Review Article

Physiologycal Responses of Rice Crop to Water Deficit and Water Excess Conditions

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Abstract

Rice (*Oryza sativa* L.) plays a major role as a staple food supporting more than three billion people, and it comprises 50% to 80% of their daily calorie intake (Khush, 2005). Water is a highly limited resource (Wang et.al, 2012) which is important for yield and productivity of rice crop. Water deficit stress affects rice at morphological (reduced germination, plant height, plant biomass, number of tillers, various root and leaf traits), physiological (reduced photosynthesis, transpiration, stomatal conductance, water use efficiency, relative water content, chlorophyll content, photo system II activity, membrane stability, carbon isotope discrimination and abscise acid content), biochemical (accumulation of osmoprotectant like proline, sugars, polyamines and antioxidants), at molecular levels. A thorough understanding of these characters that govern the yield of rice under water stress condition is a prerequisite (Pandey & Shukla 2015). Excess water is a natural disturbance affecting crop and forage production worldwide, and it provokes on most terrestrial plants. Adaptive traits of plants enable survival under soil water logging or partial submergence. It leads to oxygenation of submerged tissues (*i.e.* parts of shoots and entire root system), while leaves above water continue with carbon fixation. Thus, a better comprehension of plant functioning under water excess would help to assist breeding programs as well as to define better management decisions for cultivation of crops and forage species in lands prone to flooding. The present paper attempts to focus light on the physiological responses of rice crop to both the water stress conditions in a mini reviewed form.

Keywords

Introduction

Rice (*Oryza sativa* L.) is one of the three major food crops of the world being grown worldwide. It is the staple food for more than half of the world's population. It is a nutritious cereal crop, provides 20% calories and 15% protein requirements of world population. The world dedicated 162.3 million hectares in 2012 for rice cultivation, and the total production was about 738.1 million tonnes. About 92% of the world's rice is produced and consumed in Asia. A major part of Asian rice grown under flooded irrigation, and water is the main limiting factor for increased production of rice (Akinbile *et al.,* 2011). The lower productivity of Asian rice in most of the cases is attributed to various abiotic stresses including drought and submergence.

Drought is defined as water stress mainly due to lack of rain during crop growing period. Shortage of water is the main obstacle for rice production in rainfed ecosystems since most of the rice varieties are susceptible to water stress (Mostajeran; Rahimi-Eichi, 2009). Drought stress has now become a severe threat to ensure food security in the developing world. Although water is required all over the growth periods of rice plants, there are some critical growth stages when drought stress impacts seriously, creates a massive reduction in quality and quantity of yield (Islam *et al.,* 2011). The effect of drought on agriculture is extensive as it is limiting crop growth and yield. Other than that, drought stress also is involved with many biochemical, molecular and physiological changes that influence various cellular and whole plant processes, and reduce quality and quantity of yield (Prasad; Staggenborg, 2008).

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Excess water leading to submergence stress is a common environmental challenge for agriculture sustainability in many regions throughout the world. The negative impact of submergence on economic plants is mainly related to a poor gas exchange under water through impeding biochemical activities such as aerobic respiration and photosynthesis (Das *et al.,* 2005; Bailey- Serres and Voesenek, 2008; Colmer and Voesenek, 2009). Young rice seedlings are too small to escape by means of underwater leaf elongation and cannot successfully develops a canopy above the water surface. There is a large variation in the depth, duration and frequency of submergence which are dictated by the local topography. Therefore, rice plants should have adaptability to a particular target submergence environment. The major morphological and physiological submergence tolerant traits are slow leaf elongation, less chlorosis, high carbohydrate reserve storage during submergence and prompt re-adaptation to the aerial environment after de-submergence (Setter *et al.,* 1997; Ito *et al.,* 1999; Ram *et al.,* 2002; Jackson and Ram, 2003).

Drought Stress in Rice

Drought, as an abiotic stress, is multidimensional in nature, and it affects plants at various levels of their organization (Wentworth et al., 2006). In fact, under prolonged drought, many plants will dehydrate and die. Water stress in rice plant reduces the plant-cell's water potential and turgor, which elevate the solutes' concentrations in the cytosol and extracellular matrices. As a result, cell enlargement decreases leading to growth inhibition and reproductive failure (Ali, et al., 1999). This is followed by accumulation of abscisic acid (ABA) and compatible osmolytes like proline, which cause wilting. At this stage, overproduction of reactive oxygen species (ROS) and formation of radical scavenging compounds such as ascorbate and glutathione further aggravate the adverse influence. Drought not only affects plant water relations through the reduction of water content, turgor and total water, it also affects stomatal closure, limits gaseous exchange, reduces transpiration and arrests carbon assimilation (photosynthesis) rates (Razak, et al., 2013). Synthesis of new protein and mRNAs associated with the drought response is another outcome of water stress on plants. Under the water stress cell expansion slows down or ceases, and plant growth is retarded. However, water stress influences cell enlargement more than cell division. Plant growth under drought is influenced by altered photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism, and hormones. Some aspects of drought induced effect on

morphological, physiological, biochemical, molecular, yield and its associated traits as well as acclimation and tolerant mechanisms of rice to drought stress are discussed below.

Effects of Drought on Morphological Characteristics

Plant experiences drought stress either when the water supply to roots becomes difficult or when the transpiration rate becomes very high. It severely impairs growth, development and ultimately the production of rice. When water stress occurs, plants react by slowing down or stopping their growth. This is a normal plant reaction to lack of water, and it acts as a survival technique (Zhu, 2002). Plant growth and development reduces as a consequence of poor root development, with reduced leaf-surface traits form, shape, composition of cuticular wax, leaf pubescence and leaf color, which affect the radiation load on the leaf canopy, delay in or reduced rate of normal plant senescence as it approaches maturity, and inhibition of stem reserves (Blum, 2011). Drought affects both elongation as well as expansion growth (Shao *et al.,* 2008), and inhibits cell enlargement more than cell division (Jaleel *et al.,* 2009). It impairs the germination of rice seedlings (Jiang and Lafitte, 2007; Swain *et al.,* 2014) and reduces number of tillers (Mostajeran and Rahimi-Eichi, 2009; Ashfaq *et al.,* 2012; Bunnag and Pongthai, 2013) and plant height (Sarvestani *et al.,* 2008; Ashfaq *et al.,* 2012; Bunnag and Pongthai, 2013; Sokoto and Muhammad, 2014).

Adaptaion of Rice Based on Morphology

- *Flag Leaf*

For grain filling to occur under drought, either a relatively uncompromised or a favourably reprogrammed function of flag leaf is required to maintain synthesis and transport of photo assimilates. Thus, various traits of flag leaf (Biswal and Kohli, 2013) have been proposed for selecting drought tolerant plant, i.e. higher flag leaf area, relative dry weight, excised leaf weight loss, residual transpiration, leaf glaucousness, canopy temperature depression, chlorophyll content, late senescence and higher carbon isotope discrimination (CID).

- *Leaf Rolling*

It is one of the acclimation responses of rice, and is used as a criterion for scoring drought tolerance. Leaf rolling is hydro nasty that leads to reduced light interception, transpiration and leaf dehydration (Kadioglu and Terzi, 2007). It may help in maintaining

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internal plant water status (Turner *et al.,* 1986; Abd Allah, 2009; Gana, 2011; Ha, 2014).

- *Root Traits*

Have been claimed to be critical for increasing yield under water stress. The structure and development of rice root system largely determine crop function under drought. Under mild water deficit, the root growth usually maintains while shoot growth is inhibited. This is because of the facts on the adjustment and re-establishment of water potential gradient through osmotic alteration and increase in loosening ability of the cell wall, which permit roots to resume growth under low water potential. Root dry mass and length are good predictors of rice yield under drought (Fageria and Moreira, 2011; Feng *et al.*, 2012).

Effects of Drought on Biochemical Characteristics

As water deficit occurs, plants accumulate different types of organic and inorganic solutes in the cytosol to lower osmotic potential, thereby maintaining cell turgor (Rhodes and Samaras, 1994). This biochemical process is known as osmotic adjustment which strongly depends on the rate of plant water stress. Osmotic adjustment is achieved by the accumulation of proline, sucrose, glycinebetaine and other solutes in cytoplasm, improving water uptake from drying soil. Of these solutes, proline is the most widely studied because of its considerable importance in the stress tolerance. Drought also induces the accumulation of soluble sugars (Shehab *et al.,* 2010; Usman *et al.,* 2013; Maisura *et al.,* 2014). Other biochemical response includes increase in the antioxidant activity which improves drought tolerance by scavenging reactive oxygen species.

- *Role of Proline*

Proline plays a highly beneficial role in plants exposed to various stress conditions (Verbruggen and Hermans, 2008). Proline acts as osmolyte and its accumulation contributes to better performance and drought tolerance (Vajrabhaya *et al.,* 2001). Besides acting as an excellent osmolyte, proline plays three major roles during stress, i.e., as a metal chelator, an antioxidative defence molecule and a signaling molecule (Hayat *et al.,* 2012). Proline accumulation might promote plant damage repair ability by increasing antioxidant activity during drought stress.

Role of Polyamines

Polyamines (PAs) are small positively charged molecules (Fuell *et al.,* 2010; Takahashi and Kakehi, 2010), which are involved in the response to drought (Calzadilla *et al.,* 2014). Most ubiquitous PAs in plants are putrescine (Put), spermidine (Spd) and spermine (Spm). They stabilize membranes, regulate osmotic and ionic homeostasis, and act as antioxidants and interact with other signal molecules. Under drought stress conditions, higher PAs contents in plants are related to increased photosynthetic capacity, reduced water loss, improved osmotic adjustment and detoxification.

- *Role of Antioxidants*

A common effect of drought stress is the disturbance between the generation and quenching of reactive oxygen species (ROS) (Smirnoff, 1998; Faize *et al.,* 2011). ROS includes superoxide radical, hydroxyl free radical, hydrogen peroxide and singlet oxygen, and causes peroxidation of lipids, denaturation of proteins, mutation of DNA, disrupt cellular hemeostasis and various types of cellular oxidative damage. Plant cells are protected against the detrimental effects of ROS by a complex antioxidant system comprising of the non-enzymatic as well as enzymatic antioxidants. Ascorbate (AsA) and glutathione (GSH) are served as potent non-enzymatic antioxidants within the cell. The enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidise (GPX), enzymes of ascorbate-glutathione cycle, ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) (Noctor and Foyer, 1998). These antioxidants are critical components of the ROS scavenging system in plant, and their expressions can improve drought tolerance in rice (Wang *et al.,* 2005). With increasing levels of drought stress in rice, the activities of AsA, GSH, APX (Selote and Khanna- Chopra, 2004), SOD, MDHAR, DHAR, GR (Sharma and Dubey, 2005), phenylalanine ammonia-lyase and CAT (Shehab *et al.,* 2010) consistently increase. The increases in the activities of these antioxidant defence enzymes represent the protective activity to counteract the oxidative injury promoted by drought conditions in rice. The activities of SOD, POD and CAT can effectively diminish the ROS, and thereby reducing negative impact of drought (Lum *et al.,* 2014; Yang *et al.,* 2014).

Effects of Drought at Molecular Level

At the molecular level, the response to drought stress is a multigenic trait. Through high-throughput molecular studies, a number of genes that respond to

drought stress at the transcriptional level have been reported (Shinozaki and Yamaguchi-Shinozaki, 2007). Some of these genes in rice have been found to protect plants from desiccation through stress perception, signal transduction, transcriptional regulatory networks in cellular responses or tolerance to dehydration (Wang *et al.*, 2005). The products of these stress-inducible genes are classified into two groups.

I.   The first group includes proteins that directly protect against stress, probably by protecting cells from dehydration, such as the enzymes required for the biosynthesis of various osmoprotectants, late embryogenesis abundant (LEA) proteins, antifreeze proteins, chaperones and detoxification enzymes.

II. The second group are those that regulate gene expression and signal transduction in the stress response, which include transcription factors and protein kinases (Seki *et al.*, 2003).

This drought induced regulatory and functional genes have been used to increase drought tolerance through gene transfer. Thus, it is important to analyze the functions of stress inducible genes not only to understand the molecular mechanisms of stress responses, but also to improve the stress tolerance of crops by gene manipulation.

Effects of Drought on Physiological Characteristics

Drought stress affects various physiological processes and induces several physiological responses in plants, which help them to adapt to such limiting environmental conditions. Optimization of these physiological processes is prerequisite for increased water productivity under water stress (Serraj *et al.*, 2009). The knowledge of these physiological responses of rice under drought conditions may contribute to ongoing studies on providing drought resistance in rice. An important physiological response of plants to drought is its ability to maintain turgor pressure by reducing osmotic potential as a tolerant mechanism (Maisura *et al.*, 2014). Water deficit affects rice physiology in countless ways like it affects plant net photosynthesis (Centritto *et al.*, 2009; Yang *et al.*, 2014), transpiration rate (Cabuslay *et al.*, 2002), stomatal conductance (Ji *et al.*, 2012; Singh *et al.*, 2013), water use efficiency (Cha-um *et al.*, 2010), intercellular CO_2, photosystem II (PSII) activity (Pieters and Souki, 2005), relative water content (Biswas and Choudhuri, 1984; Pirdashti *et al.*, 2009; Cha-um *et al.*, 2010) and membrane stability index (Kumar S *et al.*, 2014). All these parameters reduce under water stress in rice

(Farooq *et al.*, 2010; Akram *et al.*, 2013; Ding *et al.*, 2014).

•   *Effects of Drought on Photosynthesis*

Photosynthesis is the main metabolic process determining crop production, and is affected by drought stress. Drought induced reduction in photosynthetic rate of rice has been well documented (Ji *et al.*, 2012; Lauteri *et al.*, 2014; Yang *et al.*, 2014). The major components limiting photosynthesis are the CO_2 diffusional limitation due to early stomatal closure, reduced activity of photosynthetic enzymes, the biochemical components related to triose-phosphate formation and decreased photochemical efficiency of PSII. Change in any of these components alters the final photosynthesis rate. Stomatal (*g*s) and mesophyll conductance (*g*m) to CO_2 often decrease in response to drought (Centritto *et al.*, 2009). Thus, the ability to maintain the *g*m values under water-deficits determines the drought tolerance of rice varieties (Lauteri *et al.*,2014). Activity of PSII is crucial in providing reducing power and ATP. If PSII activity exceeds the demand, over-reduction of the photosynthetic electron transport chain may occur, and this stimulates the formation of reactive oxygen species. Therefore, there must be balance between photochemical activity and the demand for photo assimilates. Drought severely impairs PSII activity in the flag leaf of rice plants (Pieters and Souki, 2005). This may be due to drought induced degradation of D1 polypeptide, leading to the inactivation of the PSII reaction center. Severe drought conditions limit photosynthesis due to a decline in Rubisco activity, which is an enzyme of the Calvin cycle (Bota *et al.*, 2004; Zhou *et al.*, 2007). However, the amount of Rubisco activase, which rescues Rubisco sites from dead end inhibition by promoting ATP-dependent conformational changes, enhances under the drought stress as a protective mechanism. The up-regulation of this enzyme might alleviate the damage on Rubisco by drought stress (Ji *et al.*, 2012). Recently, it has been observed that introduction of enzymes involved in photosynthesis of C4 plants in rice enhances the photosynthesis and crop productivity under stress. It is speculated that drought tolerance is greatly enhanced in transgenic rice plants over expressing C4 photosynthesis enzymes like pyruvate orthophosphate dikinase and phosphoenolpyruvate carboxylase (Zhou *et al.*, 2011; Gu *et al.*, 2013). This is attributed to the fact that the enzymes involved in C4 photosynthesis are more tolerant to drought than those involved in C3 photosynthesis. This approach opens up new avenue in developing drought tolerance in rice.

•   *Effects of Drought on Photosynthetic Pigments*

Drought causes many changes related to altered metabolic functions, and one of those is either loss of or reduced the synthesis of photosynthetic pigments. This results in declined light harvesting and generation of reducing powers, which are a source of energy for dark reactions of photosynthesis. These changes in the amounts of photosynthetic pigments are closely associated to plant biomass and yield (Jaleel *et al.*, 2009). Chlorophyll is one of the important pigments of photosynthetic apparatus which absorbs light and transfers light energy to the reaction center of the photosystem. Both chlorophyll a and b are prone to soil drying. However, other pigment carotenoids have additional roles in chloroplast photosystem structure, light harvesting and photoprotection, and partially help the plants to withstand adversaries of drought. Decreases in chlorophyll content and the maximum quantum yield of PSII (Fv/Fm) have been reported in many studies on drought stressed rice (Pirdashti *et al.*, 2009; Cha-um *et al.*, 2010; Sikuku *et al.*, 2012; Ha, 2014; Maisura *et al.*, 2014). Yang *et al.*, 2014) speculated that the reductions in chlorophyll content and the Fv/Fm of autotetraploid lines were less pronounced under drought than their corresponding diploid lines, suggesting that autotetraploid rice is more tolerant to drought stress. This reduction in chlorophyll content may occur due to stress-induced impairment in pigment biosynthetic pathways or in pigment degradation, loss of the chloroplast membrane, and increased lipid peroxidation.

Chlorophyll-a is a universal pigment and Chlorophyll-b is found in the higher plants. A decrease in chlorophyll a content has the ability to change the reaction energy of light radiation decreases such that photosynthesis is inhibited. Chlorophyll b acts as a photosynthetic antenna that collects light. The higher amount of Chlorophyll-a and Chlorophyll-b attributes to the accumulation of solutes in the cell sap through passive accumulation resulting from reduced cell size which significantly does osmotic adjustment ($\Delta\psi\pi$). Chlorophyll content in 12 different rice varieties grown under three different water regimes were reported by Chutia and Borah (2012).

- *Effects of Drought on Water Relations*

A key factor determining plant productivity under drought conditions is water use efficiency (WUE), and it is mentioned as a strategy to improve crop performance under water limited conditions (Araus *et al.*, 2002). Agronomic parameters like photosynthetic rate, relative water content (RWC) and stomatal conductance show strong positive correlations with WUE, whereas transpiration rate expresses negative correlation with WUE under drought in basmati rice varieties (Akram *et al.*, 2013). CID has been suggested as an indirect tool for selecting plants having higher WUE and yield potential. The physiological basis for CID variation in C3 plants is related to the variation in the internal CO_2 concentration (Ci) to ambient CO_2 concentration (*C*a) ratio. High CID values resulting from high Ci/Ca will lead to low transpiration efficiency. Under drought conditions, CID is negatively correlated to transpiration efficiency (Dingkuhn et al, 1991; Scartazza *et al.*, 1998; Cabuslay *et al.*, 2002; Kondo *et al.*, 2004) and WUE (Impa *et al.*, 2005) at the leaf level in rice. The discrimination against the heavier carbon isotope, ^{13}C, is calculated as the ^{13}C/^{12}C ratio in plant material relative to the value of the same ratio in the air assimilated by plants. CID has been proposed by several authors as an indirect selection criterion for yield under drought (Condon *et al.*, 2002; Akhter *et al.*, 2010; Mohankumar *et al.*, 2011). In general, water stress increases carbon isotope ratio ($\delta^{13}C$) and decreases CID values in rice (Kondo *et al.*, 2004; Zhao *et al.*, 2004; Impa *et al.*, 2005; Centritto *et al.*, 2009). Genotypic variation has been reported for $\delta^{13}C$ or CID values in rice. The japonica genotypes show higher $\delta^{13}C$ values or lower CID values than the indica ones (Takai *et al.*, 2009; Xu *et al.*, 2009; This *et al.*, 2010). Recently, much attention has been focused on the differences in $\delta^{13}C$ between plant organs. $\delta^{13}C$ of different parts in rice plant is affected differentially under drought. The differences in carbon isotope composition among plant parts are related to the differences in fractionation processes during transport, the synthesis of metabolites, and the chemical composition of different organs, such as the amounts of lipids and lignin (Brugnoli and Farquhar, 2000). Kano-Nakata *et al.*, (2014) suggested that among various plant organs, the $\delta^{13}C$ value of panicles may be the best indicator of plant water status in rice under drought.

Effects of Drought on Stress Hormone (Abscisic Acid)

Abscisic acid (ABA) is a growth regulator and is also involved in stress tolerance. Several studies have confirmed its role in mediating plant responses against drought stress conditions through a series of signal transduction pathways. A dynamic accumulation of ABA in response to water stress has been well studied in rice (Wang *et al.*, 2007; Ye *et al.*, 2011; Ashok Kumar *et al.*, 2013). ABA imparts drought stress tolerance in part by inducing a significant increase in antioxidant enzymes (Latif, 2014; Li *et al.*, 2014), and improving protein transport, carbon metabolism and expression of resistance proteins (Zhou *et al.*, 2014). Exogenous ABA application in

rice enhances the recovery of the net photosynthetic rate, stomatal conductance and transpiration rate under drought, with increased expression of various drought responsive genes (Teng *et al.,* 2014). ABA regulates stomatal movement (Ahmad *et al.,* 2014), and it is an important component of drought tolerance strategy for reduced water loss by closing stomata. The mechanism of action involves ABA receptor and responsive proteins. The genes for soluble ABA receptors have been identified as PYR/PYL/RCARs (pyrabactin resistance/PYR1-LIKE/regulatory components of ABA receptors) (Ma *et al.,* 2009; Park *et al.,* 2009), and play major roles in ABA mediated regulation of SnRK2 kinase (sucrose nonfermenting1-related protein kinases 2) activity (Gonzalez-Guzman *et al.,* 2012). This SnRK2 regulates guard cell channel activities by activation of the anion channel (Geiger *et al.,* 2009; Lee *et al.,* 2009), inducing depolarization of the guard cell membrane, resulting in the outward movement of potassium ions as well as closures of stomatal pores (Kim *et al.,* 2010). ABA also induces the expression of many genes whose products are involved in the response to drought. These genes are mainly activated by a group of transcription factors, which specifically bind to promoters containing ABA-responsive elements (Antoni *et al.,* 2011; Fujita *et al.,* 2011; Rushton *et al.,* 2012). These ABA-induced genes encode proteins involved in stress tolerance while ABA-repressed gene products are associated with growth. All these indicate the central role of ABA in plant tolerance to drought stress.

Effects of Submergence on Rice

In a broad sense, the term flooding is often used to depict different situations in which the water excess can range from water saturated soil (*i.e.* water logging) to deep water columns causing complete submergence of plants. Water logging corresponds to the full saturation of the soil pores with water, and with a very thin – or even without - a layer of water above the soil surface. Hence, under waterlogged conditions, only the root system of plant is under the anaerobic conditions imposed by the lack of oxygen, while the shoot is under atmospheric normal conditions. Flooding is the situation in which there is a water layer above the soil surface. This water layer can be shallow or deep, so that it can provoke partial or complete submergence of plants. Under partial submergence conditions, plants have a portion of their shoots underwater, besides having their roots completely immersed in water-saturated soil. Under complete submergence, plants confront the most stressful scenario because both, shoot and root plant compartments, are underwater, and in this case, the chances to capture atmospheric oxygen and to continue with carbon fixation are restricted. This situation is worsened in turbid water and/or with deep water columns above plants because the irradiance available to sustain underwater photosynthesis for survival is drastically reduced (Mommer *et al.,* 2004; Colmer & Pedersen, 2008; Vashist *et al.,* 2011).

• *Plant Responses to Partial Submergence*

Plants develop a suite of anatomical, morphological and physiological responses in order to deal with partial submergence imposed by flooding (Armstrong, 1979; Kozlowski & Pallardy, 1984; Vartapetian & Jackson, 1997; Striker *et al.,* 2005; Colmer & Voesenek, 2009). The most common anatomical response is the generation of aerenchyma in tissues (Justin & Armstrong, 1987; Seago *et al.,* 2005), which facilitates the transport of oxygen from shoots to roots (Colmer, 2003a). At morphological level, usual responses to flooding include adventitious rooting , increases in plant height and consequently, in the proportion of biomass above water level (Naidoo & Mundree, 1993; Grimoldi *et al.,* 1999). This also helps to facilitate the oxygenation of submerged tissues through the aerenchyma tissue (Laan *et al.,* 1990; Colmer, 2003a). At physiological level, flooding modifies water relations and plants carbon fixation. Closing of stomata, with or without leaf dehydration, reduction of transpiration and inhibition of photosynthesis, are responses that can occur in hours or days, depending on the tolerance to flooding of each plant species (Bradford & Hsiao, 1982; Else *et al.,* 1996; Insausti *et al.,* 2001; Striker *et al.,* 2005; Mollard *et al.,* 2008; 2010). The following sections show the main plant responses at those levels associated with tolerance to flooding.

• *Anatomical Traits of Tolerance to Partial Submergence*

Rice roots under submerged condition (traditional cultivation) consist of more aerenchyma and air spaces than plants under irrigated condition. Interestingly, the roots of plants grown in irrigated condition for four months generally had less aerenchyma than those of plants grown in submerged system for two months (Figure C-F). A decrease in root's aerenchyma was observed in all cultivars in irrigated condition compared to the submerged treatment (control). The existence of aerenchymas helps the plants under conditions of excess water in the soils to maintain aerobic respiration by

maintaining O_2 diffusion (Colmer, 2003). Although, under flooded condition, the formation of aerenchyma consider as a favourite characteristic, It can be appeared as a significant weakening factor under irrigated treatment (Striker *et al.*, 2007a). Roots commonly suffer mechanical stress during their lifespan (Bennie, 2002) due to water level fluctuation. The advantage of increased root porosity for oxygenation could endanger the mechanical strength of the roots, which helps them resist the subsequent soil shrinkage associated with the decrease of soil water content immediately after flooding. However, anatomical features that facilitate growth in waterlogged soils may cause limitations for root functioning under well-drained conditions (Stirker, 2007). Aerenchyma formation may weaken the root structure. After flooding, when the soil becomes more compacted, the aerenchymatous structure may collapse under external pressure and the amount of functional root tissue may be reduced (Engelaar *et al.*, 1993).
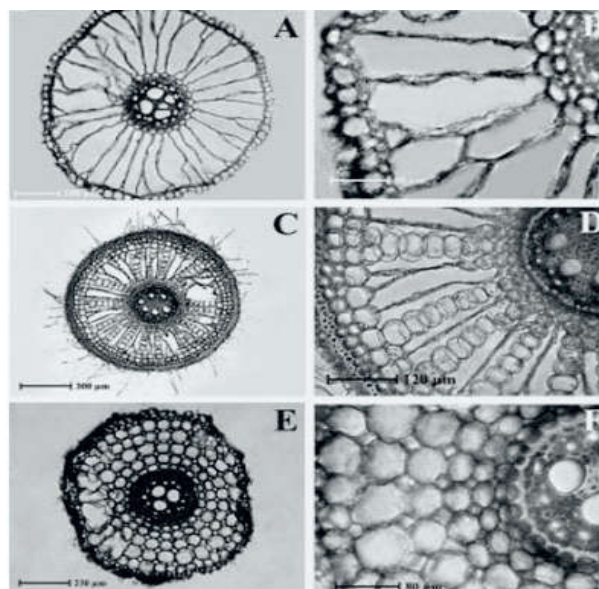

Fig. 1: Sections of roots of rice (*Oryza sativa L.*) plants cultivar Zayande-Rood (A-F). Aerenchyma formation at submergence (A and B), irrigated (2 months under treatment) (C and D) and irrigated (4 months under treatment) (E and F). The cross-sections were obtained at 20 mm from the root tip (Reproduced from Mostajeran *et al.,* 2008 with due permission).

• *Morphological Responses of Rice Tolerance to Partial Submergence*

Submergence induces morphological changes in roots and shoots. In roots, the formation of adventitious roots is highlighted as a common response of flood-tolerant species. These adventitious roots, which have high porosity, help plants to continue with water and nutrient uptake under partial submergence conditions, replacing in some way the functions of older root system (Kozlowski &

Pallardy, 1984). The two first mechanisms appear to be triggered by ethylene, which is thought to increase the sensitivity of plant tissues to auxin (Bertell *et al.,* 1990; Liu & Reid, 1992). In graminaceous species the morphological responses are analogous to those developed by dicots. The morphological responses to partial submergence is the increase in the tiller insertion angle (Insausti *et al.,* 2001) followed by the elongation of the leaf sheaths, and lastly (but not always) elongation of leaf blades (Insausti *et al.,* 2001; Mollard *et al.,* 2008; 2010). The higher leaf sheath length of flooded plants is the result of a higher number of longer parenchymatic cells with respect to control plants (Insausti *et al.,* 2001). Another specific change at shoot level implies stem hypertrophy, which is a white spongy tissue with large volumes of intercellular gas spaces (Armstrong *et al.,* 1994). This tissue is secondary aerenchyma that forms externally from a phellogen, and is homologous to cork (Shimamura *et al.,* 2010). Its role seems to be increasing air space which allows for increased movement of gases between water and plant tissues (Teakle *et al.,* 2011).

• *Physiological Responses of Rice to Partial Submergence*

❖ *Plant Water Relations*

In flood sensitive plants a few hours after the soil becomes flooded, the water uptake by roots is reduced (Bradford & Hsiao, 1982; Jackson & Drew, 1984). Here, the reduction of water absorption under flooding is a consequence of a reduction of the root hydraulic conductivity (Else *et al.,* 1995; Else *et al.,* 2001; Islam & McDonald, 2004) that seems to be associated with the acidification of the cell cytoplasm and the gating of aquaporins (Tournarie-Roux *et al.,* 2003). It appears that the excess of protons provoking such acidification, determines conformational changes of the mentioned water channels that trigger their closure (Tournarie-Roux *et al.,* 2003; Verdoucq *et al.,* 2008). So, the reduction of water uptake under water excess of the soil in flooding sensitive species shows the paradoxical response of wilting of leaves (Bradford & Hsiao, 1982; Else *et al.,* 1996), as it can be seen under drought. In this type of species, unable to tolerate short-term flooding, plants die (without recovery) when the water recedes. In flood-tolerant plants, the plant water relations during flooding can vary depending on the season of occurrence and naturally on species-specific responses (Crawford, 2003; Lenssen *et al.,* 2004).

❖ *Photosynthesis Responses*

A common response to submergence is the

reduction of plant carbon fixation (*i.e.* rate of photosynthesis; Jackson & Drew, 1984). In the short term, photosynthesis can drop as a result of a restriction of CO_2 uptake due to stomata closing (Jackson & Hall, 1987; Huang *et al.,* 1994; Malik *et al.,* 2001; Striker *et al.,* 2005; Mollard *et al.,* 2010). Several works have shown correlation between stomatal conductance and carbon fixation in flooded plants indicating that stomatal aperture can be a limiting factor for photosynthesis (Vu & Yelenosky, 1991; Liao & Lin, 2001; Mielke *et al.,* 2003). Stomata closing under submergence can occur in response to leaf dehydration where the guard-cells lose their turgor (Bradford & Hsiao, 1982; Striker *et al.,* 2007b), but it can also occur without noticeable changes in the leaf water potential responding to a hormonal (non-hydraulic) regulation (Jackson & Hall, 1987; Jackson, 2002; Striker *et al.,* 2005).

❖ *ROS under Flood Stress*

In the last case, the available evidence supports the idea of stomatal closure mediated by action of abscisic acid (ABA) in leaves (Else *et al.,* 1996; Jackson *et al.,* 2003), but not synthetized and transported from the roots, as it happens under drought stress (Davies & Zhang, 1991). If flooding continues in time, a decrease in the photosynthetic capacity of mesophyll cells *per se* (Liao & Lin, 1994; Yordanova & Popova, 2001) leads to a further reduction of photosynthesis. Such lower photosynthetic capacity can be attributed to a

(i) lower leaf chlorophyll content (Yordanova & Popova, 2001; Manzur *et al.,* 2009; *cf.* leaf greenness of flooded *vs.* control plant),

(ii) a reduced activity of carboxylation enzymes, and

(iii) an oxidative damage on photosystem II by reactive oxygen species (Yordanova *et al.,* 2004).

In addition, the low photon utilization of flooded plants (Titarenko, 2000 as cited in Yordanova *et al.,* 2004) could result in the production of reactive oxygen species (ROS) (Asada and Takahashi, 1987). The main ROS are superoxide, single oxygen, hydrogen peroxide and hydroxyl radical, which are very reactive and provoke damage to lipid membranes and proteins (Foyer *et al.,* 1994; Noctor & Foyer, 1998). To manage the level of ROS for protecting cells, plants have antioxidants like ascorbate, glutathione and tocopherols, and enzymes (*i.e.* peroxidases, superoxide dismutase, glutathione reductase, catalase) with ability to scavenge ROS and regenerate the antioxidants (Asada, 2006; Murchie & Niyogi, 2011). However, under flooding stress, the scavenging

capacity can be over passed due to the higher production of ROS, thus generating oxidative damage on the proteins of the photosynthetic apparatus (Yordanova *et al.,* 2004). If it is scaled up, the negative effects of flooding on photosynthesis from the leaf level to the plant level can lead to a low growth rate in flooded plants. Such a reduction in growth, determines a low demand of triose phosphate for sucrose biosynthesis as well as a slowdown on the phloem transport of this sugar (Pezeshki, 1994; Pezeshki, 2001; Sachs & Vartapetian, 2007). Consequently, starch starts to accumulate in the chloroplasts (Wample & Davies, 1983) leading to a negative feedback on photosynthesis rate (Liao & Lin, 2001).

Plant Responses to Complete Submergence

Complete submergence is one of the most stressful scenarios that plants can confront in environments prone to soil flooding (Mommer & Visser, 2005; Colmer & Voesenek, 2009). In addition to oxygen deficiency for roots occurring during water excess in soil, rice subjected to complete submergence are restricted from obtaining enough oxygen for sustaining tissue aeration, even though in some species, oxygen can partially be supplied by underwater photosynthesis (Mommer *et al.,* 2004; Colmer & Pedersen, 2008; Vashist *et al.,* 2011). As a result, aerobic metabolism for energy production shifts to the much less efficient anaerobic/fermentative pathways (Gibbs & Greenway, 2003; Voesenek *et al.,* 2006; Kulichikhin *et al.,* 2009). Besides, depending on the turbidity of the water, light reduction can constrain carbon gain by photosynthesis (Sand-Jensen, 1989; Colmer & Pedersen, 2008). Therefore, complete submergence can cause a drastic energy and carbohydrate crisis that can threaten plant survival (Voesenek *et al.,* 2006; Bailey-Serres & Voesenek 2008; 2010). According to Colmer & Voesenek (2009), this stress can be classified depending on water depth and duration of the submergence. With respect to water, shallow floods are those of less than 0.5-1 meter of water column, in which submerged plants have chances to surpass the water level if they respond elongating their shoots (Setter & Laureles, 1996; Lynn & Waldren, 2003; Hattori *et al.,* 2010). On the other hand, deep floods are those of more than 1 m of water column, in which the effort of trying to de-submerge the plant shoots is useless, because the chances to surpass the water are non-existent. In these cases, the pursued benefit of developing a shoot elongation response is not outweighed by the incurred cost, because the plant exhausts its carbohydrates reserves, dying before reaching the water surface. In contrast, plants that

remain quiescent are able to succeed in front to deep submergence, surviving by using carbohydrates reserves to maintain a basal metabolism until water subsides (Schlüter & Crawford, 2001; Ram *et al.,* 2002; Manzur *et al.,* 2009; Striker *et al.,* 2011b).

Conclusion

Abiotic stresses can directly or indirectly affect the physiological status of an organism by altering its metabolism, growth, and development. To facilitate the development of tolerant varieties which can survive and give better yields under drought conditions, a thorough understanding of the various morphological, biochemical, physiological and molecular characters that govern the yield of rice under water stress condition is a prerequisite. Most physiological and metabolic processes are affected by water deficits which include stomatal regulation, photosynthesis, translocation, PSII activity, chlorophyll content, etc. Maintenance of these processes for prolonged period of time under stress is a desired character. Since, ABA is an important component of signalling under stress, efficient ABA signalling also ensures tolerance. Further, the enhancement of the naturally occurring antioxidant components (enzymatic and non-enzymatic) may be another strategy for reducing oxidative damage. Knowledge of how plants are affected by water stress at molecular scale, and development of varieties tolerant to different regimes of water stress is important for the sustainable production of rice crop.

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Special Note!