfer to dioxygen (amino acid oxidases and glucose oxidase) can contribute to H_2O_2 accumulation (Apel and Hirt, 2004).

Tolerance

Conventional breeding and Genomic approaches

To overcome environmental stresses as well as high yield and biomass, conventional breeding approaches have been utilized with some success. Wild relative and germplasm with higher degree of tolerance have been utilized in breeding program to evolve varieties of different field crops showing enhanced tolerance to abiotic stress and improved yield. DNA markers have enormous potential to improve the efficiency and precision of conventional plant breeding through marker-assisted selection (MAS). The level of genetic diversity within *G. hirsutum* has been found to be higher than the other three cultivated cotton species (Wendel *et al.*, 1994; Abdurakhmonov *et al.*, 2008). So far, studies have indicated that this diversity does not represent in the present cultivated germplasm of upland cotton. The success of plant breeding depends on the genetic variability, which rises from the genetic relationship and the genetic diversity between and within plant groups (Rana and Bhat, 2005; Abdellatif and Soliman, 2013). Use of molecular markers accelerates these breeding processes. These markers facilitate the generation of new varieties and allow association of phenotypic traits with genomic loci. Genetic diversity is a fundamental source of crop existence and its improvement (Xiao *et al.*, 2009). Information of genetic diversity and relationships among breeding genome, their polymorphic nature, and codominance has a significant impact on crop improvement. Recently molecular markers have come up as a quite fascinating technology for identifying molecular phylogenetics, genetic

linkage mapping, conservation of gene order, genetic fidelity and genetic diversity (Belaj *et al.*, 2006; Joshi and Dhawan, 2007; Preetha and Raveendren, 2008). Since our upland cotton (*G. hirsutum*) possesses a large and complex genome, it requires a large collection of DNA markers to get maximum genome coverage (Nisar *et al.*, 2007; Xiao *et al.*, 2009) for its genome characterization. Transcription factors are found in all organisms, because they are essential for the regulation of the gene expression. Different types of transcription factors exist and an organism with a larger genome usually contains more transcription factors than one with a smaller genome. Elucidation of the mechanism of the gene expression for a particular trait is a major focus of molecular biologists to find out how different types of transcription factors are involved in the gene expression. Recently, Saibo *et al.* (2009) have described the role of a number of transcription factors involved directly or indirectly in the regulation of genes involved in photosynthesis. For example, a transcription factor LONG HYPOCOTYL 5 (HY5), a bZIP-type, was reported to be mainly involved in the regulation of *CAB* gene expression by light, although it may also exhibit a significant role in abiotic stress tolerance (Maxwell *et al.* 2003, Saibo *et al.* 2009).

This transcription factor, despite controlling the expression of *Chla/b* binding protein 2 (CAB2) (Maxwell *et al.* 2003), regulates the expression of the gene for the Rubisco small subunit (RbcS1A) (Chattopadhyay *et al.* 1998, Lee *et al.* 2007). There is another transcription factor, OsMYB4, the over expression of which has been reported to be involved in high accumulation of glycine betaine, which in turn increases stress tolerance in *Arabidopsis thaliana* (Mattana *et al.* 2005), because glycine betaine can stabilize Rubisco structure under high-saline regimes (Sakamoto and Murata 2002, Yang *et al.* 2005, Khafagy *et al.* 2009). Thus, the over expression of this transcription factor has an indirect effect on the regulation of photosynthetic genes under stressful environments. In maize, the expression of photosynthetic genes has been reported to be partly controlled by two factors DOF1 and DOF2. From the expression studies, it was evident that DOF1 is an activator of transcription, whereas DOF2 is a repressor (Yanagisawa and Sheen 1998). However, DOF1 was found to enhance the expression of the maize C4-PEPC gene. From the above, it is evident that development of transgenic lines of C_3 plants over expressing C_4 photosynthetic enzymes is a meaningful approach to improve photosynthetic capacity of C_3 plants and to bring it to the level of C_4 plants. However, the extent, to which C_4 enzymes transferred to C_3 plants play a role in effectively fixing CO_2 , depends on a number of factors including the localization of introduced C_4 enzymes within the leaf tissues and coordination of C_4 enzymes with already CO_2 fixing pathways or other allied pathways operative in C_3 plants. It has been observed that although overexpression of a single C_4 enzyme can modulate the photosynthetic metabolism in C_3 plants, in most cases, it does not have significant effects on photosynthesis. Furthermore, little success of attaining photosynthetic capacity in C_3 plants equivalent to that of C_4 plants by transferring C_4 genes to C_3 plants could have been due to non-transformation of C_3 leaf anatomical structure to that of C_4 leaf. This may be the main reason of a low effectiveness of the attempts to bring C_3 photosynthetic capacity at par with that of C_4 through genetic engineering.

Thus, alternatively, efforts should be made to improve the efficiency of CO₂ concentrating processes in C₃ plants by enhancing the activities of key enzymes through genetic manipulation. However, transgenic C₃ plants over expressing multiple C₄ enzymes are now in the focus of most scientists to improve photosynthetic capacity in C₃ plants (Miyao 2003, Begonia and Begonia 2007, Kajala *et al.* 2012). Little information is available in the literature on the components involved in either the perception or signaling involved in a stress response. This necessitates a comprehensive elucidation of the signal transduction pathways induced by different stresses so that appropriate programmes can be devised to improve plant tolerance to a variety of abiotic stresses including the functioning of the photosynthetic system. Thus, identification of signaling components involved in the stress adaptation in plants is a meaningful approach to identify transcriptional activators of adaptive mechanisms to stressful environments that are promising for improvement of crop tolerance. Keeping in view the current and future scenario of climate change it is imperative to breed crops for economic use that can cope with environmental hazards efficiently. Moreover, identification of germplasm sources carrying desired traits, and their behavior in suitable genetic backgrounds and environments.

Future Directions

Approaches with proteomics will be necessary to clarify the structural predictions of genome sequence information and to assess the protein modifications and protein–ligand interactions that are relevant to stress tolerant phenotypes. Ultimately, the functional determination of all genes that participate in stress adaptation or tolerance reactions are expected to provide an integrated understanding of the biochemical and physiological basis of stress responses in plants. Armed with such information from established models, it will be possible to rationally manipulate and optimize tolerance traits for improved crop productivity well into the twenty-first century.

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