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Review

Waterlogging stress in plants: A review

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Waterlogging is the major obstacle for sustainable agriculture. Plants subjected to waterlogging suffer from substantial yield losses. Under natural environmental conditions, plants often get exposed to transient or permanent waterlogging. Flooding induces a number of alterations in important soil physio-chemical properties like soil pH, redox potential and oxygen level. Thus, the plants growing on the waterlogged soil face the stressful environment in terms of hypoxia (deficiency of O_2) or anoxia (absence of O_2). These oxygen deficient conditions substantially hamper plant growth, development and survival. Plants under O_2-restrictive environment exhibit metabolic switch from aerobic respiration to anaerobic fermentation. It is evident from the available literature that most of the genes expressed under flooding stress are potentially involved in the synthesis of enzymes known to play active role in the establishment of this fermentative pathway. Plants undergo this metabolic change in order to get continuous supply of Adenosine triphosphate (ATP). Under waterlogged conditions, plants exhibit several responses including hampered stomata conductance, net CO_2-assimilation rate and root hydraulic conductivity. Furthermore, plants grown under waterlogged conditions often face the oxidative damage induced by the generation of reactive oxygen species. These reactive oxygen species in turn affects the integrity of membranes and induce damage to the efficiency of photosystem II, thereby, causing considerable decrease in net photosynthetic rates. Moreover, these perturbations in physiological mechanisms may affect the carbohydrate reserves and translocations. In fact, waterlogging tolerant and sensitive plant species could be discriminated on the basis of their efficient carbohydrate utilization. Waterlogging is also known to induce adverse effects on several physiological and biochemical processes of plants by creating deficiency of essential nutrients like nitrogen, magnesium, potassium, calcium. Apart from these waterlogging-induced alterations in physiological mechanisms, plants growing under flooded conditions also exhibit certain morphological changes entailing the formation of adventitious roots, initiation of hypertrophied lenticels and/or establishment of aerenchyma. Therefore, the aim of this review is to highlight the major morphological, physiological and biochemical adaptations of plants to tolerate the flooding stress.

Key words: Hypoxia, anoxia, fermentation, Adenosine triphosphate (ATP), reactive oxygen species (ROS), antioxidants.

INTRODUCTION

In tropical and subtropical regions, excessive rainfall is the major constraint for crop production. Elevated levels of water in soil create hypoxic conditions (decrease in the level of oxygen) within a short period of time. As a result plant roots suffer from anoxia, complete absence of oxygen (Gambrell and Patrick, 1978). However, plants tolerant to waterlogging (flooding) stress exhibit certain adaptations, for example, formation of aerenchyma and adventitious roots. Furthermore, the formation of adventitious roots is due to the interaction of plant hormones, auxin and ethylene (McNamara and Mitchell, 1989). Oxygen deficiency inhibits the root respiration of plants which results in substantial reduction in energy status of root cells. Since oxygen is a terminal electron acceptor in aerobic respiration, in its absence, Kreb's cycle and electron-transport system are blocked. Therefore, plants under waterlogged conditions use alternate pathway for energy extraction. This alternate pathway uses fermentative metabolism to produce Adenosine triphosphate (ATP), thereby, resulting in enhanced accumulation of ethanol.

Moreover, the activity of alcohol dehydrogenase (ADH) is also increased (Davies, 1980; Vartapetian, 1991).

In fermentation, plants could get only two ATP per glucose molecule, whereas, 36 ATP molecules are produced per glucose molecule in aerobic respiration. Flood-tolerant plants are able to maintain their energy status using fermentation. In addition, the maintenance of cytosolic pH is of prime importance. In waterlogged plants, initial decline in cytosolic pH has been observed and this decline is attributed to the production of lactic acid during fermentation. This initial decrease in pH helps the plant to switch from lactate to ethanol fermentation by activation of alcohol dehydrogenase and inhibition of lactate dehydrogenase (Chang et al., 2000). As under hypoxic or anoxic conditions oxygen is lacking, therefore, alternative electron acceptor is required. For example, nitrate has been considered as terminal electron acceptor of plant mitochondria under anoxic or hypoxic conditions (Vartapetien et al., 2003). It has also been suggested that nitrate reduction is an alternate respiratory pathway and is important for the maintenance and energy homeostasis of the cell in the oxygen deficient environment (Igamberdiev and Hill, 2004).

WATERLOGGING-INDUCED ALTERATIONS IN PHYSIOLOGICAL MECHANISMS

One of the first plant responses to waterlogging is the reduction in stomata conductance (Folzer et al., 2006). Plants exposed to flooding stress exhibit increased stomata resistance as well as, limited water uptake leading to internal water deficit (Parent et al., 2008). In addition, low levels of O_2 may decrease hydraulic conductivity due to hampered root permeability (Else et al., 2001). Oxygen deficiency generally leads to the substantial decline in net photosynthetic rate (Ashraf et al., 2011). This decrease in transpiration and photosynthesis is attributed to stomata closure (Ashraf and Arfan, 2005). However, other factors such as reduced chlorophyll contents, leaf senescence and reduced leaf area are also held responsible for decreased rates of photosynthesis (Malik et al., 2001). In this context, Yordanova et al. (2005) reported fast stomata closure in barley plants when subjected to flooding conditions. Similarly, when pea plants were subjected to flooding conditions, a prompt closure of stomata was recorded (Zang and Zang, 1994). This stomata closure of pea plants was attributed to the abscisic acid (ABA) transport from older to younger leaves or denovo synthesis of this hormone.

Furthermore, prolonged exposure of plants to flooding conditions could result in root injuries which in turn restrict photosynthetic capacity by inducing certain alterations in biochemical reactions of photosynthesis. These biochemical alterations include restricted activity of ribulose bisphosphate carboxylase (RuBPC), phosphoglycollate and glycollate oxidase (Yordanova and Popova, 2001), demolition of chloroplast membrane inhibiting photosynthetic electron transport and efficiency of photosystem II (Titarenko, 2000). It is evident from the literature that flooding causes a marked reduction in photosynthetic capacity of a number of plants, for example, *Lolium perenne* (McFarlane et al., 2003), *Lycopersicon esculentum* (Bradford, 1983; Jackson, 1990) *Pisum sativum* (Jackson and Kowalewska, 1983, Zhang and Davies, 1987), and *Triticum aestivum* (Trought and Drew, 1980). However, plants exhibit certain adaptation under waterlogging stress to maintain photosynthetic capacity (Li et al., 2004). Moreover, flood-induced destruction of chlorophyll has been investigated widely by a number of researchers (Jackson et al., 1991; Huang et al., 1994; Ashraf et al., 2011). This decrease in chlorophyll directly or indirectly affects the photosynthetic capacity of plants under waterlogged conditions (Ashraf et al., 2011).

The adverse effects of waterlogging on different gas exchange attributes of plants have been reported in some earlier studies. For example, Ashraf and Arfan (2005) reported decrease in photosynthetic rate, water use efficiency and intrinsic water use efficiency of 32-day okra plants when subjected to waterlogged conditions. It is a general consensus that stomata regulation controls the CO_2 exchange rate of plants under waterlogged conditions (Ashraf and Arfan, 2005; Ashraf et al., 2011). Furthermore, water potential of plants is also controlled to some extent by stomata regulations (Liao and Lin, 1996). However, there are contrasting reports on the involvement of stomatal regulation in maintenance of water potential. For example, waterlogging caused a marked reduction in stomata conductance of bitter melon. This reduction in g_s resulted in increased leaf water potential (Liao and Lin, 1994). In contrast, Ashraf and Arfan (2005) found no significant correlation between stomata conductance and water potential of okra plants under waterlogged conditions. In fact, these authors were of the view that osmotic potential and pressure potential are the main factors that determine water potential.

Waterlogging stress is also known to cause marked perturbation in different chlorophyll fluorescence attributes of plants. Since chlorophyll fluorescence is an excellent physiological marker that determine the primary processes involved in photosynthesis such as energy transfer due to excitation, absorption of light and photochemical reactions occurring in the PSII (photosystem II) (DeEll et al., 1999; Saleem et al., 2011). Therefore, changes in chlorophyll fluorescence parameters determine the function and stability of photosystem II (Jimenez et al., 1997; Abdeshahian et al., 2010). The plants subjected to waterlogged conditions exhibit certain alterations in this physiological marker. For example, when Cork oak (*Quercus variabilis*) and China wingnut (*Pterocarya stenoptera*) were subjected to waterlogging stress, a prominent decrease in maximum quantum efficiency (*Fv/Fm*) was recorded (Hua et al., 2006). Likewise, decrease in the maximum quantum yield of PS II photochemistry (Fv/Fm) was also recorded in flied beans when subjected to varying days of waterlogging stress (Pociecha et al., 2008). PSII photochemistry was also impaired due to waterlogging in *Medicago sativa*. The decrease in Fv/Fm indicated the sensitivity of photosynthetic apparatus to abiotic stress and also inability of the plants to regenerate rubisco under stressful conditions (Smethurst et al., 2005).

OXIDATIVE DAMAGE INDUCED BY REACTIVE OXYGEN SPECIES (ROS)

Despite the fact that oxygen is important for life on earth, its reduction by any means could result in the production of ROS perturbing several cellular metabolic processes of plants (Ashraf, 2009; Ashraf et al., 2010). Lethal reactive oxygen species include superoxide (O_2^-), hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH). Singlet oxygen generated due to the reaction of oxygen with excited chlorophyll, is also considered as potential ROS (Ashraf and Akram, 2009). These ROS are extremely reactive in nature and induce damage to a number of cellular molecules and metabolites such as proteins, lipids, pigments, DNA etc (Ashraf, 2009). ROS are also produced in plants under normal conditions or non-stressed conditions but their concentration is very low. However, when plants are facing some environmental stress like waterlogging stress, the concentration of ROS is elevated to a level that is damaging for several cellular metabolic reactions of plants such as photosynthesis, efficiency of PS II (Ashraf, 2009). For example, elevated cellular levels of hydrogen peroxide result in inhibition of calvin cycle (Ashraf and Akram, 2009).

ROS are free radicals possessing one or more unpaired electrons. This is not a stable configuration; therefore, the radicals react with other cellular molecules to produce more free radicals (Foyer and Halliwell, 1976; Hideg, 1997). Generation of reactive oxygen species occurs via different mechanisms, for example, when molecules of aerobic system come in contact with the ionizing radiations, this interaction results in the production of ROS. It is now a well established fact that electrons flowing through electron transport chain may leak from their proper rout and in the absence of any electron acceptor, these electrons react with oxygen to produce reactive oxygen species (Ashraf, 2009). Different celluar organelles such as mitochondria, chloroplasts and peroxisomes are considered as the sites for production of reactive oxygen species (Sairam and Srivastva, 2002).

ANTIOXIDANT DEFENSE MECHANISM OF PLANTS UNDER WATERLOGGED CONDITIONS

All the plants have the ability to detoxify the adverse effects of ROS by producing different types of antioxidants. Generally, antioxidants are categorized into enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants include ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), glutathione reductase (GR), whereas, ascorbic acid, glutathione, tocopherols and carotenoids are included in non-enzymatic antioxidants (Gupta et al., 2005).

A marked alteration in the endogenous levels of different enzymatic and non-enzymatic antioxidants has been recorded in a number of studies. For example, when mungbean plants were subjected to waterlogging stress, the activities of various enzymatic antioxidants such as glutathione reducatse (GR), superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) decreased markedly (Ahmed et al., 2002). These authors also stated that oxidative damage was not directly involved in the impairment of photosynthetic machinery of plants under waterlogged conditions. Likewise, waterlogging-induced reduction in the activity of one of oxygen processing enzyme SOD has also been reported in corn (Yan et al., 1996). In contrast, increase in the activities of different enzymatic antioxidants was recorded in maize seedlings when subjected to varying degree of waterlogging stress (Tang et al., 2010). Similarly, when pigeon pea genotypes were exposed to waterlogging stress, the activities of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) increased markedly (Kumutha et al., 2009). From these reports, it is amply clear that plants when exposed to waterlogged conditions employ antioxidant defense system to get through the damaging effects of oxidative stress induced by ROS.

EFFECT OF WATERLOGGING ON NUTRIENT COMPOSITION

Waterlogging reduces the endogenous levels of nutrient in different parts of plants (Ashraf et al., 2011). Oxygen deficiency in the root zone causes a marked decline in the selectivity of K^+/Na^+ uptake and impedes the transport of K^+ to the shoots (Armstrong and Drew, 2002). It has also been reported in the literature that hypoxic conditions cause decrease in the permeability of root membranes to Na^+ (Barrett-Lennard et al., 1999). Generally, waterlogging causes acute deficiencies of essential nutrients such as nitrogen, phosphorous, potassium, magnesium and calcium (Smethurst et al., 2005). In this context, Boem et al. (1996) reported a marked decline in the uptake of N, P, K and Ca in canola when exposed to short period of waterlogging stress. Likewise, reduced endogenous levels of N, P and K have been reported in maize (Atwell and Steer, 1990). When *M. sativa* was subjected to flooding stress, a marked reduction in leaf and root nutrient composition (P, K, Ca, Mg, B, Cu and Zn) was recorded in plants (Smethurst et al., 2005). Similarly, Stieger and Feller (1994) reported reduced concentrations of P, K and Mg in wheat shoots due to waterlogging. In contrast, the endogenous levels of calcium remained unaffected in wheat under waterlogged conditions. However, decrease in calcium contents along with other nutrients (N, P, K and Mg) were also recorded in different organs of wheat under waterlogged conditions (Sharma and Swarup, 1989). Similarly, Tarekegne et al. (2000) recorded a marked reduction in Cu, Zn, P and K uptake in waterlogging susceptible wheat genotype when compared with the tolerant genotypes. These researchers were of the view that genotypes that possess the ability to avoid waterlogging-induced nutrient deficiency, particularly Zn and P deficiency should be selected. Moreover, the hampered efficiency of PS II is attributed to the deficiencies of N, P, K, Mg and Ca (Smethurst et al., 2005). It is evident from the literature that adverse effects of waterlogging are not due to the toxic levels of Na and Fe but reduced concentrations of N, P, K, Ca and Mg are the major contributors (Sharma and Swarup, 1989; Smethurst et al., 2005).

MORPHOLOGICAL AND ANATOMICAL CHANGES

Waterlogging stress is also known to cause a number of morphological and anatomical changes in plants. For example, the presence of hypertrophied lenticels is a common anatomical change observed in different woody species under flooding stress (Yamamoto et al., 1995). Radical cell division and expansion near stem base results in hypertrophic growth. In addition, it is also believed to be associated with ethylene and auxin production (Kozlowski, 1997). The lenticels are thought to be involved in the downward diffusion of O_2 as well as, the compounds produced as by-products of anaerobic metabolism (ethanol, CO_2 and CH_4). Although, the actual physiological role of lenticels is still unclear, their presence is often linked to waterlogging tolerance in plants (Parelle et al., 2006). Moreover, the number of hypertrophied lenticels is more under the water surface that supports the argument stating their involvement in maintenance of plant water homeostasis and deviating from the argument that dictates their role as important facilitators of oxygen entry toward the root system. Their potential role in the plant water homeostasis is evident from their active involvement in partially replacing the decaying roots and facilitating water intake for the shoot (Parent et al., 2008).

Formation of adventitious roots potentially replacing the basal roots is considered as one of the potential morphological adaptations depicted by plants under waterlogging stress (Malik et al., 2001). These specialized roots maintain the continuous supply of water and minerals when the basal root system fails to do so (Mergemann and Sauter, 2008). Furthermore, the deterioration of the main root system is taken as the sacrifice providing energy for the development of well adapted root system (Dat et al., 2006). In addition, the formation of adventitious roots is associated with waterlogging tolerance of plants (Steffens et al., 2006).

Another important morphological response of plant is the development of lacunae gas spaces (aerenchyma) in the root cortex. The formation of aerenchyma is considered as an adaptive response of the plant under flooding stress (Evans, 2004). There are two types of processes involved in the development of aerenchyma. The first is constitutive development of aerenchyma as it is not linked with the abiotic stress. It is formed by the cells separated during tissue development. This type of cell death occurring as a result of cell separation is termed as shizogeny, regulated developmentally and independent of external stimulus. It is formed as a result of highly regulated tissue specific pattern of cell separation. The second type of aerenchyma development is known as Isogeny since it is formed due to partial breakdown of the cortex that resembles programmed cell death and its formation depends on the external stimulus like abiotic stress (Pellinen et al., 1999).

GENETIC VARIATION FOR WATERLOGGING TOLERANCE

Plants under waterlogged conditions exhibit marked up and/or down-regulation of a number of genes. By investigating the induced expression of these genes in low oxygen environment, it is possible to identify certain gene products. Then these potential genes involved in conferring waterlogging tolerance can be isolated and introduced into the transgenic plants in order to identify their possible contribution in stress tolerance. Early studies performed by isotopic labeling of maize roots with ^{35}S-methionine clearly indicated the synthesis of anaerobic polypeptides when plants were subjected to low oxygen environment (Sachs et al., 1980). The anaerobic polypeptides include the enzymes involved in fermentation, that is, pyruvate decarboxylate, alcohol dehydrogenase and lactate dehydrogenase.

Moreover, there exists a marked variation in genetic resources of potential crops for flooding tolerance. For example, it has been widely reported in the literature that genetic differences exists in wheat for waterlogging tolerance (Gradner and Flood, 1993; Ding and Musgrave, 1995). Setter et al. (1999) showed that there exists a significant genetic diversity among 14 wheat varieties when exposed to flooding stress under glasshouse conditions. Similarly, genetic variation has also been reported in many other plant species, for example, oat (Lemons e Silva et al., 2003), cucumber (Yeboah et al., 2008), Soybean (VanToai et al., 1994) and maize(Anjus e Silva et al., 2005).

SHORTGUN APPROACHES TO INDUCE WATERLOGGING TOLERANCE

Scientists from different geographical regions of the world are actively involved in making the plants tolerant to flooding stress by the use of exogenous application of nutrient and plant hormones. For example, recently, Ashraf et al. (2011) reported that exogenous application of potassium in soil and as foliar spray alleviated the adverse effects of waterlogging on cotton plants. Likewise, Ashraf and Rehman (1999) reported that application of nitrate in soil proved useful in mitigating the harmful effects of waterlogging on different physiological attributes of maize. Likewise, Yiu et al. (2009) found that exogenous application of spermidine and spermine provoked several biochemical and physiological adaptations in onion when exposed to flooding stress. In this context, exogenous application of uniconazole was also helpful in circumventing the damaging effects of waterlogging in wheat and oil seed rape plants (Webb and Fletcher, 1996; Zhou et al., 1997). Therefore, the use of these organic and inorganic compounds offers an excellent platform for inducing tolerance to flooding stress.

CONCLUSION

It can be inferred from the aforesaid discussion that waterlogging is one of the major constraints for sustainable agriculture. Its effects are evident on the entire plant as well as, cellular levels. There is the need to screen available germplasm for waterlogging tolerance and use the genes responsible for inducing tolerance in other potential crops so as to make them resistant as well. Waterlogging causes deficiency of several essential nutrients. Therefore, exogenous application of these nutrient or other plant hormones could be used so as to alleviate the adverse effects of waterlogging.

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