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Root Adaptation Traits under Water Logging Conditions

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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ABSTRACT

A problem known as "waterlogging" occurs when the soil is saturated, which can seriously hinder plant growth and development. Waterlogging limits the amount of oxygen that can reach the roots of the plant, which affects the physiological and biochemical changes that occur in the plant. Plants, however, have developed a variety of adaptive strategies to deal with this kind of stress. Several morphological adaptations are displayed by plants to withstand waterlogging. Aerenchyma development, adventitious roots, and a shallow root system are a few of these. Plants respond to waterlogging stress by undergoing metabolic changes at the biochemical level. Increased ethylene synthesis, a stress hormone, controls the formation of aerenchymas and adventitious root growth, among other adaptive responses. In addition, plants store osmoprotectants such as soluble carbohydrates and proline to preserve the osmotic balance within their cells and prevent harm from waterlogging. Plants are able to tolerate waterlogging stress because of complex interaction of morphological, physiological, and biochemical adaptations together. In order to produce resilient crop varieties and sustainable agricultural techniques, it is imperative to comprehend the underlying mechanisms determining root architectural features under waterlogging circumstances. Subsequent

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investigations aimed at clarifying the molecular mechanisms behind plant reactions to waterlogging will aid in the creation of novel approaches to lessen the deleterious consequences of this environmental stressor.

Keywords: Waterlogging; submergence; abiotic stress; waterlogging tolerance.

1. INTRODUCTION

Plant throughout its life cycle is affected by different kind of stresses, like abiotic and biotic stresses. It can be witnessed that the root system of the plant is exposed to the various kind of abiotic stress as compared to the shoot system, therefore it can be seen that the root system of the plant is much more affected by abiotic stresses than the aerial parts of the plant. Plant stresses such as drought, waterlogging, salinity, extreme temperatures, nutrient deficiency, etc. are considered under abiotic stress. Globally, there is a drastic shift in the climatic conditions accelerating the unfavorable conditions that favors the abiotic stresses which eventually affects the crops grown in the field. The major shift is seen in the rainfall patterns that have been unpredictable leading to exposure of a plant to severe abiotic stress, flooding (either submergence or waterlogging) being one of them and is caused by increase in the frequency and the quantity of the rainfall occurring over a period of time due to change in the climatic conditions. [1,2]

Agriculture around the globe is affected by the rising incidence of adverse weather conditions that is majorly accelerated by global warming leading to extreme events that alter water availability in the layers of the soil, altogether being big threats to food security [3] and this effect of climate change affect the agriculture sector globally as agronomic crop production is highly sensitive to extreme weather conditions. [4] Whenever the soil layers are saturated with water and water content of the surface layer of the soil exceeds 20% of the field carrying capacity, it leads to free standing water on soil surface. [5,6]

Flooding in the agricultural fields is usually due to irregular patterns of heavy rainfall over a period of time and also can be caused by over flowing of a water body due to many biological and unbiological factors. Flooding has negative effects on various aspects of the society such as economic and social aspects which may include loss of livestock and seeds stock and destructions of infrastructure and machineries and tools as well. [7,8]

Gas exchange between the soil and air decreases when it experiences waterlogging. O2 levels in saturated soil will drop quickly as a result of the water's slow gas diffusion. This situation leads the oxygen in the soil to rapidly deplete, and the soil may quickly become anoxic (without oxygen) or hypoxic (with little oxygen). Insufficient soil oxygen put stress upon roots, resulting in a significant oxygen deficit that causes an energy deficit and toxin buildup, which in turn can reduce the yield of plants directly by affecting root metabolism as well as indirectly by affecting the availability of essential nutrients to the plant. [9,10].

2. WATERLOGGING

Waterlogging term refers to flooding of the soil, and is one of the abiotic stresses that are characterized under flooding. It occurs due to infiltration of water that accumulates over the soil layer due to either rainfall or flooding and exceeds the rate of surface drainage and evapotranspiration. [11] It can also be defined as the condition in which soil contains excessive water and limits the flow of gases found in the soil pores. [12,2].

Due to the massive loss of yield and output, waterlogging has a greater impact on agricultural land and a variety of negative economic effects. This economic loss brought on by waterlogging has social repercussions that last a lifetime. The accumulation of water is a problem where water fills soil pores and affects air circulation. The water displaces gases that are in the soil pores, which then slowly seep into the waterlogged soil and cause a decline in available oxygen (hypoxia) in the rhizosphere, or root zone. The availability of oxygen to plant roots and soil microorganisms is hindered by the unsteady dispersion of oxygen and other gases in the soil. Under hypoxic conditions, the oxygen that is available is quickly absorbed by plant roots. [13, 2].

Waterlogging limits the overall growth and development of the plants thereby reducing the crop productivity. The main reasons responsible for the occurrence of the waterlogging is accumulation of water over the top layer of soil due to poor drainage system of the field and extreme rainfall events. Events of waterlogging conditions are expected to increase due to heavy and unpredictable rainfall patterns [14,2].

Long-term waterlogging has a negative impact on the plant's growth at every stage of its life cycle and ultimately reduces output. Waterlogging, has a real impact on how oxygen is distributed in tissues and how different gases are distributed between cells. These factors restrict the exchange of oxygen and aerobic respiration in mitochondria, which has a real impact on how the plant typically functions biochemically and physiologically. [8] The plant's rate of development at the vegetative stage under waterlogged situations is slowed down, suggesting that this stage is the most vulnerable stage [15,16].

Sensitive plant species' growth, metabolism, and endurance are hampered by waterlogging because it causes a lack of oxygen, causing the production of adenosine triphosphate (ATP) [14]. Reactive oxygen species, also known as ROS, and deadly metabolites, such as H_2S, N_2, Mn^{2+} , and Fe^{2+}, build up in the soil as a result of an oxygen deficiency or absence (hypoxia and anoxia, respectively) that is caused by anaerobic bacteria, which in turn influences the stress hormones, such as ethylene and abscisic acids, in roots [17,18].

Some plants are modified and develop features to endure such situations under stresses for their survival such as morphological modifications and physiological adaptations. It is necessary for the plant to modify itself and adapt to such changes in order to maintain agricultural fields, improve the crop productivity, and adaptation of crop to changing climate [19,16].

It is important to develop waterlogging tolerant crops by using various breeding methods such as screening and thereby developing better knowledge on the physiological mechanisms of the plants in response to waterlogging that will help in further development of techniques, and methods to develop improved tolerant crops [20, 2].

With chlorophyll deterioration, leaf senescence, and yellowing limit the ability of leaves to collect light and ultimately cause a loss in photosynthetic rate, waterlogging causes leaf stomata to close. As a result, oxygen availability in saturated soil decreases significantly, which inhibits root respiration, reduces root activity, and leads an energy shortage. Through glycolysis and ethanol fermentation, plants are momentarily able to retain some level of energy production during hypoxia brought on by waterlogging. Through extended period of waterlogging and anaerobic respiration the toxic metabolites like lactic acid, ethanol, and aldehydes accumulates, along with an increase in reactive oxygen species (ROS), particularly hydrogen peroxide, eventually leads to cell death and plant senescence [17,18].

Soil waterlogging may occur during times of exce ssive rain, submerging soil roots in water.The sh oots may potentially become partially or entirely s ubmerged during flooding situations.The diffusion of gases dissolved in water is 104 times slower t han that of gases in air, which is one of the prima ry effects of this altered situation. Gas diffusion is crucial for plants; for photosynthesis to take place, CO2 has to enter the chloroplasts, and for respiration to occur, O2 must diffuse quickly into the mitochondria. [5,21] The initial impact of water logging is seen in the soil as a change from an aerobic condition (oxygen rich) to anaerobic condition (oxygen deprived) caused by inadequate aeration, which has an impact on both the growth and survival of roots [9].

3. WHAT IS ROOT ARCHITECTURE?

In 1880, Charles Darwin introduced the concept of root system layout when he wrote about root, that it bends under the force of gravity. The three cellular processes in roots that underlie root architecture are curving, elongating, and branching. Together, they control just how roots are distributed throughout the soil and throughout time, which affects how well-anchored and how easily the plants are able to absorb water and nutrients. The term "root architecture" refers to the arrangement of roots in the soil profile with time and space [22,16].

The formation of biotic relationships at the rhizosphere, water and nutrient intake, soil anchoring, and other critical adaptation processes are all carried out by plant root systems. Therefore, modifications to the root system's design can have a significant impact on how well plants can absorb nutrients and water. However, in the field, root systems are exposed to a range of stresses that interact with plant genetics and alter the root system architecture [8,23].

Due to the fact that gases diffuse 10,000 times more slowly in water than in air, oxygen levels in waterlogged soils begin to decline as diffusive influx is unable to keep up with the demand from root and microbial respiration. Lack of oxygen in the soil's rooting zone may directly impact plant growth by restricting root aerobic respiration. The root system experiences hypoxia (reduced oxygen level) or even anoxia (lack of oxygen) when it is wet. Even in roots with aerenchyma cells, which are known to help plants with internal O2 diffusion, severe hypoxia is seen. Plants begin to produce energy through fermentation rather than less effective aerobic respiration as a result of O2 depletion. The shoot's ability to absorb nutrients and water is constrained, and root growth is hindered in this energy crisis [8, 14].

Root system architecture (RSA) is essential for plant fitness and survival. For greater agricultural adaptability, it is crucial to create crop genotypes with effective root systems for increased abiotic stress tolerance. Breeding plans for rainfed environments prioritise root features that overcome abiotic restrictions as they are essential for conserving structural and functional properties. Improved water and nutrient uptake may be facilitated by root characteristics such as deep root systems, higher root density in the subsoil, enhanced root hair length as well as density, and/or xylem diameters [22,24].

4. EFFECT OF WATER LOGGING ON THE PLANT AS A WHOLE

Plants subjected to water stress may alter their physiological metabolisms, such as photosynthesis, antioxidant enzyme systems, and hormone levels, as a way of coping with their extreme circumstances. They will also alter the morphology of their leaves and roots. Waterlogging lead to hypoxia, which is a condition that results in an insufficient amount of oxygen in the soil environment, and anoxia, which is a condition that refers to a complete lack of oxygen in a specified soil environment, which completely stops root respiration and affects key metabolic activity of the plants *by causing a lack of important minerals like nitrogen, magnesium, potassium, and calcium, which negatively impacts a number of physiological and biochemical processes in plant.* Such condition also hinders root hydraulic conductivity, stomata conductance, and net CO2-assimilation rate. Roots may thrive in such a condition by triggering biochemical or anatomical modification, modification that increases overall oxygen movement inside the plant and improve the root and shoot growth under anoxic environment of the soil [25].

The primary indicators of a plant's response to water stress are its leaves and roots, and they are best able to demonstrate this through their surface morphological traits and internal anatomical structure. Under conditions where oxygen is scarce, plants display a metabolic transition from aerobic metabolism to anaerobic fermentation. This biochemical alteration is necessary for plants to obtain a constant supply of the hormone adenosine triphosphate (ATP). For respiration, which produces the energy (ATP) needed for cellular operation, development, and the transportation of nutritional ions, roots need oxygen (O_2) Roots have to continue to function in order to supply the shoots with water as well as nutrients when the soil becomes partially submerged by water. While new adventitious roots from stem nodes may also arise, they are better adapted to low soil oxygen levels and must survive and adapt if at all possible. Additionally, some roots may protrude above the soil into the water [14,26].

In extreme circumstances, leaves display evidence of etiolation, atrophy, curling up, senescence, and even abscission; other symptoms of waterlogging stress include curling, yellowing, withering, falling off, rotting, etc. There are two ways that leaves can respond to waterlogging stress: one is to thicken, and the other is to thin out [27,28].

The stomata of leaves closes, while chlorophyll deterioration, leaf senescence, and yellowing make leaves less able to absorb light, which ultimately causes a drop in the rate of photosynthetic activity. The oxygen rate of diffusion in water is only 1/10,000 that of air, and waterlogging causes air to be drawn out of soil pores, preventing the exchange of gases between the soil and atmosphere. Due to the severely restricted oxygen availability in wet soil, root respiration is repressed, root activity is lowered, and energy is depleted. Through glycolysis and ethanol fermentation, plants are momentarily able to retain some level of energy production during hypoxia driven by waterlogging. It has been indicated that roots could improve adaptability by creating air cavities in the aerenchyma to expand storage space, and block the entry of soil toxins into plants. As a result of root anaerobic respiration, which limits sugar transfer from the stem into the root by reducing the consumption of sugar in the root, and the accumulation of photoassimilated products in leaves, which can act as a negative feedback inhibitor to the photosynthetic rate, leaf carbohydrates may accumulate quickly within a few days for plants that are not well adapted to waterlogging. In such circumstances, roots either induce anatomical or biochemical adaptation to survive. Plants that suffer from water stress will adapt to their unfavorable surroundings by changing several physiological processes and morphological features, including photosynthesis, antioxidant enzyme systems, hormone levels, and the morphology of their leaves and roots [27-29].

But over time, waterlogging and anaerobic respiration cause a buildup of toxic metabolites like lactic acid, ethanol, and aldehydes as well as an increase in reactive oxygen species (ROS), particularly hydrogen peroxide, which ultimately causes cell death and senescence in plants [30] Inhibited gaseous exchange might further impact a plant's ability to tolerate waterlogging by causing hormones to accumulate or degrade quickly [20,17].

For respiration, which gives rise to ATP needed for cell growth and maintenance as well as for the transportation of nutritional ions, roots need oxygen (O_2). In order to provide nutrients and water to the shoots, roots have to keep functioning even when the soil becomes soggy. While new adventitious roots that are more suited for little soil O2 can also arise from stem nodes, the aerobically formed roots that are currently there must endure and, if possible, adapt. Adaptive reactions to waterlogging require the induction of ethylene. By enhancing stomatal conductance, exogenous ethylene can boost photosynthesis [31,14].

Plants respond primarily to water stress through their leaves and roots, and the strongest indicators of their ability to adapt to harsh circumstances are their internal organelles and external morphological traits [32,26].

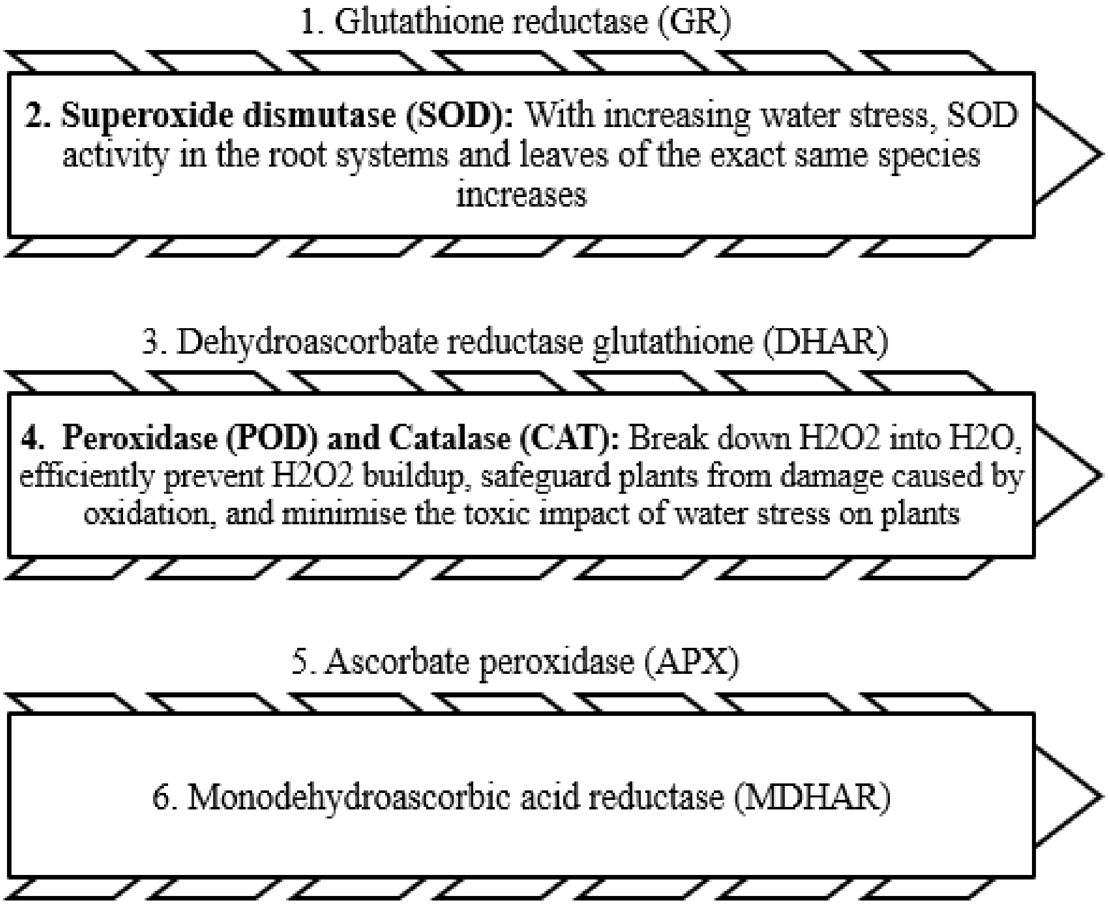

Fig. 1. The enzymatic antioxidants include

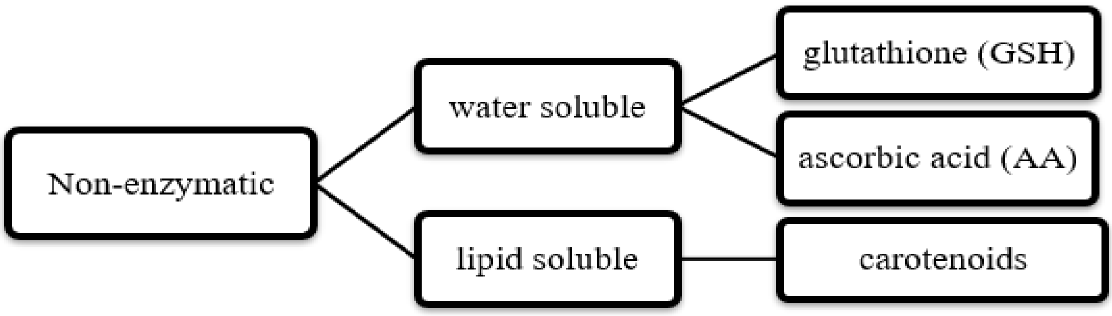

Fig 2. The non-enzymatic antioxidants include

5. ADAPTATION OF PLANT AT MORPHOLOGICAL LEVEL

The morphological changes that occur are mainly caused by adventitious roots (ARs) or other aeration tissues, rapid apical meristematic tissue elongation, constraints to radial oxygen loss (ROL), and the formation of air films in the upper cuticle, as reported by several studies [20,33].

Since waterlogging significantly slows down the rates at which oxygen and carbon dioxide permeate through roots and stems, it hinders both photosynthesis and respiration, making most plants vulnerable to it. Nevertheless, certain plants undergo unique morphological changes that mitigate the damage caused by disrupted energy metabolism and root respiratory depression in wet environments. As a waterlogging response, certain plants keep a gas film on the surface of their leaves when submerged. The gas film keeps aerobic respiration and photosynthesis going by promoting the entry of O2 in the dark and CO2 in the light [34,35].

Radical oxygen loss (ROL) is defined by Yamachi et al. (2018) as the loss of O2 that occurs both longitudinally through respiration when O2 passes through the aerenchyma and laterally through leaking into the intercellular spaces of the rhizosphere. Plants have the ability to form a barrier against root-tip oxidation loss (ROL), which reduces both O2 redirection and leakage to the intercellular gaps in the rhizosphere [26].

The rapid apical meristem expansion of plants is another defense mechanism against waterlogging. Delicate stems and internodes can extend quickly, allowing for fast air contact and escape from the oxygen-deprived environment and regular respiration [17]. This reaction is known as "low oxygen escape syndrome" (LOES).

The formation of adventitious roots (ARs) is a commonly documented adaptive modification in morphology. The plant's roots can access oxygen in the stagnant water owing to the adventitious root formation. After extended waterlogging, ARs form in the hypocotyl internodes or at the base of the stem, facilitating gas exchange and the absorption of water and nutrients. AR generation can maintain metabolic cycles and support healthy development and growth by partially replacing the primary roots that die under hypoxic stress. Since the newly formed ARs have more aerenchyma than the parent roots, they have better total oxygen absorption and diffusion potential roots [36,26].

Under water-logged conditions, adventitious roots can produce root hairs, expand the root structure's surface area, thin the cuticle, and form a well-developed aerenchyma, which serves as an extra layer of lignified vascular bundle cell barrier and increases the root's ability to transfer oxygen from the stem base to the root tip. Because of this, various plant species under stress from waterlogging have distinct mechanisms for growing adventitious roots, and plants that can withstand waterlogging are more likely to be able to do so. Certain studies suggest that roots may improve adaptability by creating air gaps in the aerenchyma, which increases storage capacity and keeps soil toxins out of plants [37-40].

In wheat roots under hypoxia, nitric oxide levels increase, which appears to promote ethylene synthesis, ROS production, and cortical cell death in order to promote the growth of stimulated aerenchyma. In rice, constitutive aerenchyma formation in roots is regulated by both ethylene-dependent and ethylene-independent pathways. Auxin signaling regulates the constitutive aerenchyma formation in rice roots [41-43].

6. ADAPTATION OF PLANT AT PHYSIOLOGICAL LEVEL

Research has shown that plant hormones are critical in helping plants adapt to damaging environmental stressors. An imbalance of hormones is brought on by hypoxia and inadequate oxygenation of the submerged tissue. These roots are always located near the top layers of the water, which probably have more oxygen in them. According to Justin and Armstrong (1987), most species found in damp settings have large interconnected spaces between cells called aerenchyma, which are filled with gas and often stretch from the shoots to near the tip of the roots. Adventitious roots that grew at or below the surface of the water became more evident in stagnant conditions after the floodwaters had passed. These roots are more adapted to waterlogging conditions because they have far larger intercellular spaces than the initial roots [15,44].

Plants produce reactive oxygen species (ROS) as signal transmitters to regulate the expression of genes and proteins in plant cells during normal physiological activities. ROS include superoxide anion radicals (O_2), singlet oxygen (O2), hydroxyl radicals (-OH), and hydrogen peroxide (H_2O_2). here is a constant state of dynamic equilibrium between the production and elimination of ROS. [6,45]

7. ANTIOXIDANT DEFENSE MECHANISM OF PLANTS UNDER WATERLOGGED CONDITIONS

In response to stress, plants increase their antioxidant defense mechanism to prevent cell damage. Enzymatic and non-enzymatic antioxidants are the parts of the antioxidant defense system.

8. ADAPTATION OF PLANT AT BIOCHEMICAL LEVEL

Soluble proteins and root anaerobic proteins (ANPs) are created in response to waterlogging stress. Plants can also respond to anoxia by altering the process by which root protein is produced. The proteins produced expressly in reaction to anaerobiosis are known as anaerobic polypeptides, or ANPs for short. Total soluble protein and RNA primary metabolites showed a negative correlation with the duration of waterlogging, as reported by Das and Sarkar (2001). Protein chemistry and the molecular approach have been used to study a number of ANPs. The anaerobic root proteins were initially described and identified from the maize root. All of them participated in the procedures that mobilize starch or sucrose for the process of fermentation of ethanol, which is necessary to keep producing energy in the absence of oxygen. They are therefore essential for surviving in anoxia [9].

9. ROLE OF PLANT HORMONES UNDER WATERLOGGING STRESS

Plant hormones are essential physiological cues in the process of developing waterlogging tolerance. All aspects of a plant's life cycle are mostly regulated by endogenous plant hormones, and a healthy plant's physiological development, growth, and metabolism depend on maintaining the correct ratio of several hormones. The plant regulates its response to waterlogging by adjusting the balance between the production and distribution of plant hormones through precise signaling. Plant hormones are essential physiological cues in the process of developing waterlogging tolerance [46,43].

1. **Ethylene (ET):** This hormone is particularly vulnerable to waterlogging and becomes more elevated in anoxic environments. Ethylene is a gaseous hormone found in plants that is less soluble in water than in air due to its extremely low water diffusion rate. Rapid ET buildup is one important way that plants deal with waterlogging, according to Alpuerto et al. (2016) and Hartman et al. (2019a, b). ET synthesis is necessary for the emergence of adventitious roots in stressed plants. Under waterlogging, ET accumulates in roots because of its continuous production and slow rate of water diffusion. With the development of lysogenic aerenchyma, ET promotes programmed cell death [5,10,47].

2. **Abscisic Acid** (ABA): ABA regulates the quantity of guard cells, which directly affects stomata and, ultimately, the water potential of plants. ABA is therefore

thought to be an important hormone in reactions to water stress. Abscisic acid plays a role in the emergence of root aerenchyma during waterlogging. Waterlogging led to an accumulation of ET in the lower stem, which consequently lowered the amounts of ABA in the stem and AR primordia. This demonstrates that, in contrast to ET, ABA negatively regulated the growth of ARs under waterlogging [48,49].

3. **Auxin (IAA):** It is necessary for plants to grow and flourish. As a precursor to waterlogging, auxin production can drive auxin transport to flooded parts of the plant. Conversely, an increase in auxin concentration can initiate ET biosynthesis, which in turn promotes auxin transport. Auxin buildup can then trigger ARs by initiating cell division. [50,51].

4. **Gibberellin** (GA): It is one of the essential hormones in plants that regulates growth and development. The main functions of GAs are to control cell size and number, which in turn controls several processes related to plant growth and development. Research has shown that GA has a critical role in increasing rice's ability to withstand waterlogging. The findings show that under saturated conditions, GA plays a crucial role in promoting internode elongation in rice [20,52].

5. **Salicylic Acid** (SA): It is a common phenolic compound found in plants that regulates the antioxidant system of cells by encouraging the production of genes linked to stress, enhancing the capacity of plants to cope with difficult conditions. Salicylic acid (SA), a signal molecule that can alter the physiological characteristics of wet plants, may be important for a plant's resistance to the stress of waterlogging. An adequate SA level can promote the growth of ARs and aerenchyma, which is positively correlated with plants' resistance to waterlogging, according to research by Bai et al. [53,39].

6. **Jasmonic Acid** (JA): It has been connected to the defense response against abiotic stress and is a key regulator of plant growth. The dynamic between JA and ET is essential for the formation and development of the aerenchyma and root system under conditions of waterlogging stress. When the chemical methyl jasmonate was sprayed on the leaves, the amount of ET increased, suggesting that exogenous JA can raise ET levels, which is beneficial for lowering waterlogging stress [32,52].

10. SCOPE AND FUTURE APPLICATIONS IN WATERLOGGING STRESS TOLERANCE

The ability to withstand waterlogging becomes increasingly important for sustainable agriculture as a result of climate change and an increase in rainfall occurrences. [54,21,55] Future studies would need to concentrate on

A. Genetic Variability and Breeding: [56-58]

i. Identifying genetic markers associated with waterlogging tolerance guides crop breeding efforts.
ii. Developing waterlogging-tolerant crop varieties through selective breeding.
iii. Enhancing root traits that improve waterlogging resilience.

B. Precision Phenotyping:

i. Advanced phenotyping techniques assess root responses to waterlogging stress.
ii. High-throughput methods screen large populations for desirable root traits.

C. Crop Breeding: [40,59]

i. Developing waterlogging-tolerant crop varieties.
ii. Developing crop lines with improved root traits will enhance resilience to water stress.

D. Climate Change Adaptation: As climate change leads to more frequent and intense rainfall events, understanding waterlogging tolerance becomes essential. Sustainable agriculture requires crops resilient to changing environmental conditions [24,60]

In summary, unraveling the intricate mechanisms of root adaptation to waterlogging stress will empower us to develop resilient crops and ensure food security in a changing climate.

11. DISCUSSION

Water logging is a severe abiotic stress that negatively impacts plant growth and productivity. It occurs when excessive water accumulates in the soil, displacing air and reducing oxygen availability to the roots. This oxygen deficiency disrupts vital plant processes like respiration, nutrient uptake, and energy production [9,61,2].

Under water-logged conditions, plants undergo various morphological, physiological, and biochemical adaptations to cope with the stress. One crucial morphological adaptation is the formation of aerenchyma, which are air-filled spaces that facilitate internal oxygen transport from the shoot to the root system. Plants with efficient aerenchyma development can maintain root respiration and nutrient acquisition under water-logged conditions [37,62].

Another important adaptation is the production of adventitious roots, which emerge from non-root tissues like stems or hypocotyls. These roots have a higher density of aerenchyma and can improve oxygen and nutrient uptake when the primary roots are compromised [36,26]. Additionally, some plants exhibit a shallower root growth angle, allowing roots to explore the upper, more oxygenated soil layers [8].

Physiologically, plants regulate various processes like stomatal conductance, hydraulic conductivity, and antioxidant defense systems to maintain cellular homeostasis under water logging [43,54]. They also undergo metabolic changes, such as increased ethylene synthesis, which controls the formation of aerenchyma and adventitious roots [55,42].

At the biochemical level, plants accumulate osmoprotectants like soluble carbohydrates and proline to maintain osmotic balance within cells [27]. They also produce anaerobic polypeptides (ANPs) and root anaerobic proteins (RAPs) to facilitate energy production through fermentation pathways in the absence of oxygen [63,56].

Plant hormones play a crucial role in coordinating these adaptive responses. Ethylene, abscisic acid, auxin, gibberellin, salicylic acid, and jasmonic acid are involved in regulating root growth, aerenchyma formation, and stress tolerance under water-logged conditions [53,50,64].

12. CONCLUSION

Water logging is a significant abiotic stress that poses a severe threat to crop productivity worldwide [9]. Plants have developed intricate mechanisms to adapt to water-logged conditions, involving morphological, physiological, and biochemical changes. The formation of aerenchyma, adventitious roots, and a shallow root system are key morphological adaptations that facilitate oxygen and nutrient uptake under hypoxic conditions [37,36,8]. Physiologically, plants regulate various processes like stomatal conductance, hydraulic conductivity, and antioxidant defense systems to maintain cellular homeostasis [64,25]. At the biochemical level, they produce osmoprotectants, ANPs, and RAPs to cope with the stress [27,34,64]. Plant hormones, particularly ethylene, abscisic acid, auxin, gibberellin, salicylic acid, and jasmonic acid, play crucial roles in coordinating these adaptive responses [54,51,65]. Understanding these mechanisms is essential for developing water logging-tolerant crop varieties and sustainable agricultural practices. Further research into the molecular mechanisms underlying plant responses to water logging will aid in developing novel strategies to mitigate the deleterious effects of this environmental stressor and ensure food security in the face of climate change [56].

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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