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Waterlogging tolerance: A review on regulative morpho-physiological homeostasis of crop plants

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Abstract

The natural environment is being drastically affected by climate change. Under these severe environmental conditions, the growth and productivity of agricultural crops have reduced. Due to unpredictable rainfall, crops growing in the field are often exposed to waterlogging. This leads to significant crop damage and production losses. In this review paper, the morphological and physiological adaptations such as development of aerenchyma, adventitious roots, radial root oxygen loss barrier, and changes in chlorophyll fluorescence parameters of crops under waterlogging are discussed. This will help to understand the effects of waterlogging on various crops and their adaptation that promotes crop growth and productivity. To meet the food requirements of a growing population, the development of waterlogging tolerant crops by screening and plant breeding methods is necessary for plant breeders. Better knowledge of physiological mechanisms in response to waterlogging will facilitate the development of techniques and methods to improve tolerance in crops.

Key words: *antioxidants, cellular metabolites, climate change, photosynthesis, waterlogging*

INTRODUCTION

Global changes in climatic conditions, including extreme availability of water and temperature, have exacerbated the harshness and unpredictability of environmental conditions unfavourable to the development and survival of plant species in natural habitats. Agricultural food crops face problems with extreme weather events in times of climate change, leading to a significant decline in crop productivity and yield. In a highly dynamic and generous environment, plants must constantly regulate their metabolism to maintain growth and development. Therefore, it is necessary to identify the plant traits associated with maintenance in changing climate and enhancing the resilience of plant varieties under deleterious stress conditions.

Flooding is one of the abiotic stressors that can be observed worldwide and has a significant impact on plant productivity and biodiversity [BAILEY-SERRES, BRINTON 2012; HIRABAYASHI *et al.* 2013]. The frequency of floods has increased by about 65% in the last 25 years and causes greater climatic adversity worldwide than other severe climatic events [CONFORTI *et al.* 2018]. Increasing flood events due to global warming are detrimental to plant communities and affect the distribution of plants in natural ecosystems [BAILEY-SERRES *et al.* 2010]. In addition, one-tenth (about 12 mln ha) of flooded cropland loses its productivity during each flood event [SHABALA (ed.) 2017].

India, surrounded by the Arabian Sea, the Bay of Bengal and Indian Ocean is very prone to floods. According to Geological Survey, flood prone areas in India cover 12.5% of the country's land area (the top states indicated in Figure 1 are affected by waterlogging/flooding). In India, about 8.11 mln ha of area and 3.57 mln ha of arable land are affected by floods with a total loss of 13.400 mln rupees and 177.41 USD [Map of India undated]. Rajasthan, a state of India, generally has a water deficit, but in the last 30 years, flood events have increased. There are many districts in Rajasthan which are considered flood prone areas including Ajmer, Barmer, Jodhpur, Pali, Sirohi, Udaipur, Chittorgarh, Jaipur, Kota, Sri-Ganganagar etc. which are located near the river

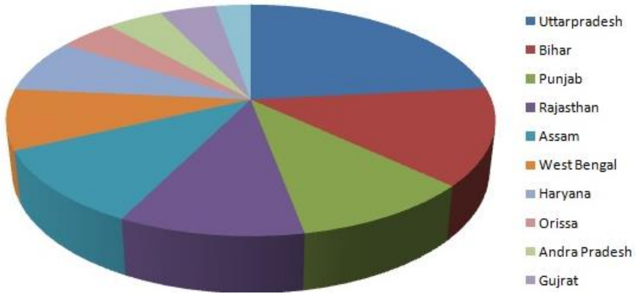

Fig. 1. Land area liable to flooding in India; source: Maps of India [undated]

basins of Ghaggar, Banas, Luni and Chambal [RajRAS 2020]. Due to these floods and waterlogging, the crops grown in these areas are drastically affected and suffer from various adverse conditions.

Long-term waterlogging has negative effects on all growth stages of the plant throughout its life cycle and ultimately leads to productivity losses [ARGUELLO *et al.* 2016; HERZOG *et al.* 2016; STRIKER, COLMER 2017; WANG *et al.* 2017; ZHANG *et al.* 2016]. Waterlogging, flooding, or inundation legitimately influences the distribution of oxygen in tissues and the distribution of various gases between cells restricts the exchange of oxygen and respiration in mitochondria (aerobic respiration) and in this way really affects the typical biochemical as well as physiological performance of the plant [LIU *et al.* 2012; VOESENEK, BAILEY-SERRES 2013]. The lower energy production leads to high accumulation of lethal compounds (e.g. aldehydes and alcohols) in the tissues [TAMANG *et al.* 2014]. The reduction in the rate of development of the plant at the vegetative stage under waterlogged conditions indicates that it is the most vulnerable stage [XU *et al.* 2013], as observed in soybean, cereals, canola, and wheat [ANDRADE *et al.* 2018; WOLLMER *et al.* 2018; ZHOU *et al.* 2020].

Conventionally, plant breeding methods for the resilience of waterlogging were founded as evaluating the extent of agronomic and morphological attributes, but now physiologically based methods and cellular mechanisms are fundamental key parts of waterlogging resistance in plants. Creation of tolerant varieties to waterlogging is a major need of plant breeders [SHABALA 2011]. Biotechnological systems have used molecular information to create varieties impervious to flooding or to provide alternative methods for flood-prone soils, such as bioethanol and biomass production [FUKAO *et al.* 2019]. The serious effects of waterlogging stress on crop performance, development and improvement are of much greater concern, particularly in the context of global climate change [WANG *et al.* 2017, XU *et al.* 2018].

Under these circumstances, plant resilience to adverse environmental conditions is determined not only by acclimation to the stress level itself, but also by recovery from a stressed condition. In a highly dynamic and generous environment, plants need to constantly regulate their metabolism to maintain growth and development [YEUNG *et al.* 2018].

To balance food supply with increasing population and develop a better agricultural system, this is a challenge for researchers and plant breeders for the future. For the production of waterlogging tolerant crops and to improve agricultural practices, more efforts are certainly expected to overcome these future difficulties. Although data availability is there with respect to various abiotic stresses, no attention has been paid to waterlogging stress [TEWARI, MISHRA 2018]. Therefore, the present review mainly focuses on the morphological and physiological adaptations of crops under waterlogging to understand the effects of waterlogging on various crops and their adaptations that promote plant growth and productivity.

EFFECT OF FLOODING AND OTHER ASSOCIATED STRESSES

Flood stress is a condition in which multiple stressors are created for plants, either water logging (*i.e*., only the roots are affected and a condition in which there is an excessive amount of water in the soil pores) or submersion stress (*i.e*. entire plant shoots being completely submerged in water) are among the major abiotic stresses that occur intensively due to unpredictable and intense rainfall patterns and poor drainage of the water system [BALAKHNINA *et al.* 2015; LIMAMI *et al.* 2014; PHUKAN *et al.* 2016]. After a flood event, when flood waters recede, plants were acclimatized to the reduced light and low oxygen levels in turbid water and suddenly switched from aerobic to anaerobic conditions. This switch from hypoxia to normal oxygen levels causes other additional stresses on the plants, namely, oxidative stress and dehydration due to root dysfunction, often leading to extreme dehydration of the plants [MAUREL *et al.* 2010]. These results show that plant survival after flooding requires tolerance to several other combined stresses, namely flooding, desiccation, and reoxygenation. This is particularly evident for plants that need to recover from flooding (as shown in Fig. 2).

In the spring and winter seasons, excessive rainfall events can lead to prolonged waterlogging and flash flood in summer in many areas of world [KREUZWIESER, RENNENBERG 2014]. Waterlogging affects agricultural land on a larger scale and has a wide range of economic consequences because of the enormous loss of yield and production. This economic loss due to waterlogging is associated with lifelong social consequences. Waterlogging is a water condition that fills the pores and alters the condition of soil air circulation. Gases present in the soil pores are displaced by the water and gradually diffuse into the waterlogged soil, resulting in a decrease in accessible oxygen (hypoxia) in the rhizosphere. The slow dispersion of oxygen and various gases in the soil limits the accessibility of oxygen to plant roots and soil microorganisms [BALAKHNINA *et al.* 2015]. Plant roots rapidly consume accessible oxygen under hypoxic conditions [PARAD *et al.* 2013]. Waterlogging leads to a lack of oxygen that generates adenosine triphosphate (ATP), and in this way limits the development and metabolism as well as the endurance of sensitive plant species [JOSHI *et al.* 2020]. Oxygen deficiency or absence in the soil (hypoxia and anoxia, respectively) produced by anaerobic microorganisms leads to the accumulation of lethal metabolites (including H_2S, N_2, Mn^{2+}, Fe^{2+}) and reactive oxygen species (ROS) and affects stress hormones (e.g., abscisic acids and ethylene) in roots [CARVALHO *et al.* 2015; LORETI *et al.* 2016; SAUTER 2013].

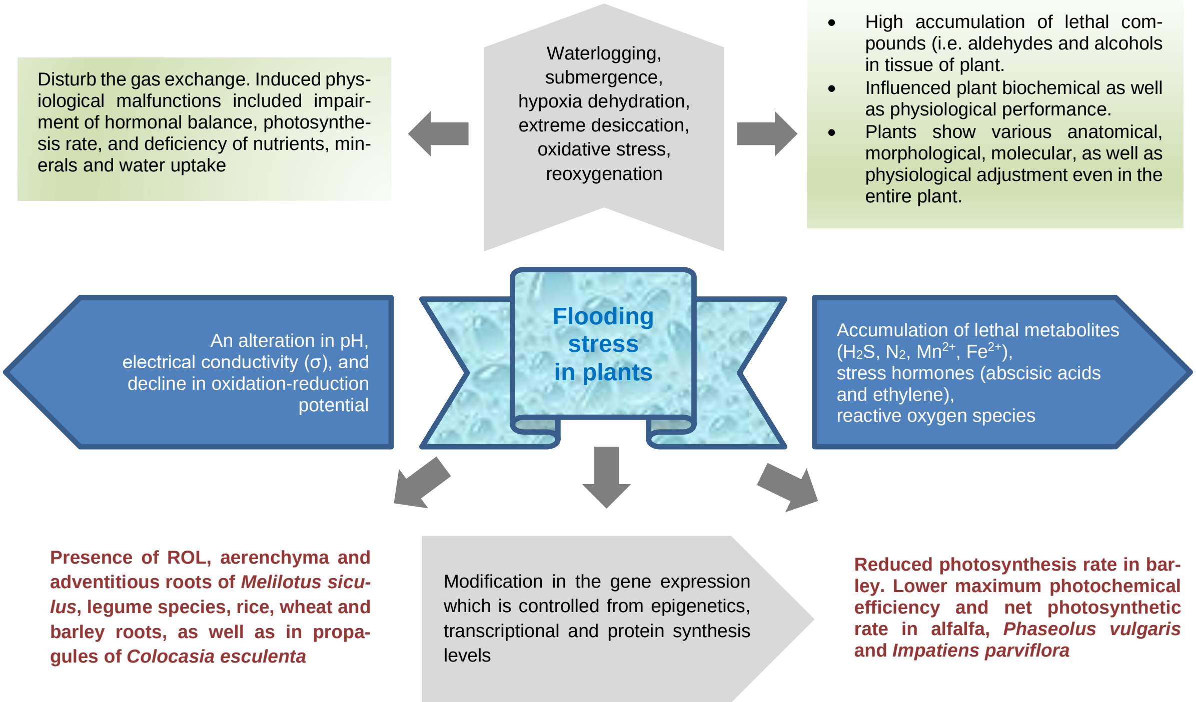

Fig. 2. Flooding stress: types, consequences, effect on soil as well as plant metabolism and responses of different plants to survive in these adverse conditions; source: own elaboration

Waterlogging, soil erosion, water flow, and pedoturbation affect both physicochemical and biochemical soil properties. The usable accumulation of humic substances changes with increasing soil wetness [FERRONATO *et al.* 2019]. In the presence of waterlogging, the existing root can be affected by the lack of oxygen and the resulting low ATP formation due to the loss of oxidative phosphorylation [BAILEY-SERRES, VOESENEK 2010].

In cold waterlogged rice fields, reduced soil temperature, less irrigated plow layer, and reduced availability of nutrients lead to a decrease in average yield [LIU *et al.* 2016]. In waterlogged soils, a change in pH, electrical conductivity (CE) and a decrease in oxidation-reduction potential (ε) have been observed [PEZESHKI, DELAUNE 2012; TOKARZ, URBAN 2015]. Physiological activities of plants are altered by waterlogging, i.e., respiration [YAMAUCHI *et al.* 2017], photosynthesis [ARGUS *et al.* 2015; LI *et al.* 2019], nutritional traits [LIU *et al.* 2016], plant growth and survival.

PLANT RESPONSES UNDER WATERLOGGING CONDITION

The resistance mechanisms of plant species to waterlogging depend mainly on the growth stage of the plant, the duration of exposure, and the degree of waterlogging [ROMINA *et al.* 2014; SHAO *et al.* 2013; WU *et al.* 2018]. The ability of plant species to tolerate waterlogging is mainly related to the evolutionary developed resistance to the stressor [BORELLA *et al.* 2019].

During waterlogging, plant responses vary by species, some of the plant species are tolerant, for example, rice (*Oryza sativa*), while others are highly sensitive, for example cucumber (*Cucumis sativus*) [XU *et al.* 2017]. Highly sensitive plant species have adopted different mechanisms for survival [BAILEY-SERRES, COLMER 2014; ZHOU *et al.* 2020].

Some anatomical, morphological, molecular, as well as physiological adaptations have been observed in crop plants during waterlogging stress that help plants to withstand these conditions [ARGUELLO *et al.* 2016; HERZOG *et al.* 2016; JOGAWAT 2019; ZHANG *et al.* 2016; 2019b].

Under waterlogged conditions, the plant has adapted various resistance mechanisms, such as the development of aerenchymas, expanded accessibility of soluble sugars, higher activity of the glycolytic pathway, fermentation enzymes, and the development of (ROS) scavenging enzymes to protect against oxidative stress [ANEE *et al.* 2019; ARMSTRONG *et al.* 2019; LAMBERS, OLIVEIRA 2019]. Plant responses to waterlogging are supported by hormones such as ethylene and abscisic acid and rely on species-specific adaptations that may be genetically determined [PHUKAN *et al.* 2016].

During congestion stress, plants respond with altered gene expression controlled by epigenetics, transcription and protein synthesis [JUNTAWONG *et al.* 2014; LEE *et al.* 2011; MUSTROPH *et al.* 2010]. The altered gene expression changes plant morphology and physiology. Some of the other responses are altered plant metabolism, restricted plant growth, altered nutrient uptake, increased disease susceptibility, and reduced crop yield [DOUPIS *et al.* 2017].

In response to waterlogging, many crops have adapted anatomically, morphologically, physiologically and even at the molecular level. However, in this review, only the morphological, anatomical, and physiological adaptations in different crops were discussed.

MORPHOLOGICAL AND ANATOMICAL ADAPTATIONS IN CROP PLANTS

The high photosynthetic rate as well as the persistence of plants in waterlogged soil are often associated with a number of anatomical and morphological changes, including the production of aerenchyma in root tissues, the appearance of adventitious roots, and the development of a barrier to root radial O_2 loss (ROL) [SAUTER 2013; VOESENEK, BAILEY-SERRES 2015; YAMAUCHI *et al.* 2017].

To adapt to waterlogging, various morphological as well as anatomical adaptations have been reported in plants, e.g., the formation of thick Casparian strips and the formation of aerenchyma in the taproot of wheat, barley, and rice [LI *et al.* 2019; SAUTER 2013; SHIONO *et al.* 2019] and the formation of adventitious roots (ARs) in bittersweet (*Solanum dulcamara*), were observed under waterlogging conditions [EYSHOLDT-DERZSÓ, SAUTER 2019].

Roots are highly sensitive organs of plants in flooded soils [PANOZZO *et al.* 2019; SAUTER 2013]. In roots, some morphological and anatomical changes are perceived that are important for the maintenance of root function under a hypoxic condition. The formation of aerenchymatous tissue facilitates roots to maintain aerobic respiration by initiating the distribution of various gases from the aboveground shoot to the waterlogged roots of plants.

The waterlogging resistance responses in woody plants are the formation of new adventitious roots, the development of aerenchymatous cells and the hypertrophy of lenticels [KREUZWIESER, RENNENBERG 2014].

Increases in stem diameter, reduced biomass accumulation in roots, and delayed flower development have been reported in different genotypes of soybean during waterlogging [GARCIA *et al.* 2020].

Other mechanisms to cope with hypoxia or anoxia conditions are the increase of nitrogen concentration in plant leaves and in certain areas of willow (*Salix* sp.) leaves [RODRÍGUEZ *et al.* 2018]. In the vegetative phase, a decrease in grain yield is observed in wheat under prolonged waterlogging [DING *et al.* 2020]. Significant reduction in length and dry weight under waterlogging has been reported in rice and wheat roots [NGUYEN *et al.* 2018]. Metabolic balance under excessive water treatment can be maintained by increasing aerial roots in sorghum (*Sorghum bicolour* L.) [ZHANG *et al.* 2019a].

The presence of aerenchymatous tissue and a barrier to radial oxygen loss in the cortical part of the root and nodules under waterlogging was observed in tolerant legume species. The permeability of the O_2 diffusion barrier (ODB) of nodules was increased in tolerant cultivars improving tolerance to waterlogging [STRIKER, COLMER 2017]. Some of the additional adaptations in legumes are alternative nodulation mechanisms and metabolic regulation in response to hypoxia [ROBERTS *et al.* 2010]. The formation of nodules above adventitious roots is also observed in messina (*Melilotus siculus*), a tolerant species [KONNERUP *et al.* 2018]. In certain species of legumes, there is a clear difference in the mechanisms of adaptation in a flood-prone zone [STRIKER, COLMER 2017].

Some crop species, e.g., rice, can induce stem elongation in waterlogged conditions to reach soil level. These strategies rely on morphological changes to overcome limiting (for normal growth processes) stress conditions [RUMANTI *et al.* 2020]. Ethylene biosynthesis is increased and it accumulates in the hypoxic root due to slow gas movement into the rhizosphere [SASIDHARAN, VOESENEK 2015]. Ethylene promotes morphological adaptation in plants, for example, the development of aerenchyma and adventitious roots. There is no evidence for the formation of obstruction in radial O_2 loss (ROL) by ethylene signalling.

- **Aerenchymatous tissue development in various plant parts**

Aerenchyma can provide a complete aeration channel for the transport of oxygen from leaves to plant roots; it can also remove other gases such as methane (CH_4), carbon dioxide (CO_2), nitrogen (N_2), and ethylene (C_2H_2), allowing plant roots to grow normally even in waterlogged soil [SHIONO *et al.* 2019]. In many lowland and aquatic plants, a specific tissue that forms air spaces/channels (aerenchyma) is observed to survive under submerged, emerged, and floating conditions.

Two categories of aerenchyma are found in taproots of waterlogging-tolerant plants: primary aerenchyma (in wheat, maize, and rice, formed by schizogenic and lysogenic cell disruption), present in primary tissues, and secondary aerenchyma, formed in secondary tissues (in roots of soybean) [TAKAHASHI *et al*. 2014; YAMAUCHI *et al*. 2018].

The development of secondary aerenchymatous tissue (spongy tissue with many gas spaces formed in the phellem) in plant roots, stems, root nodules, and hypocotyls of some plants (legumes) increases the exchange of gases between submerged soil tissues and the atmosphere [PEDERSEN *et al*. 2021].

The two types of aerenchyma give enlarged spaces for gas dispersion. Schizogenic aerenchyma develops by the disintegration of the adjacent acts (spread columns) of the cells of the bark and by the spread of the preexisting intercellular spaces, followed by the division and enlargement of the cell [TAKAHASHI *et al*. 2014].

In wheat seedlings, the development of aerenchymatous tissue in the seed roots has been demonstrated, originating from centrally located bark cells, e.g. pre-erenchymatous cells, and extending to the surrounding cells [XU *et al*. 2013]. In *Melilotus siculus* (a waterlogging-tolerant plant species), secondary aerenchyma (aerenchymatous phellem) developed in roots and hypocotyls [TEAKLE *et al*. 2012].

In maize (*Zea mays*) and its tolerant to the waterlogging ancestor *Zea nicaraguensis*, enhanced aerenchyma formation is associated with tolerance to waterlogging [WATANABE *et al.* 2017].

In a grafting experiment in bitter melon (*Momordica charantia* L.), increased aerenchyma formation suggests that grafting improves tolerance to waterlogging [PENG *et al.* 2020]. The formation of aerenchyma is also observed in the graft roots of taro (*Colocasia esculenta*) under moisture conditions [ABIKO, MIYASAKA 2020].

The formation of aerenchyma has also been reported in many xerophytic plants under waterlogging stress [HAQUE *et al.* 2010]. Treatment with ACC (1-amino-cyclopropane-l-carboxylic acid), *i.e*., a precursor of ethylene biosynthesis in plant roots, promoted internal oxygen movement to the root tip and facilitated aerenchyma formation in plants, suggesting that ethylene induces all adaptive responses under waterlogging [YAMAUCHI *et al.* 2014]. In rice roots, an exogenous supply of ACC (1-amino cyclopropane-l-carboxylic acid) produces aerenchyma, suggesting that ethylene is the key enzyme for the development of waterlogging-tolerant responses [YAMAUCHI *et al.* 2014]. On barley (*Hordeum vulgare*) root tips grown under fully aerated and enriched nutrient solution, ethephon (ethylene-producing chemical) treatment promoted the build-up of aerenchyma [SHIONO *et al.* 2019]. Ethylene was also shown to play a significant role in the development of aerenchyma in plants subjected to waterlogging stress.

- **Development of novel adventitious roots (ARs) as an alternative of primary root**

Adventitious root production is an adaptation to waterlogging stress that increases the dispersion of gasses and decreases separation for oxygen dispersal [SAUTER 2013]. To survive in waterlogged soil, the development of ARs is a significant change for plants to continue the normal function of primary roots as these roots are damaged by waterlogging [YAMAUCHI *et al*. 2014]. Recently, they formed adventitious roots with aerenchyma, are developed from the stem to restore root work in plant species, such as water and supplement uptake, and adhere to the surface [SAUTER 2013].

Adventitious roots (ARs) are connected to the stem by aerenchyma, which facilitates oxygen diffusion from floodwater to aerial shoots [AYI *et al*. 2016]. The adventitious roots originate from the basal region of the stem or the waterlogged part of the hypostyle [BAILEY-SERRES *et al*. 2012; SAUTER 2013]. A high rate of adventitious root development under waterlogging is observed in maize and its waterlogging-tolerant stem variety, Zea nicaraguensis [WATANABE *et al*. 2017].

These roots generally transform into basal roots when the primary root structure is no longer able to supply water and minerals to the shoot [YANG *et al*. 2016]. Adventitious roots regularly emerge from the basal part of the stem or in the area where lenticels are abundant, and their development is lateral and parallel to the water-soil surface in Sedum spectabile cultivars [ZHANG *et al*. 2019c]. In sesame (Sesamum indicum), adventitious roots represent a tolerance strategy to waterlogging [WEI *et al*. 2013].

Adventitious root development is constrained by complex genetic events at each developmental stage, such as during root primordia development, root emergence, and continuous growth. Genetically controlled factors of adventitious root development have been recognized in rice [BELLINI *et al*. 2014]. The formation of floating adventitious roots depends on several ecological parameters, such as water depth (e.g. whether or not part of the aboveground shoot is flooded), oxygen levels, light penetration and, in addition, the concentration of dissolved CO_2 (the last two affect the carbohydrate status of plants) during flooding.

Adventitious roots are formed in cucumber by treatment with auxin such as indole-3-acetic acid (IAA) and ethylene (C_2H_2). In cucumber, induction of ARs by auxin is ethylene-dependent, but induction by ethylene is auxin-independent [QI *et al*. 2019]. The amount of adventitious roots was increased in soybean cultivars in response to overwatering [KIM *et al*. 2019]. In maize seedlings, waterlogging induced the development of adventitious roots to increase tolerance under this stress [YU *et al*. 2019].

Ethylene is the key inducer for all versatile responses to waterlogging in tomato (*Solanum lycopersicum*) plants. Ethylene promoted the formation of AR primordia on the hypocotyl surface in tomato [VIDOZ *et al.* 2010]. Ethephon (ethylene releasing compound) treatment increased the development of adventitious root in the grain of barley [SHIONO *et al.* 2019].

Nitric oxide (NO) is involved in resistance to waterlogging by increasing adventitious root production in several plant species. To study the effects of NO, sodium nitroprusside (a donor of NO) was used in suaeda (*Suaeda salsa*). It shows that NO signalling expands resistance under waterlogging conditions and increases adventitious root development in *Suaeda salsa* [CHEN *et al.* 2016]. Also, the generation of reactive oxygen species is a major element of signaling related to the emergence of adventitious roots under waterlogging stress [STEFFENS, RASMUSSEN 2016].

- **Development of barrier for radial root oxygen loss (ROL)**

Some marsh plants form a structural boundary that blocks the escape of oxygen from apical root regions, termed the barrier to radial oxygen loss [EJIRI, SHIONO 2019]. Environmental signals activate the induction of the ROL barrier in the root, a factor that, together with the gas-filled porosity of the tissue, promotes internal air circulation [COLMER *et al*. 2019].

Induction of the radial O_2 loss barrier promotes longitudinal O_2 dispersion and may also prevent phytotoxin invasion [PEDERSEN et al. 2021]. Induction of the ROL barrier lowers the level of oxygen transported through aerenchymatous tissues to the root tip and allows root development in anoxic soil [EJIRI, SHIONO 2019].

Plant roots of some species establish a ROL barrier under waterlogged conditions (inducible ROL barrier), while the remaining species allow oxygen to escape under aerated conditions (constitutive ROL barrier). The inducible ROL barrier is formed by suberin and lignin deposits in the outer parts of the roots in the outer cell space (apoplast). Some wetland plant species such as Echinochloa (a weed plant grown in rice paddies) establish a constitutive ROL barrier, i.e. it is present even in the absence of waterlogging. A constitutive ROL boundary is not present in barnyard grass (*E. oryzicola*), which is commonly found in rice fields under aerated conditions. However, 90% of the sclerenchyma was very woody; it released oxygen from the lower part of the roots. A larger percentage (approximately 55%) of root exodermis cells not formed by suberin lamellae was observed in this plant. These results suggested that suberin is an important component in the formation of the constitutive ROL barrier [EJIRI, SHIONO 2019].

Waterlogged soils are composed of monocarboxylic acids produced by anaerobic microorganisms. These organic acids accumulate as phytotoxins and enhance the formation of radial root oxygen loss barrier in rice roots [COLMER *et al*. 2019]. In shorter roots, this barrier formation is weaker than in longer roots of plant species. This suggests that the age and growth stages of the root tissue influence this formation of the ROL barrier [SHIONO *et al*. 2011].

A barrier to radial root oxygen loss formed by lateral roots emerging from adventitious roots was investigated in Zea nicaraguensis using root peeling electrodes and O_2 microsensors. Stimulation of the barrier to radial oxygen loss associated with tolerance to waterlogging in this plant. The barrier of ROL is also present in lateral roots, requiring a re-evaluation of the function of roots as a site of oxygen loss [PEDERSEN *et al*. 2021].

Hordeum marinum (a wild related variety of wheat) is tolerant to waterlogging by creating a barrier to root decline radial oxygen O_2 loss. It increases the porosity of the root (gas volume/root volume), which is associated with tolerance to waterlogging [KONNERUP *et al*. 2017].

At the time of root radial oxygen O_2 loss barrier formation, the first stage is electron-dense material development in hypodermal and exodermal cell walls [SHIONO *et al*. 2011]. A transcriptome study conducted in rice using laser micro dissected tissues of the root outer cell wall suggested that many genes involved in suberin biosynthesis, but not lignin biosynthesis, were up-regulated during ROL barrier development in rice plant roots [SHIONO *et al*. 2014].

In rice roots, the introduction of the ROL barrier is coupled with high expression of genes associated with suberin, and it is also responsive to phyto-toxins in waterlogged soils [YAMAUCHI *et al*. 2018]. In addition, the accumulation of malate in rice root may form a ROL barrier, suggesting that malate is also important for the biosynthesis of fatty acids (FAs), which provide substrates for suberin biosynthesis [KULICHIKHIN *et al*. 2014].

Surprisingly, other toxic compounds produced in waterlogged soils as a product of metabolic activity of anaerobic microorganisms also developed ROL barrier in plant roots of submerged species; some of these compounds were organic acids and iron metal (Fe^{2+}) [KOTULA *et al*. 2017]. Further studies are needed to explain the signalling cascades and biochemical control during ROL barrier development and to show the effects of the rigid ROL barrier and root morphology (role of lateral root) on the uptake of water and minerals in the persistent waterlogging and subsequent drainage system (with the roots recovering growth) [YAMAUCHI *et al*. 2017].

PHYSIOLOGICAL REACTIONS OF CROP PLANTS UNDER WATERLOGGING

Physiological disorders caused by waterlogging include impaired hormonal balance, photosynthetic rate, and lack of nutrients, minerals, and water uptake, which cause poor development when flooded. Waterlogging causes stomata closure associated with photosynthetic efficiency of plants, disrupting gas exchange and ultimately reducing yield and productivity [YU *et al.* 2015; ZHU *et al.* 2016].

Plants also show a decrease in stomatal conductance (g_s) under waterlogging [BARICKMAN *et al.* 2019; POSSO *et al.* 2018], often caused by reduced assimilation of net CO_2 and chlorosis of the leaf [DE SOUZA *et al.* 2013; POSSO *et al.* 2018]. Reduced net CO_2 accumulation is caused by restricted uptake of water (H_2O) and nutrients (P, Ca, Mg, Fe, Mn, Mo, etc.), which reduce plant development, growth and organic matter accumulation [MARASHI 2018; PLOSCHUK *et al.* 2018; YE *et al.* 2018].

Stress due to waterlogging affects the activity of photosynthetic enzymes, alters the structure of chloroplasts, and damages the reaction centers (RCs) of photosynthesis [LIN *et al.* 2016; REN *et al.* 2016; ZHENG *et al.* 2009]. Decreased chlorophyll contents (especially chlorophyll a and b) have been observed in water-soaked grown plants [BANSAL, SRIVASTAVA 2015]. This leads to an overall decrease in photosynthetic rate (P_N) and ultimately a decrease in crop yield and production [ZHANG *et al.* 2019a]. Under waterlogging/flooding conditions, several ROS were produced as a result of oxidative damage due to excessive reduction in the electron transport chain [LAL *et al.* 2019].

Bermuda grass (*Cynodon dactylon*) exposed to waterlogging shows reduced leaf photosynthesis, a decrease in transpiration rate (E), reduced stomatal conductance (g_s), and loss of root fresh weight [XIAO, JESPERSEN. 2019]. Lower stomatal conductivity affects plant root water uptake from soil water and is the most important limiting factor for plant development [BARICKMAN *et al.* 2019].

In maize, a significant reduction in transpiration, stomatal conductance, and photosynthetic rate (P_N) was observed due to excessive soil moisture. Other physiological parameters were also weakened under waterlogging in dryland crops [TIAN *et al.* 2019]. Similar results were also reported in winter wheat (*Triticum aestivum*) [ABID *et al.* 2018]. Reduction in leaf gas exchange was also observed in soybean crop [GARCIA *et al.* 2020].

- **Waterlogging induced anaerobic respiration and alteration of cellular metabolites**

Waterlogging stress represents a hypoxic state (below 21% O_2) in which a shift from the oxygenated to the low-energy anaerobic state occurs to support plant growth. It involves various biochemical adaptations, the pathways of anaerobic digestion, and the formation of defensive compounds for the removal of phytotoxic products [EVANS, GLADISH 2017] which are important for plant persistence under waterlogged conditions.

There are two types of anaerobic respiration, one is ethanolic fermentation and the other is lactate fermentation [DU *et al.* 2018]. In ethanolic fermentation, a two-step process is involved in which first pyruvate decarboxylase (PDC) decarboxylates pyruvate to acetaldehyde and then alcohol dehydrogenase (ADH) converts acetaldehyde to ethanol by producing oxidised nicotinamide adenine dinucleotide (NAD^+). In lactate fermentation, lactate dehydrogenase (LDH) catalyzed pyruvate to lactate using reduced nicotinamide adenine dinucleotide (NADH) [ZHANG *et al.* 2017].

Fermentation leads to the accumulation of phytotoxins and depletion of carbohydrate reserves [LORETI *et al.* 2016; PUCCIARIELLO, PERATA. 2017]. In this condition, plants use glycolysis for energy production and mobilization of stored sugar reserves [LORETI *et al.* 2016]. The primary substrates of fermentation are water-soluble carbohydrates (WSCs). The reserves of water-soluble carbohydrates WSCs can be reduced when the balance between carbohydrate metabolism and photosynthesis is altered during waterlogging [JURCZYK *et al.* 2016], and these changes affect the fermentation rate and survival of some species [CHEN *et al.* 2013; LIU *et al.* 2017].

Therefore, waterlogging and anaerobic metabolism leads to critical growth inhibition and eventual death of many plants due to energy depletion and accumulation of phyto-toxic products (such as lactate) and carbon loss (via ethanol loss from roots) [TAMANG *et al.* 2014].

Anaerobic respiratory enzymes, such as pyruvate dehydrogenase (EC 1.2.4.1), alcohol dehydrogenase (EC 1.1.1.1), and lactate dehydrogenase (EC 1.1.1.27) are critical to the defense mechanism of plants to survive in waterlogging stress. Their increased activity provides energy to drive normal root function in waterlogging for normal plant growth [BARICKMAN *et al.* 2019].

These fermentative enzymes play key roles to protect plants under the hypoxic conditions such as preventing the accumulation of fermentative products (pyruvate and lactate), also helping in NADH cycle and production of ATP at substrate level [BORELLA *et al.* 2019; BUI *et al.* 2019]. However, the enzyme lactate dehydrogenase (LDH) produces lactic acid, which lowers cytosolic pH [BANTI *et al.* 2013].

Anaerobic respiration was observed in almond (*Prunus dulcis*) during waterlogging treatment [ZHOU *et al.* 2021]. Increased activity of anaerobic respiration enzymes was studied in seedlings of wheat grown under waterlogging conditions. The enzymatic activity of pyruvate decarboxylase, alcohol dehydrogenase, and lactate dehydrogenase was increased in wheat depending on the genotypes and higher alcohol and lactate content was also observed [DU *et al.* 2018].

- **The antioxidant mechanism to defense against waterlogging induced stress**

A high level of formation of reactive oxygen species is an important phenomenon in hypoxia or anoxia and especially in oxygenation [PUCCIARIELLO, PERATA 2017]. In this situation, an imbalance of redox potential can generally trigger oxidative damage to various cellular metabolites. It leads to changes in membrane fluidity, peroxidation of unsaturated fatty acids of the cell membrane, denaturation of proteins, inactivation of enzymes, genomic damage, and irreversible metabolic changes leading to cell apoptosis [LORETI *et al.* 2016].

To survive under oxidative stress, plants generate an antioxidant defence system by increasing the activity of ROS and ROS through the enzymatic and non-enzymatic antioxidant mechanism to eliminate oxidative damage under hypoxic conditions [BALAKHNINA *et al*. 2015; IRFAN *et al*. 2010]. To counter the hazardous effects of ROS, plant species have evolved several defensive antioxidant systems. Several enzymes such as ascorbate peroxidase (APX), superoxide dismutase (SOD) and catalase (CAT) play key roles in the antioxidant mechanism [FUKAO *et al*. 2019].

Under waterlogging stress, malondialdehyde (MDA) is used as a marker of oxidative lipid damage, which is the product of lipoperoxidation of cell membranes [BALAKHNINA *et al*. 2015]. MDA is indirectly proportional to antioxidant activity, if MDA value is high, then the antioxidant ability is low and it decreases resistance during waterlogging situation.

During waterlogging, the enzymes of ROS scavenging such as catalase, glutathione reductase (GR) and peroxidase (POD) were activated in many plants. For survival under short-term waterlogging, higher levels of ROS interceptors were observed in Chinese cherry (Prunus pseudocerasus) genotypes [JIA *et al*. 2019]. Waterlogging treatment increased H_2O_2 concentration in maize genotypes [CHUGH *et al*. 2016]. More H_2O_2 content and superoxide radical was accumulated of roots in pigon pea (Cajanus cajan) genotypes [DUHAN *et al*. 2017]. In sedum genotypes, the higher activity of SOD, CAT and APX was observed during waterlogging treatment [ZHANG *et al*. 2019c].

- **Changes in photosynthetic parameters to waterlogging responses**

Dynamic monitoring of various photosynthetic and chlorophyll fluorescence parameters were studied under waterlogging conditions, it reveals the growth strategies of plants [PAN *et al*. 2019]. The maximum quantum efficiency (F_v/F_m) of photosystem II and plant phenotyping studies are evaluated using chlorophyll fluorescence under abiotic stress. Chlorophyll fluorescence and chlorophyll content were reduced in blackgrass (*Alopecurus myosuroides*) genotypes during waterlogging stress and light-harvesting complex (LHC) was damaged in blackgrass and tomato during waterlogging situation [BANSAL *et al*. 2019].

In barley, photosynthesis was reduced under early waterlogging conditions due to stomatal and non-stomatal constraints. During late waterlogging, damage to the photosynthetic machinery and reduction in mesophyll stomatal conductance by chlorophyll fluorescence was observed in barley. In addition, photosynthesis was generally reduced in oilseed rape (*Brassica napus* subsp. *napus*) during late and early waterlogging due to non-stomatal limitations [FUKAO *et al.* 2019].

A study on *Arabidopsis thaliana* investigating the damage caused by waterlogging at different temperatures showed that less effects of waterlogging were observed at lower temperatures than at higher temperatures. Waterlogging causes less damage as shown in a study at short temperature (about 16°C) compared to high temperature (about 22°C). Several photochemical properties such as chlorophyll fluorescence, electron transport rate (*ETR*), photochemical quenching (*qP*), maximum quantum yield (F_v/F_m), chlorophyll *a* and *b* content, and leaf temperature were more constant at low temperature. Malondialdehyde accumulation was also reduced in plants under waterlogging conditions at low temperature [XU *et al.* 2019].

Under waterlogging conditions, the maximum photochemical efficiency and net photosynthetic rate of leaves were lower compared to the control. In alfalfa (*Medicago sativa*), the net photosynthetic rate and maximum photochemical efficiency (F_v/F_m) were increased by pretreatment with melatonin [Zhang *et al.* 2019b]. A similar study was conducted in star magnolia (*Magnolia sinostellata*), resulting in changes in chlorophyll metabolism and photosynthesis that are beneficial for the growth of this endangered plant species [Yu *et al.* 2019].

In sorghum, photosynthesis is affected by excessive water treatment. In sorghum, *ETR*, *qP* and actual *PS*II quantum yield (*Y*II) decreased while non-photochemical quenching (*NPQ*) increased after water stress treatment. This decrease in *qP* indicates that the amount of open reaction centers of *PS*II decreased and the potential activity of *PS*II also decreased [Zhang *et al.* 2019a]. The photochemical quenching *qP* and maximum quantum yield F_v/F_m decreased significantly and *NPQ* increased slightly in cotton (*Gossypium hirsutum*) sensitive genotypes during water stress [Pan *et al.* 2019]. The value of photochemical quenching coefficient (*qP*) and reduced electron transport rate of *PS*II is also decreased in French bean (*Phaseolus vulgaris*) and the variation in the trapped amount of light energy used in organic acid formation finally reduces the effective quantum yield of photosystem II (ΦPSII) [Mathobo *et al.* 2018].

Electrolytic leakage (*EL*) and malondialdehyde (MDA) concentrations increased dramatically in alfalfa plants during waterlogging treatment, but a significant decrease in chlorophyll content was also observed. Melatonin pre-treatment strongly suppressed these responses in alfalfa [Zhang *et al.* 2019b]. The growth- and photosynthesis-maintaining mechanisms of melatonin have been previously demonstrated for many other plant species under various stress conditions [Zhao *et al.* 2017; Zheng *et al.* 2017].

In *Impatiens parviflora* (small-flowered touch-me-not plant), low light and waterlogging conditions decrease light energy absorption by photosynthetic antenna pigments, block photosynthetic electron transport, and reduce photosynthetic enzyme activity and carbon assimilation, thereby impairing photosynthesis and inhibiting growth [Quinet *et al.* 2015]. Due to re-oxygenation, ROS is overproduced in leaves, which may lead to photosynthetic imbalance, reduced stomatal opening and damage to photosynthetic pigments, and finally, during this condition, the light collection system of the electron transport chain in chloroplasts is overloaded, causing electrons to escape and accumulate ROS in the leaves of water-saturated plants [Gill, Tuteja 2010].

CONCLUSIONS

Waterlogging poses a major threat to agriculture and affects crop yields and productivity worldwide. Food crops can survive under these critical conditions by making complex anatomical, biochemical and physiological adaptations. The morphological resistance mechanism involves the production of new adventitious roots, aerenchyma, and a barrier to radial oxygen loss in the roots of the crop. A defining feature of tolerance under waterlogging is the alteration of various physiological properties such as photosynthesis, stomatal conductance and gas exchange etc. and biochemical adaptations such as increased fermentative enzyme content, energy crisis and increased glycolysis supply. Various long and short-term responses to waterlogging stress have been recognized in plants depending on the species as well as different genotypes of the species. Some of the plant species are tolerant while others are susceptible to waterlogging. These resistant species are able to grow under such conditions because they develop certain modifications that help them adapt to the conditions of waterlogging.

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