Chapter 12
Physiological and Molecular Responses to Drought, Submergence and Excessive Watering in Plants

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Contents

1 Introduction

Ecological stress is diverse and, for the most part, explicit, which causes enormous harvesting misfortunes. They include expanded UV-B radiation, high saltiness, water stress, extreme temperature, hypoxia (limited oxygen is provided in water-logged and compacted soil), lack of mineral supplement, harmful metals, fungicides, herbicides, contaminated air, topography and light temperature (Pradhan and Mohanty 2013). It can also be presented as the rapid change in atmospheric conditions that expand the recurrence of abiotic stresses like drought, floods, heavy metals or high salinity, cold and high temperatures, which cause a sudden decrease in efficiency of plant production and yield (Wang et al. 2003). The total populace is

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anticipated to ascend by 31 million every year going up to 9.1 billion by 2050, turning into a significant danger to food security (United Nations, Population Division 2002). It was assessed that there would be 70% high food prerequisite by 2050, forcing a more prominent workload on plant raisers to grow high-yielding cultivars that can withstand this high requirement. Among the abiotic stresses, water stress is intermittent and a key restricting element for development and improvement of yields (Araus et al. 2002; Dinesh et al. 2016).

Environment-based connections towards plant growth and its different interchangeable reactions are significantly connected with water (Fukao et al. 2019). Plants represent many physiological, morphological, molecular, and biochemical connections under water stress (Sourour et al. 2017). Water stress antagonistically impacts numerous plant parts physiologically, particularly photosynthesis proportions. The chances of plant development and its efficiency are severely impaired if stress last longer. The physiological and atomic components are widely contemplated for their relationship with water-stress resistance and water-use effectiveness. Furthermore, we explore how the plant functions at an atomic level to resist stress, preserve the hormone balance and its reactions and prevent excessive light damage. An understanding of the way in which these frameworks are regulated and the impact of water stress on plant viability would provide data to improve the resilience of the plant through biotechnology while preserving plant supply and nature (Bhatt and Rao 2005; Osakabe et al. 2014).

There are mainly two kinds of water stress that focus on the plant's involvement with it in general. One is when water is not in an adequate amount, mentioned as water shortage, while the other one is when water is accessible and in abundance called waterlogging/submergence. Water shortage influences plants through the decline of leaf water potential, which results in the closing of the stomata and loss of cell turgor, leading to a reduced rate of photosynthesis and transpiration and eventually resulting in plant's poor development and later wilting. Then again, waterlogging happens when the soil has a high number of the pore openings, which are engaged by water which constrains the dissemination of oxygen and gas trade between the plants, its surrounding soil and climate, followed by poor root development and their activity, therefore, influencing the plant development and endurance negatively (Pradhan and Mohanty 2013).

2 The Effect of Water Stress on Plant Growth and Its Productivity

Ecological stresses alter a wide assortment of plant reactions, extending from the metabolism of the cell and modified gene expression to changes in development and yield (Anjum et al. 2011).

2.1 Drought

In India, it was evaluated that there would be exhaustion of over 40% of accessible water by 2025, prompting a drought for horticulture crops. To understand stress better, the definitions related to various abiotic stresses are expressed thus. Heat stress is characterized as ascending in temperatures typically 10–15 °C above ideal conditions, which cause permanent harm. Low-temperature stress incorporates freezing pressure (<0 °C) or chilling pressure (<20 °C), leading to crystallized plasma layer, and when a plant's water potential and turgor are sufficiently diminished to hinder common plant activity, it is water stress (Hsiao et al. 1976). In contrast to the observational crop stand, the harvests developed in crude condition experience numerous unpredictable stresses which are responsible for the tremendous yield misfortune (Dinesh et al. 2016).

Out of all these stresses, drought or water deficit is particularly one of the terrible factors responsible for poor plant development and efficiency (Noorka and Tabasum 2015). There are various sorts of plant responses to drought: (i) stress resilience; (ii) stress escape and (iii) stress avoidance. Water deficit is an intricate character contingent upon seriousness, length of the stress phase and the plant development period (Sourour et al. 2017).

Drought is a significant ecologically restricting element at the adolescent phase of plant development and initiation. Actually, seed germination is the principal phase of development that is fragile to water shortage. Subsequently, seed germination, its vitality and sheath protecting young shoot tip of coleoptile length are beneficial for the foundation of a plant. During critical water inadequacy, elongation of the cells of higher plants may be suppressed by interference of the water stream from xylene to the extended cells (Nonami 1998). Water deficiency causes weakened mitosis; cell lengthening and expansion contributes to decreased growth and yields (Hussain et al. 2008).

Drought lessens the number of leaves per plant and individual leaf size, leaf life span by diminishing the water potential of the soil. Leaf part development relies upon leaf turgidity, heat intensity and acclimatizing flexibly for development. Water-deficit-stress encouraging the reduction of the leaf part is attributed to the concealment of the leaf extension by the reduction of photosynthesis (Rucker et al. 1995; Scott 2000).

Water-deficit stress decreases the number of days in a plant life cycle, which leads to complete flowering, shoot length and a most important decrease in the production of fresh and dry biomass (Farooq et al. 2009; Kilic and Yağbasanlar 2010). It was finalized that the length of plants, the diameter of the stem and leaf zone diminished observably with increased water-deficit stress. The decrease in plant stature could be credited to a decrease in cell expansion and more leaf ageing in the plant undergoing water stress (Manivannan et al. 2007).

Plenty of processes in plants that decide on yield, respond to water disruption. Yield has complicatedly integrated a large number of certain techniques. It is therefore difficult to determine how plants accumulate, consolidate and explain ever-changing and unpredictable processes over the entire life-long pattern of harvesting. Plant yield is the consequence of the articulation and consortium of a few plant development segments. The insufficiency of water prompts a serious decrease in yield attributes of harvest plants, presumably by disturbing leaf gas interchanging properties which not just constrained the size of the source and submerged tissues but also the loading of the phloem, movement acclimatization and dry material distributing are likewise disabled (Farooq et al. 2009). Water-deficit stress restrains the dry substance to be produced mostly because of the great extent of its inhibitory impacts on leaf elongation, leaf growth and therefore decreased light capture (Nam et al. 1998). Water-deficient stress at blooming usually causes barrenness. However, a decrease of absorbing motion to the growing ear within certain limits is important for optimum grain development, its may not be the only reason for low yield (Yadav et al. 2004).

Peduncle length has been likewise recommended as a valuable marker of yield execution in stress conditions. A paper by Kaya et al. has mentioned a positive connection between the peduncle length and plant yield (Kaya et al. 2002). Water stress can also influence productivity and its associated properties, for example, spike number per m2, plant for each spike number, 1000 plant weight and plant weight per spike, especially in the dry and semi-dry area (Bilal et al. 2015). The impact of water stress on productivity and its productivity parameters at various development stages have been noted by a few researchers (Simane et al. 1993). Actually, drought may take place all around the developing season; it does not matter whether the season is early or late; productivity is diminished generally when water stress happens during the blossoming stages; however, its impact on reduced yield is most elevated when it happens after the flowering period. In durum wheat, water stress can highly reduce the yield (Ehdaie 1995). During development, this pressure leads to a 10% decline in productivity. However, generally, there is no effect on yield due to moderate stress if provided during the early vegetative development stages (Bauder 2001).

Maize developed at high temperature combined with serious water stress during fertilization brings about 100% yield misfortune. This might be because of the decrease in the amount and nature of produced pollen, low chances of pollen survival and silk receptivity (Hall et al. 1982; Schoper et al. 1986). Normally, the decrease in crop yield relies upon tension attributes like length of subjection, the strength of stress, blend of stresses and the number of subjections (Lobell et al. 2011).

2.2 Submergence and Waterlogging

Pressure on plants forced by flooding of the humus and more profound submergence establishes one of the major abiotic limitations on development, species' dissemination and farming efficiency. Stress due to flooding is likewise a solid driver of versatile advancement. This has brought about a wide scope of biochemical, sub-atomic and morphological transformations that authorize the development and conceptive accomplishment under rambling or for all-time overflowed conditions that are profoundly harming to most of the plant species (Jackson and Colmer 2005). Development and advancement of most vascular plant species are hindered by soil flooding and especially by total submergence, the two of which can bring about death (Pradhan and Mohanty 2013).

Submergence/flooding/waterlogging is viewed as one of the significant limitations for crop output or yields in numerous territories of the world (Kozlowski 1984; Pang et al. 2004; Conaty et al. 2008), which unfavourably influence roughly 10% of the worldwide land territory (Fao 2002). Soil waterlogging and submergence are abiotic stresses that impact species synthesis and efficiency in various plant networks around the world. Flooding is a complicated stress that forces a few frequent simultaneous difficulties to typical plant working. Deprivation of oxygen and carbon dioxide is forced by very moderate paces of dispersion across the floodwater in contrast with that in air. Partial (hypoxia) or total oxygen deficiency (anoxia) in the surrounding soil limits the development, advancement and yield, which is a significant natural outcome of waterlogging or flood stress. Submergence happens when precipitation or the supply of water to the land is stored on the surface of the soil or earth for the elongated timeframe and can likewise happen when the volume of water included through precipitation or supply is beyond what can permeate into the earth in less than 1 or 2 days. Field-grown crop plants waterlogging can happen either as ‘waterlogging of the surface’ where the top of the ineffectively evacuated soils is overflowed or ‘waterlogging of the root zone’ where the water table ascends to drench a section or whole root zone with water. In this manner, the inclination towards complete flooding has a damaging impact for almost all the terrestrial plant crops, with the exception of some resistant species, since it hampers development and can bring about early sudden death (Pradhan and Mohanty 2013) because of the quick advancement of anoxic or hypoxic conditions in water-logged soils. For nearly all variant yield, abundant water is a significant requirement to profitability in numerous districts and circumstances (Jackson 2004), unfavourably influencing plant crop (Setter and Waters 2003) and development of field species (Gibberd and Cocks 1997; Gibberd et al. 2001).

In pigeon pea, stress due to moisture brings about 50% decreases in photosynthesis at its pre-flowering stage (Choudhary et al. 2011). Yield improvement for physical stress resilience is monotonous and includes very good-quality logical information to comprehend quantitative nature of the characteristics. The plant being immobile has the capacity to start sub-atomic, physiological and structural changes to any pressure and act as indicated by it (Hasanuzzaman et al. 2013). Understanding atomic components and utilization of sub-atomic methodologies are incredibly critical to productivity improvement. In contrast to the traditional standards, the hereditary gain for each unit time has been high through sub-atomic methodologies. This prompted an expanded examination action to comprehend the scientific framework of various harvests under abiotic stresses (Cramer et al. 2011).

The current analysis or assessment is an endeavour to achieve the pathways and crosstalk engaged with reaction to various abiotic stresses and arrangements more about the progressions that happen at an atomic level.

3 Plant's Physiological and Molecular Response Against the Major Water Stresses

3.1 Physiological Response Against Drought

3.1.1 Photosynthesis and Chlorophyll Content

In case of drought, the predominant impact of water stress is restricting photosynthesis due to the closure of the stomata which limits uptake of the CO_2 by leaves and blocks the loss of water through transpiration which eventually leads to the decrease in leaf turgor as well as water potential (Yokota et al. 2002; Anjum et al. 2003). The restrained CO_2 accessibility is the root cause of photo damage (Cornic and Massacci 1996). Water-deficit stress controls especially photochemical productivity of photosystem PS II through the electron transport reduction, external protein removal and also by releasing ions of calcium and magnesium from their coupling (Barta et al. 2010; Zlatev and Lidon 2012). Severe water-deficit stress conditions can diminish photosynthesis because of the reduction in Rubisco activity (Bota et al. 2004). Under drought conditions, the photosynthetic electron transport chain activity is subtly adjusted towards the existence of CO_2 in the chloroplast and the changes that occur in photosystem II. Water-deficit stress ends up creating changes in the proportion of chlorophyll 'a' and 'b' along with carotenoids (Farooq et al. 2009). Chlorophyll concentration has become the ultimate source as an evaluating indicator. Actually, cultivars that are resistant to water pressure have been found to have high chlorophyll content (Sairam et al. 1997). Relating to it, Ashraf et al. found that water-deficit stress is capable of reducing concentration more in chlorophyll b than chlorophyll a (Ashraf et al. 1994).

3.1.2 Water Relation and Osmolyte Accumulation

Relative water content (RWC), water potential of the leaf, resistance of the stomata, transpiration rate, temperature of the leaf and temperature of the canopy are significant qualities that impact plant water relations (Anjum et al. 2011). Water stress is also responsible for the decrease in relative water content (Cornic 2000; Saeidi et al. 2015). Relative water content (RWC) is viewed as a proportion of water status in plants, indicator of the metabolic movement in tissues and is utilized as the most important parameter for resistance against dehydration. In fact, despite the fact that constituents of plant water relations are influenced by decreased accessibility of water, the opening and closing of the stomata is greatly influenced. In addition, alterations in the leaf temperature might be a significant element in controlling water status in leaf influenced by water-deficit stress (Anjum et al. 2011)

High relative water content or RWC is actually a process that works against water-deficit stress and is more in relation with the osmotic regulation than elasticity of the cell walls of the tissue (Ritchie et al. 1990).The osmotic change is the procedure for maintaining the turgidity in the tissue through the collection of solutes against water-deficit stress. Accumulation of solutes contributes to the osmotic modification in plants, incorporating organic acids, starches, inorganic cations and free amino acids. Potassium is the essential inorganic cation in some plants, collected during water stress and can also be the richest solute of the leaf (Jones et al. 1980; Ford and Wilson 1981). Osmotic change relies mostly on photosynthesis for the supply of suited solute. Photosynthesis is hindered bringing about less contribution of the solute for osmotic alteration. With the water constraint, osmotic modification is slowed down, yet it cannot totally prevent it from dehydration (Kramer and Boyer 1995). Osmotic modification is not perpetual, and plants frequently react quickly to decreased water presence. Osmotic regulation and turgidity maintenance allow the continuity of the root development and proficient soil moisture uptake (Sharp and Davies 1979). Even with the collection of ions and organic solutes which permit osmotic changes in meristematic and elongating activity, the shooting development may still be hindered with stress either because of osmotic changes which cannot make up for the development or because of the turgidity failure that is caused by stress (Sourour et al. 2017; Dodd and Ryan 2016).

3.1.3 Root Signalling

It is advantageous to have an immense root system to help the plant development during the early yield developmental stages and in the extraction of the water from little depths of the soil layers that is generally effectively lost due to evaporation.

Under water-deficit stress conditions, roots incite a stream of signals to the shoots through xylem, causing physiological alterations in the end, deciding the degree of transformation to the stress. Cytokinins, abscisic acid (ABA), malate, ethylene and other unidentified variables have been involved in the root–shoot signalling. This water-deficit stress ends up inducing initiated root-to-leaf signalling across the transpiration stream, resulting in closing of the stomata, which is a significant transformation to constrained supply of water in the fields (Anjum et al. 2011).

3.2 Molecular Response Against Drought

The comprehension of plant's molecular response to abiotic stresses included improvement of new devices and tools by means of gene alteration through the expression of numerous genes responsible for inducing stress. There are different kinds of proteins that will likely enhance stress resistance. Genes that encode osmolyte biosynthesis catalysts allow these osmotic compounds to work against stress, for example, the formation of proline from l-glutamic acid via D1-pyrroline-5-carboxylate (P5C) in the presence of two catalysts: P5C synthase and P5C reductase, and the degradation of proline to l-glutamic acid by these two enzymes – proline dehydrogenase and P5C dehyde. In return of drought stress, proline dehydrogenase activity is repressed while inducing P5Csynthetase, bringing about a collection of proline. Unique to plants are another set of genes which are instigated in plants when exposed to water stress. These genes which are programmed to function during growth in the desiccating seeds are named as late embryogenesis abundant genes, which are abbreviated as LEA genes. These genes in turn are responsible for encoding small hydrophilic proteins which are anticipated to ensure the protection of membranes and proteins during the dehydration of the cell. For the wheat plant, to resist or to tolerate drought stress, there are numerous genes liable for it, which produces various types of catalysts and proteins, e.g. abscissic acid (Rab), rubisco, helicase, proline, protein-rich late embryogenesis (LEA protein), glutathione-S-transferase (GST) and starch during water-deficient stress (Bray 2001).

3.3 Physiological Responses Against Submergence/ Waterlogging

First primary plant reactions to waterlogging is the decrease in stomata water flow activity (Folzer et al. 2006). Plants presented to stress due to flooding have increased resistance of stomatal conductance also show restricted water uptake, prompting shortage of water internally (Parent et al. 2008). What is more, low degrees of O_2 may diminish water-driven conductivity due to hampered root penetrability (Else et al. 2001). Lack of oxygen is responsible for considerable decrease in the net rate of photosynthesis (Ashraf et al. 2011). This reduction in the rate of transpiration and photosynthesis is responsible for the closing of the stomata (Ashraf and Arfan 2005). It can also have different other factors because of which rate of transpiration is being reduced, for example, chlorophyll substance reduction, senescence of the leaf and decreased leaf volume (Malik et al. 2001).

Besides, if plants are exposed to flooding for a long time, this condition could bring about root damages which as a result leads to certain changes in the biochemical response of photosynthesis due to reduction in the photosynthetic capacity overall. The biochemical modifications consist of restrained activities of ribulose bisphosphate carboxylase (RuBPC), glycolate oxidase and phosphoglycolate (Yordanova and Popova 2001), damaged membrane of chloroplast restraining photosynthetic electron transport and effectiveness of photosystem II (Titarenko 2000). It is clear from the research that waterlogging ends up causing a noticeable decrease in photosynthetic limit in various plants, for instance, *Lycopersicon* *esculentum* (Bradford 1983; Jackson 1990), *Lolium perenne* (McFarlane et al. 2003), *Triticum aestivum* (Trought and Drew 1980) and *Pisum sativum* (Jackson and Kowalewska 1983; Zhang and Davies 1987). Flooding stress is likewise known for causing clear shifts in various fluorescence of the chlorophyll which are the characteristics of plants. Chlorophyll fluorescence has always been a fantastic physiological marker that decides the essential procedures associated with photosynthesis, for example, absorption of light, photochemical responses taking place in the PSII (photosystem II) and transfer of energy because of excitation (DeEll et al. 1999; Saleem et al. 2011). Thus, changes in the parameters of the chlorophyll fluorescence decide the working and steadiness of photosystem II (Jimenez et al. 1997; Abdeshahian et al. 2010). The plants exposed to flooding situations display certain adjustments in this physiological marker; for example, when China wingnut (*Pterocarya stenoptera*) and Cork oak (*Quercus variabilis*) were exposed to flooding stress, a noticeable reduction was observed in the maximum quantum effectiveness (Fv/Fm) (Yinghua et al. 2006). Similarly, reduction in the utmost yield of quantum of PS II photochemistry (Fv/Fm) was as well noted in field beans when exposed to differing long stretches of flooding stress (Pociecha et al. 2008). PSII photochemistry was also damaged due to flooding in Medicago sativa. The reduction in Fv/Fm showed the affectability of photosynthetic instruments to abiotic stress and furthermore failure of the plants to recover rubisco under distressing conditions (Smethurst et al. 2005).

3.4 Molecular Response Against Submergence/Waterlogging

Plants under flooding stress display notable gene regulation for a number of genes which can be up-regulated or down-regulated. Through an examination of the prompted gene expression in low-oxygen condition, the identification of some gene products becomes possible. At that point, these potential genes engaged with granting water-logging resilience can be segregated and brought into the transgenic plants so as to recognize their conceivable commitment in stress resistance. Early examinations conducted by the isotopic marking of maize roots with 35S-methionine unmistakably showed the formation of anaerobic polypeptides when plants were exposed to low-oxygen conditions (Sachs et al. 1980). The anaerobic polypeptides incorporate the proteins related to fermentation, that is, alcohol dehydrogenase, pyruvate decarboxylation and lactate dehydrogenase. Besides, there prevails a noticeable variety of potential crop's genetic reservoir for water-logging resilience. As such, it has been reported worldwide in the research literature that there are genetic differences prevalent for wheat plants against water-logging resistance (Gardner and Flood 1993; Ding and Musgrave 1995). Setter et al. demonstrated that there is a huge gene variation among 14 varieties of wheat when presented to water-logging stress under glasshouse state (Setter et al. 1999). Likewise, genetic variability has additionally been accounted for in numerous other plant varieties, such as cucumber (Yeboah et al. 2008), oat (Lemsons e Silva et al. 2003), maize (Anjos et al. 2005) and soybean (VanToai et al. 1994).

4 The Actions of the Regulatory Transcription Network and Abiotic Stress in Drought

Drought and irregular climate change influence plant development globally and that incredibly influences the plant yield. The decline in the production of plant products is a major threat to the increasing population (Bray et al. 2000). Drought has a significant impact on rice, wheat, maize and soybean production, the main staple food worldwide (Nakashima et al. 2009). Therefore, the production of crops that withstand stress, especially in areas where these stresses occur frequently, will be of great significance. Recently, some advancement has been made towards recognizable proof of pressure-related qualities possibly fit for expanding the resistance of plants to abiotic stress. In order to enhance the plant's drought-tolerance properties, molecular techniques are important for understanding the molecular mechanisms in the response to drought. In the plant, abscisic acid (ABA) is the main player for developing resistance to water-limiting conditions such as drought (Finkelstein et al. 2002; Yamaguchi-Shinozaki and Shinozaki 2006; Nakashima et al. 2009; Nakashima et al. 2014). To develop plant resistance against abiotic stress, it is very important to understand the communication between various regulatory networks and factors affecting the expression of regulatory genes. Along with ABA, transcription factors (TFs) and related genes are also known to be a key molecule in handling abiotic stress (Nakashima et al. 2009).

For example, ABRE (ABA-responsive element), a cis-element, which regulates gene expression under stress conditions, is a major TF, is found in the ABA promoter regions in *Arabidopsis*. Gene expression requires a group of ABRE or group of coupling elements (CE) and ABRE (Fujita et al. 2011, 2013). They regulate the transcriptional activity by ABA-dependent phosphorylation. To facilitate a response to a water crisis, ABRE plays an essential role in signalling the network. Therefore, overexpression of ABRE develops resistance to water-limiting stress. This regulatory network is ABA-dependent. We will look at another example of ABA-independent regulatory network and will understand how crosstalk between both impacts development of resistance against abiotic stress. Dehydration-responsive element binding (DREB) proteins is a transcription factor in the ABA-independent gene promoter region in *Arabidopsis* (Liu et al. 1998), managing stress-responsive behaviours in a large number of *Arabidopsis* genes. Research suggests that overexpression of DREB in adverse conditions improves tolerance, but in normal conditions, it leads to growth defects. (Liu et al. 1998; Kasuga et al. 1999). The chance of growth defects was, however, eliminated by DREB, regulated by another promoter, RD29A (Kasuga et al. 1999).

Research also suggests that DREB proteins interact physically with AREB proteins and that ABA-dependent DREB TF is functional as a CE for ABRE in ABA-dependency gene expression (Kim et al. 2011; Narusaka et al. 2003; Lee et al. 2010). Molecular analyses demonstrated that TFs and their crosstalk work in response to drought and tolerance. It is essential to take advantage of these properties to grow drought-resistant crops. Therefore, different combinations of TFs can produce different transgenes, specific to the particular area, depending on the weather conditions.

5 Adaptations of the Plant to Withstand Excess Water Stress

Other factors that influence crop are excessive rain, which results in waterlogging; whether it is temporary or permanent, it adversely affects the plant growth. Waterlogging leads to depletion of oxygen level, degradation of roots, changes in soil PH and redox potential (Gambrell and Patrick 1978; Ashraf 2012). Such physical and chemical changes under stress reflect aerobic respirations' shift to anaerobic fermentation. Under stress conditions, genes coding for enzymes involved in fermentation are expressed abundantly because in fermentation, each glucose produces only two ATP instead of 36 ATP, which is produced during aerobic respiration (Chang et al. 2000). Research also suggested that the plant faces oxidative damage caused by the generation of reactive oxygen species (ROS) due to the lack of oxygen (hypoxic conditions) that hinders the survival of the plant by affecting the rate of photosynthesis (Ashraf et al. 2011). In response to waterlogging, plants look for alternative pathways to save energy and withstand damages such as root hydraulic conductivity, closing stomatal conductance and change in net CO_2 assimilation rate (Folzer et al. 2006; Else et al. 2001).

In a situation of waterlogging, the plant changes its physiological processes, for example, reducing stomach conductance to reduce the water intake (Parent et al. 2008), which substantially reduces photosynthesis. Studies have suggested that abscissic acid (ABA) transport from older to younger leaves has been allocated to support the closure of the stomach (Ashraf 2012). Due to lack of water intake, hypoxic conditions result in reduced root strength and permeability; also destroys the chloroplast membrane, which eventually reduces the efficiency of photosystem II and CO_2 exchange; restricts the activity of glycolate oxidase, ribulose bisphosphate carboxylase (RuBPC) and phosphoglycolate; and controls the CO_2 exchange rate of plants (Yordanova and Popova 2001; Smethurst et al. 2005; Titarenko 2000; Ashraf and Arfan 2005; Ashraf et al. 2011; Tardieu et al. 2010).

As already mentioned, oxidative damage caused by waterlogging is handled by the plant by producing enzymes like ascorbate peroxidase (APX), glutathione reductase (GR), etc., which neutralize reactive oxygen species. Sometimes, non-enzymatic antioxidants such as ascorbic acid are also used by plants (Gupta et al. 2005). Waterlogging leads to nutritional deficiencies because of the reduction in root permeability for Na + (Barrett-Lennard et al. 1999). Studies highlight the factors that hamper the efficiency of PS II, and deficiencies of N, P, K, Mg and Ca are interconnected and they adversely affect plant survival (Smethurst et al. 2005). To survive unfavourable water condition, plants also undergo morphological change such as lenticels (Yamamoto et al. 1995), adventitious roots (Malik et al. 2001) and development of lacunae gas spaces (Aerenchyma) (Evans 2004), which try to maintain oxygen, water intake and gas exchange rate respectively to maintain homeostasis. As discussed above, waterlogging is a major problem, and the development of waterlogging-tolerant plants needs a deep understanding of genes which are produced during water-stress conditions.

6 Conclusion

The abundance of water (hypoxia/anoxia) or water supply deficiency seriously impacts plants by water stress and causes numerous physical, social, physiological and molecular changes. Drought and waterlogging are multidimensional stresses which cause a broad range of plant reactions. The analysis of the various components of stress, especially low-oxygen stress, organ expression, ion channels, ROS signalling, shooting length alterations, aerenchyma, adventitious roots, the crosstalk between pathways dependent on and independent of abscisic acid (ABA) and transcription factors play an important role in the development of tolerance at the molecular level. All these changes greatly affect the rate of photosynthesis which ultimately affect the crop yield. The challenge for today's and future agriculture is to increase the supply of food to meet the demand of the growing population. Therefore, in-depth research on transduction, signalling events and how crosstalk between regulatory networks work at the molecular level to minimize the effects of diverse types of abiotic stresses can be helpful in understanding how the plant cell transits from stress to the recovery process and develops crops tolerant to stress.

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