Chapter 11
Waterlogging and Crop Productivity

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Abstract Climate change is having a major impact on the natural world. Waterlogging occurs when free water covers the soil surface of crops. As an abiotic stress, flooding has a significant impact on around 16% of agricultural production regions globally. Both growth and yield of agricultural crops are gradually reduced due to harsh environmental conditions. Flooding disturbs the physiochemical properties of the soil that ultimately reduce the growth and physiological characteristics of the crops. Waterlogging induces oxygen loss barriers, which alter the uptake mechanism of nutrients. By developing root systems and secondary aerenchyma, the effects of waterlogging can be alleviated. Under hypoxic conditions, formation of the aerenchyma increases in most cereal crops. Some plants produce metabolic energy through the fermentation process in response to hypoxia rather than through oxidative respiration. This chapter will help understand the effects of waterlogging on crops and provide solutions to mitigate these effects to promote plant growth and productivity. To fulfill the food requirements of the growing world, it is mandatory to grow waterlogging-tolerant crops.

Keywords Waterlogging · Productivity · Anoxia · Hypoxia · Tolerant

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1 Introduction

One of the most significant stresses that plants encounters is waterlogging, which inhibits aerobic respiration growth, particularly vegetative growth and seed germination. Waterlogging stress causes plants to regulate their morphological structure, energy expenditure, endogenous hormone production, and signaling techniques (Ali et al. 2013). Waterlogging occurs when free water saturates the upper layer of the soil (Ashraf et al. 2011; Kaur et al. 2018). By combining water absorption by the roots and transpiration from the leaves, plants can grow normally. Adequate water is a necessity for typical plant growth; however, saturation of the soil's water-holding capacity or even oversaturation easily leads to waterlogging. Inhibition of root respiration and accumulation of toxins in case of waterlogging stress has a negative impact not only on vegetative growth but also on reproductive growth, ultimately leading to yield losses or even to complete crop failures (Zhou et al. 2007; Javaid et al. 2022a, b). Closure of the stomata during waterlogging as well as chlorophyll breakdown, leaf senescence, and yellowing make leaves less able to absorb light, which ultimately causes a decrease in the photosynthetic rate (Yan et al. 2018). Despite the reality that most plants struggle when they are flooded, they can adapt to the harm imposed by such environmental stresses using a variety of techniques (Doupis et al. 2017; Yin et al. 2019). The hypoxic condition in the rhizosphere reduces the oxygen intake by creating an anaerobic environment, which further results in plant mortality (Fukao et al. 2019). Plants' ability to tolerate waterlogging depends on their ability to tolerate anaerobiosis and chemical toxicity (Liu et al. 2020; Javaid et al. 2022b). Heavy rainfall and inadequate soil drainage are two of the main causes of waterlogging (Sundgren et al. 2018). Under waterlogging conditions, hypoxia, or a lack of oxygen, is a significant contributor to damage (Sanghera and Jamwal 2019; Javaid et al. 2020).

In plants, waterlogging has drastic effects, as shown in Fig. 11.1. Reactive oxygen species (ROS), including singlet oxygen and superoxide radicals, are produced in large quantities as a result of anaerobic respiration brought on by waterlogging (Zheng et al. 2017; Mehmood et al. 2018). Production of ROS initially aids in adaptive responses, including the development of the aerenchyma and adventitious roots, but excessive ROS under waterlogging stress causes severe oxidative damage (Shahzad et al. 2018; Tyagi et al. 2022). The gas exchange between plant roots and the atmosphere is severely hampered by waterlogging (Wollmer et al. 2018). The roots switch from aerobic respiration to anaerobic fermentation when the oxygen in soggy soil is quickly depleted, and CO_2 and ethylene concentrations rise. This has an adverse effect on several metabolic processes in plants, including the root cells' ability to synthesize adenosine triphosphate (ATP) (Pampana et al. 2016; Kaur et al. 2020). Therefore, waterlogging hinders mitochondrial respiration and diffusion of oxygen in plant tissues. This significantly slows down plants' regular physiological and biochemical processes (Phukan et al. 2016; Sarwar et al. 2018).

According to estimates, 12% of the world's arable land may experience regular flooding, which would reduce crop yields by about 20% (Kubik and Maurel 2016).

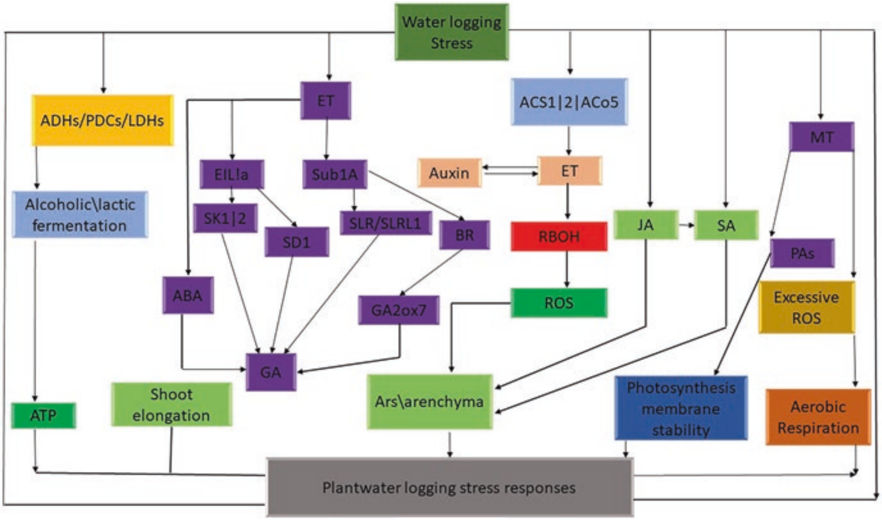

Fig. 11.1 Schematic diagram showing the genetic responses of waterlogging stress (Pan et al. 2021)

The Yangtze watershed, the plains of Huang-Huai-Hai, Sanjiang, and Songnen in China, and irrigated areas of the United States, India, Pakistan, Argentina, and Europe are among the places where soil waterlogging is predicted to become more frequent and severe in the near future as a result of global climate change (Ploschuk et al. 2018). Waterlogging is a major hazard worldwide, impacting 16% of American soils as well as agricultural regions in Russia, Pakistan, Bangladesh, China, and India (Manik et al. 2019).

One of the main abiotic stressors that significantly lowers agricultural output and has become a serious issue globally is waterlogging (Zhang et al. 2016; Jia et al. 2019). Around 17 million square kilometers of land are at risk of flooding, according to the National Aeronautics and Space Administration (NASA) (Leonardo 2019). Improved waterlogging tolerance is one of the main goals of barley breeding programmers in China and Japan, and, with the anticipated climate change, its significance will also grow in northern Europe (Karimi et al. 2018). Depending on the stage of growth, at present, waterlogging is said to diminish grain production by 20–25% or more (Ramirez-Cabral et al. 2016; Shrestha et al. 2021).

In all, 25% of the irrigated land in Pakistan has been impacted by salt and waterlogging. Moreover, 6.17 MH of land have been affected by temporary flooding or chronic waterlogging and 1.16 MH of the land have salt problems in addition to waterlogging problems (Dollinger and Jose 2018). In Pakistan, 230 MH of agricultural land are irrigated, and around 20% of the area, or 45 million hectares, is salty soil. According to estimates, waterlogging affects between 0.2 and 0.4% of all farmed lands each year as a result of poor management techniques (Harris et al. 2016).

Submergence is one of the abiotic stresses that affects 10–16% of soils and reduces the yields of the most important agricultural crops by about 80% (Liliane and Charles 2020). Being sessile, plants are vulnerable to a variety of abiotic stressors, including waterlogging, drought, salinity, heat, cold, and acidity, which can reduce production by 30–100%, depending on their severity (Choudhary et al. 2018). Due to the accelerating rate of global climate change, waterlogging will pose a significant threat to modern agriculture in the future, offering a challenge to researchers for the creation of submergence-tolerant crop cultivars with improving yield and quality (Hartman et al. 2019). In the past few decades, climate change has raised the likelihood of the occurrence of extreme weather events like droughts and flooding (Stott et al. 2016). According to estimates, flooding affects 10–12% of the world's agricultural regions, resulting in losses of more than $74 billion each year (Menéndez et al. 2020). Depending on the duration of the waterlogging, the type of soil, the varieties, and the stage of plant development, the yield reduction caused by waterlogging ranges from 20% to 25% (Tong et al. 2021), as shown in Fig. 11.2.

Waterlogging affects about 15% of the maize (*Zea mays* L.)-producing area, which reduces the yield by 20–30% (Du et al. 2017). It affects about 10–15 MH of the wheat (*Triticum aestivum* L.)-sown area, which results in yield losses of 20–50% (Manik et al. 2019). Flash floods and submergence affect more than 16% of the world's rice (*Oryza sativa* L.) cropland (Neog et al. 2016). Waterlogging affects between 10 and 15 million acres of wheat worldwide each year, resulting in yield

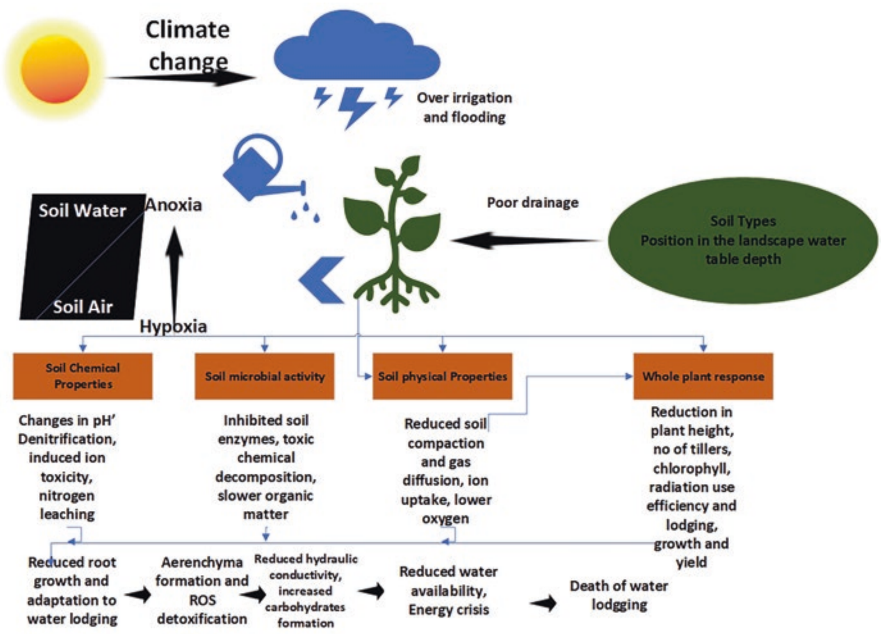

Fig. 11.2 Morphological, physiological, physical, and chemical mechanisms implicated in plant growth responses to waterlogging (Liu et al. 2020)

losses of 20–50% (Aryal et al. 2016). Other grain crops, including barley, canola, lupins, field peas, lentils, and chickpeas, also experience yield losses due to waterlogging.

2 Effects of Waterlogging

Root hypoxia is categorized as a stress that makes tomato (*Solanum lycopersicum* L.) and cucumber (*Cucumis sativus* L.) sensitive to waterlogging (Hou et al. 2019). However, genetic differences in their resistance to this stress have been found (Safavi-Rizi et al. 2020). Legumes are continually faced with a variety of stresses, the most important of which is waterlogging, which can result in yield losses of between 25 and 30% per year (Pasley et al. 2020).

Submergence in legumes can reduce photosynthesis, prevent biological nitrogen fixation by interfering with nodule development, result in nutritional deficiencies, increase the accumulation of toxic compounds, and, finally, induce plant mortality (Oves et al. 2016). Pigeon pea, cluster bean, lentil, soybean, pistachio, and chickpea are among the legume crops that are susceptible to submersion, mainly during the vegetative phases (Adak et al. 2016).

2.1 Effects of Waterlogging on Crop Productivity

One of the main abiotic stressors that impacts crop development is waterlogging (Lone et al. 2018). In many areas, waterlogging of the soil is a significant abiotic stress that significantly restricts crop development and lowers yield (Tian et al. 2021). It has turned into the primary obstacle to crop production in Australia's temperate high rainfall zone (HRZ), especially in areas with duplex soils (Ali et al. 2013; Franklin et al. 2020). The loss in the growth rates of some crops due to waterlogging makes crop production insufficient to fulfill the predicted food demand. Water is necessary for all plants to survive, but too much water, waterlogging, or floods causes stress and obstructs the passage of gases between the soil and the environment. Therefore, persistent waterlogging has a deleterious impact on nearly every stage of plant development throughout its life span and ultimately results in yield loss (Wang et al. 2017).

A valuable economic crop with an unpredictable growth habit and frequent waterlogging issues is cotton (*Gossypium hirsutum* L.). Cotton plant growth and development are negatively impacted by waterlogging stress, as is nutrient uptake. Reduced soil temperature, a less irrigated plowing layer, and decreased nutrient availability all contribute to a decline in the average production in cold, moist rice fields (Liu et al. 2016). Electrical conductivity, oxidation–reduction potential, and pH have all been found to vary in waterlogged soils (Tokarz and Urban 2015; Raja et al. 2022).

2.2 Waterlogging-Induced Anaerobic Respiration

Low oxygen levels (below 21% O_2) cause a transition from an oxygenated to a low-energy anaerobic state that supports plant development under waterlogging stress. It entails a number of biochemical adjustments, anaerobic digestion pathways, and the production of protective chemicals for the elimination of phytotoxic metabolites (Evans and Gladish 2017), which are crucial for plant survival under soggy conditions. Anaerobic respiration comes in two types: ethanolic fermentation and lactate fermentation (Du et al. 2017).

Pyruvate decarboxylase (PDC) initially converts pyruvate to acetaldehyde in the ethanolic fermentation process, and alcohol dehydrogenase (ADH) next turns acetaldehyde into ethanol by generating oxidized nicotinamide adenine dinucleotide (NAD^+). Lactate dehydrogenase (LDH) converts pyruvate to lactate during lactate fermentation by utilizing decreased nicotinamide adenine dinucleotide (NADH) (Zhang et al. 2017). Phytotoxins build up during fermentation, and carbohydrate stores are depleted (Loreti et al. 2016; Pucciariello and Perata 2017). In this situation, plants use glycolysis to generate energy and release sugar reserves that have been accumulated (Loreti et al. 2016). Fermentation's main feedstocks are water-soluble polysaccharides (WSPs). When the balance between carbohydrate metabolism and photosynthesis is off during waterlogging, the reserves of water-soluble carbohydrates (WSCs) can be reduced (Jurczyk et al. 2016), and these changes have an impact on the rate of fermentation and the survival of few species (Chen et al. 2013; Liu et al. 2017). Therefore, due to energy depletion, accumulation of phytotoxic chemicals (such lactate), and carbon loss (through ethanol loss from the roots), waterlogging and anaerobic metabolism cause severe growth inhibition and ultimately lead to the death of many plants (Tamang et al. 2014).

2.3 Effects of Waterlogging on Nutrient Composition

The fundamental cause of limited plant growth in damp soil is nutrient inadequacy, which ultimately results in wilting (Onyekachi et al. 2019). Waterlogging prevents the soil from absorbing the majority of necessary nutrients, which results in deficits of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca) (Kathpalia and Bhatla, 2018). According to the early development stage as opposed to a later growth stage, the impacts of waterlogging on N, P, and K nutrition are more pronounced. After 65 days of waterlogging, the N concentration in cotton leaves reduced by 30% (Zhang et al. 2021). According to cotton roots, the stems and leaves had lower concentrations of N, K, and Ca^{2+} under waterlogging stress but higher amounts of Mn^{2+}, Fe^{2+}, and Mg^{2+}. The decrease in oxygen availability in the root zone, which affects root respiration and, in turn, the capacity of the roots to absorb nutrients may be the cause of this nutritional imbalance. Additionally, roots' ability to store energy is diminished in waterlogging circumstances, which prevents these nutrients from being actively transported to other organs (Tavanti et al. 2020).

Reduced root respiration under hypoxia may also result in root cell death, a reduction in cell permeability, and prolonged hypoxia, even the total loss of roots. Thus, it is clear that waterlogging prevents most key nutrients from being absorbed, creating a nutritional imbalance, even if other vital elements have been found to accumulate more often. As a result, nutritional imbalance contributes to yield loss under waterlogging conditions. In the presence of hypoxia, a reduction in root respiration may also result in root cell death, a reduction in cell permeability, and, in the case of chronic hypoxia, even in total loss of the roots (Xiao et al. 2020).

2.4 Crop Germination

When waterlogging occurs during seed germination or at the blossoming stage, the seedling dies and no more growth occurs. Sorghum seedling growth is impacted by waterlogging in a short range but increased death rate of seedling (Kyu et al. 2021).

2.5 Crop Morphology

Waterlogging is one of the biggest issues in agricultural productivity, which affects approximately 12% of the world's agricultural land. Crop productivity is decreased by waterlogging. Maize productivity is decreased as waterlogging periods increase (Huang et al. 2022). When organic substances are broken down, oxygen is required to create energy for productivity. The aerobic bacteria and roots in soil nearly lose most of their capacity to make energy when the oxygen level is low; as a result, they cease growth and may even die (Antar et al. 2021). Most crops and plants on land are aerobic organisms that depend upon the fast availability of oxygen either from underground or from aerial tissues. Waterlogging, which occurs when too much water is absorbed by the soil, severely affects crop development and yield, and, in many parts of the world, it has become a serious abiotic stress (Wei et al. 2013). Flooding or waterlogging inhibits root and shoot growth, reducing the overall yield (Tiryakioglu et al. 2015). Reduction in chemical reactions, energy currency, and other mechanism in crops are shown in Fig. 11.3.

2.6 Crop Productivity

Reduction in crop yield is due to the absence or loss of oxygen and/or denitrification or leaching of nitrogen and diseases can cause damage to the crops (Kaur et al. 2020). According to the stage of the affected crop and the intensity of the floods, the average yield loss due to waterlogging is estimated to be 15–25%, but it can reach up to 40% (Gomathi et al. 2015). Waterlogging, even when temporary and

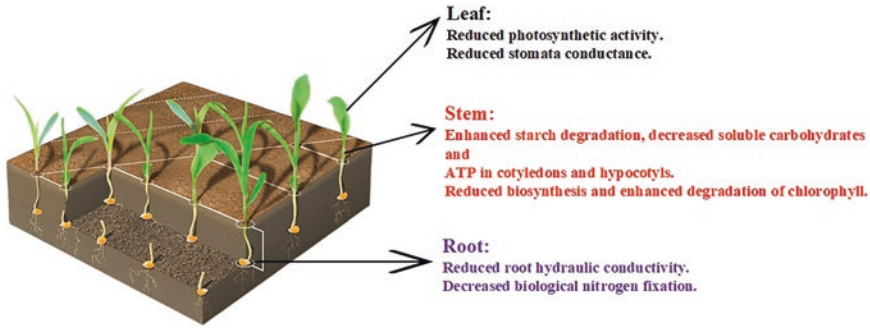

Fig. 11.3 Waterlogging effects on different parts of a plant (Manik et al. 2019)

short-lived, can have a significant impact on the development and production of dry land crops. There is reduction in the dry masses of both the shoots and roots (Robin et al. 2021). There is reduction in root growth due to waterlogging in wheat (Ploschuk et al. 2018). Wheat's grain production of the winter season can be reduced by almost 20 days at 32–94% by waterlogging, 52% in green gram, and 54% in chickpea (Basu et al. 2019). More number of enzymes such as ascorbate peroxidase (APX), superoxide dismutase (SOD), and catalase (CAT) have been proven to be harmful to tobacco rice, wheat, mung bean, sunflower, and sweet potato under waterlogging conditions (Hasanuzzaman et al. 2020). Earlier in the season, long-term waterlogging can result in reduction of crop productivity by up to 30% (Liu et al. 2021).

2.7 Crop Physiology

Waterlogging can have an impact on a number of physiological processes, including water and root–shoot hormone absorption interactions (Tong et al. 2021). They also reduce movement of ion across the roots, which results in shortage of nutrients and element toxicity such as in manganese (Mn), iron (Fe), sodium (Na), aluminum (Al), boron (B), and superoxide dismutase (SOD) (Kathpalia et al. 2018). In wheat, waterlogging decreases the rate of photosynthesis, total productivity, leaf extension, and the number of grains per spike (Du et al. 2023). Under temporary or permanent flooding conditions, quick waterlogging typically first causes deficiency of oxygen (anoxia or hypoxia) in plants and then results in chlorosis, leaf shrinking, and damage of the roots (De Oliveira 2021). Waterlogging causes a shortage in the supply of oxygen, and it has been proved to be dangerous for shoot and root systems (Zhang et al. 2021).

Oxygen-dependent activities are reduced in hypoxia, particularly in anoxia. The physiological interactions between the shoots and roots are changed, and both the uptake of carbon and the use of photosynthates are inhibited, particularly the oxygen internal transport (Nakamura & Noguchi 2020). Root hypoxia creates a photooxidative damage in leaves when production of ROS increases, like hydrogen peroxide (H_2O_2), hydroxyl radicles (OH•), and superoxide, which easily damage the leaf chloroplasts, and, also, yellowing of leaves and senescence occurs. Several well-known enzymes, including APX and SOD, reduce ROS (Kanojia & Dijkwel 2018).

The type and also the physiological age of the organism determine how waterlogging affects the respiratory rate. A higher rate of oxygen uptake in root tips is associated with respiration, which is necessary for other metabolic processes, such as the production of ATP. Under waterlogging conditions, plant roots suffer from hypoxia (a lack of oxygen), which suppresses the rate of metabolism and also lowers ATP synthesis. So, less ATP is produced and less energy is available for root growth, which inhibits vegetative growth. A reduced stomatal aperture decrease under lack of oxygen (hypoxia) also decreases the rate of photosynthesis. Senescence of the leaves, a decrease in chlorophyll concentration, and, ultimately, full inhibition of the photosynthetic process take place (Ding et al. 2022).

Photosynthesis inhibition occurs a few days before the reduction of chlorophyll contents. With more waterlogging, nitrogen contents in the leaves, shoots, and seminal roots reduce. However, adventitious roots' nitrogen content rises. Nitrogen is present in an excess amount in adventitious roots, followed by seminal roots because of the nutrient uptake ability of the aerenchyma (Mohammed et al. 2019). If the period of waterlogging increases, it causes more reduction in the photosynthetic activity of sorghum, cotton, and maize (Zhang et al. 2021). The sorghum species, especially germination-stage seeds, are extremely sensitive to water stress because they do not have enough oxygen (Zhang et al. 2020).

Due to a low amount of oxygen, electron transport chain and respiration are reduced, so, as a result, ATP production rate is decreased in sorghum. When the rate of ATP generation slows due to the lack of oxygen, permeability of the cell membrane in sorghum increased. Variations that occur in cotton by waterlogging are reduction of the rate of photosynthetic activity, leaf potential, and reduction in stomatal conductance (Pan et al. 2019). When changes in internal hormones take place, it helps in the internal connection between the shoots and roots and also affects the morphological adaptations of the stressed plants. When aerobic respiration in the root system of sugarcane is low, it negatively impacts nutrient uptake under waterlogging stress, as shown in Fig. 11.4. Moreover, it has been noted that under conditions of waterlogging, in plants, major changes in the morphology, physiology, and anatomy take place (Bhusal et al. 2020).

2.8 The Impact of Waterlogging on Different Compounds

The velocity of gas exchange between the atmosphere and the soil slows down due to the presence of too much water in the soil, which also impacts plant production and growth (Andrade et al. 2018; Garcia et al. 2020). While the amount of oxygen

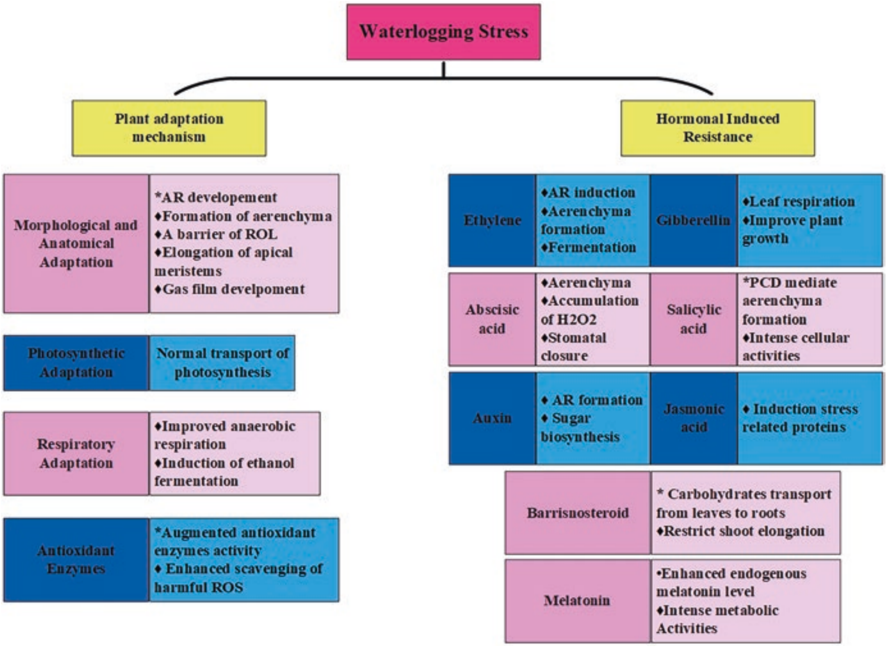

Fig. 11.4 Plants response toward waterlogging (Pan et al. 2021)

continuously drops due to waterlogging, methane, hydrogen sulfide, carbon dioxide, and ethylene increase at a rapid rate (Tyagi et al. 2022). This severely disturbs the stability of gas levels, makes a hypoxia or even anoxia conditions. It also lowers the capacity of soil for decline and also interferes with the exchange of minerals (Li et al. 2022). The absence of oxygen also reduces the aerobic nitrification and activity of the nitrifying bacteria, and, thus, conversion of nitrate into nitrogen is reduced, which results in nutrient loss (Walker et al. 2018). Additionally, under conditions of waterlogging, sulfate is quickly converted to hydrogen sulfide, thus decreasing the quantity of sulfur that plants can absorb and making them poisonous. Waterlogging also decreases oxidized substances like Fe^{2+} and Mn^{4+}, increasing the concentration of iron and manganese above what plants need for their nourishment (Kathpalia and Bhatla 2018).

2.9 Effects of Waterlogging on the Anatomy of Crops

Under waterlogging conditions, root diameter, aerenchyma number, aerenchyma width, cortex thickness, and stele width all decrease in rice plants. During flooding, the rhizosphere's limited oxygen supply has adverse effects on the plant roots. Due to the absence of oxygen, the soil increases the formation of the aerenchyma. The root aerenchyma of forage grass (*Brachiaria* spp.) is inhibited due to flooding conditions. The cortex thickness as well as the stele and diameter of the roots decrease due to flooding conditions as in rice crops (Fe et al. 2020).

3 Strategies for Improving Waterlogging Tolerance in Plants

The ability of plants to tolerate waterlogging depends on their type, water level depth, development stage at the time of waterlogging, and variety (Kaur et al. 2020). Plants can avoid the stress of waterlogging by increasing the synthesis of ethylene that leads to the formation of the aerenchyma, and, also, the surfaces of roots and adventitious roots become stronger due to this adaptative ability of plants (Wu et al. 2022).

4 Response of Plants to Hypoxic Conditions

Fundamentally, the response of plants to hypoxic conditions can be separated into three phases.

- Plant efficiently produces a group of components involved in signal transduction, and the second stage is activating.
- A metabolic adjustment occurs, which then gets involved in the fermentation process.
- The third stage depends on the strength of the plants and is involved in changing their morphology such as aerenchyma formation and root formation (Wei et al. 2013).

At their morphological and physiological stages, plants adopt different mechanisms or methods to prevent waterlogging or oxygen shortage. Some plants produce metabolic energy through the fermentation process in response to hypoxia rather than through oxidative respiration. The LDH, ADH and PDC are the parts of anaerobic proteins (ANPs) and they play a key role when respiration shifts from the aerobic to the anaerobic state. In order to maintain glycolytic metabolism under hypoxia, PDC catalyzes the irreversible changes of acetaldehyde from pyruvate and ADH transforms acetaldehyde to ethanol and stimulates NAD^+ (Borrego-Benjumea et al. 2020). From the transfer of pyruvate to lactate, LDH also creates NAD^+ (Farhana & Lappin 2023). Since the concentration of lactic acid is more harmful than alcohol, the change from alcohol to lactic acid production gives plants the capacity to survive under low oxygen conditions without having any cell injury, and this is regarded as a significant factor. Enzymes such as CAT and ascorbate peroxidase (APX) are envolved in controlling the levels of internal hydrogen peroxide (Anand et al. 2019).

5 Adaptations of Plants to Waterlogging

5.1 Morphological and Anatomical Adaptations

The majority of plants are resistant to waterlogging because it significantly reduces the rates at which oxygen and carbon dioxide diffuse through their roots and stems, inhibiting both respiration and photosynthesis. Under waterlogging conditions, certain plants undergo morphological changes; these plants alleviate the decline in the respiratory mechanism and injury caused by disturbing the energy metabolism. So, formation of the aerenchyma and adventitious roots is an important morphological adaptation, as shown in Fig. 11.4 (Pan et al. 2021).

5.2 Aerenchyma and Adventitious Root Formation

Waterlogging-induced adventitious root formation is a key process. This phenomenon is common in various plant species, including *Zea nicaraguensis*, tomato, cucumber, soybean, and wheat (Xu et al. 2017). Under hypoxic stress, new adventitious roots help in nutrient and water intake (Matsuura et al. 2022). The development of aerial roots to improve the period of waterlogging is specific for each species and depends upon water temperature, the growth period of the plants, and the duration of waterlogging (Liu et al. 2020). Waterlogging stress-sensitive species did not produce adventitious roots, whereas waterlogging-tolerant genotypes formed a greater number of adventitious roots in cucumber (Xu et al. 2017). Adventitious roots stimulated by waterlogging have a significant quantitative trait locus in them (Sanghera et al. 2019). Another characteristic of plants is to respond to water stress by the development of the aerenchyma. The aerenchyma has intercellular space, which helps plant tissues exchange gases and absorb oxygen (Luan et al. 2018). Under hypoxic conditions, the formation of aerenchyma increases in most cereal crops, including wheat, soybean, maize, and barley genotypes, which are waterlogged tolerant. This dramatically increases transparency in roots and also promotes the aerenchyma development in adventitious roots under waterlogging conditions. The aerenchyma develops in wetland plants like rice, not just in the roots but also in the leaves, stalks, and leaf sheaths (Luan et al. 2018).

5.3 Photosynthetic Adaptations

Stomatal conductivity of leaves, stomatal resistance, , closure of the stomata, and carbon dioxide uptake are all decreased when waterlogging occurs (Wu et al. 2022). Therefore, in order to continue growing and developing plants, light and CO_2 for photosynthesis are required. Under waterlogging conditions, enzymatic activities relating to photosynthesis decrease, as does chlorophyll synthesis in leaves, resulting in the senescence, shedding, and chlorosis of leaves; inhibition of new leaf development; decrease in the photosynthetic rate; and, eventually, plant death (Wu & Yang 2016). In the majority of plants, the main products of photosynthesis are sucrose and starch. The primary transport carbohydrate from the source to sink organs is sucrose, and this pathway is highly susceptible to waterlogging. The boll weight of cotton exposed to water was immediately decreased by decreasing the rate of photosynthesis, rate of transport of sucrose, and the primary activity of rubisco (Sun et al. 2022).

5.4 Adaptive Features in Tree Species

Tree species that live in habitats that face floods on a regular basis have developed a wide variety of adaptation techniques to deal with the stress caused by this waterlogging (Campbell et al. 2021). In reaction to floods, several flood-tolerant species have grown enlarged lenticels at the base of the stems (Messina & Conner 2019). In addition to allowing the plant to absorb oxygen, enlarged lenticels regulate the stem's release of gaseous chemicals into the atmosphere, such as carbon dioxide, acetaldehyde, and ethanol. Formation of adventitious roots is also an adaptive feature against waterlogging stress (Mui et al. 2021).

5.5 Adaptive Features in Soybeans and Figs

Soybean plants are capable of adapting to waterlogged soils by developing root systems and secondary aerenchyma (Goulart et al. 2020). Waterlogging stops roots from receiving oxygen, which limits respiration and significantly lowers a cell's energy status. So, to maintain ATP production, plants have adopted features under waterlogging stress conditions for the metabolic conversion of oxidative phosphorylation into anaerobic fermentation within their roots (Kaur et al. 2021). The fermentation pathways play an important role in adopting waterlogging tolerance strategies because they show a positive response when the amount of oxygen is low, but they are not used when aerobic conditions are present. So, if the fermenting pathways of plants are more effective, then they are more tolerant to waterlogging stress. Under wet stress conditions, lactic acid and ethanol are the two important fermentation pathways; two main enzymes are also involved, namely, LDH and ADH (Jitsuyama 2017).

5.6 Adaptive Features in Rice

In rice, the ratios of the cortex to the stem and the aerenchyma to the cortex relate to gaseous spaces and are necessary for the root's high capacity for oxygen transport. Transport of oxygen from the base of the shoots to the tips of the roots occurs (Yamauchi et al. 2019). Rice could develop a lysigenous aerenchyma process and barriers to the generation of radial O_2 loss (ROL) as an adaptive mechanism to waterlogging (Yamauchi et al. 2019).

5.7 Hormonal Adaptations

Waterlogging impacts the growth of the shoots by affecting root development. It disrupts the grain filling and consequently cause a decline in grain production (Wollmer et al., 2018). Due to waterlogging, abscisic acid hormones increases, while gibberellic acid and cytokinins decrease, resulting in a disturbance in the internal hormonal balance in plants. So, to avoid this situation, the hormones are applied exogenously. By stimulating a number of defense mechanisms, it has been discovered that phytohormones like cytokinin and gibberellic acid lessen the negative effects of waterlogging on crops. When cytokinin is exogenously applied, it raises its endogenous levels in plants, delays the aging of leaves, and improves photosynthetic efficiency, all of which would improve crop production. So, to overcome the negative effects in mung bean by waterlogging, cytokinin and gibberellic acid can be applied in the form of foliar treatment (Islam et al. 2021). Ethylene is a primary regulating hormone that helps combat the stress caused by waterlogging. In submerged shoot and root tissues, ethylene is produced from precursors 1-carboxylic acid (ACC) and 1-aminocyclopropane (Bashar 2018; Zeng et al. 2020).

6 Conclusions

Waterlogging is a serious problem to agriculture and reduces crop production and yield all over the world and also in Pakistan. It exerts deleterious effects on different crops. Cereal crops like barley, rice, wheat, maize, and oat are the major crops affected by waterlogging. It has major effects on the productivity of crops. It also affects the morphology, physiology, and anatomy of most crops. It induces anaerobic respiration and nutrient composition in plants. Different growth stages, especially the seedling stage, are disturbed by waterlogging. It also disturbs the photosynthetic activity in plants and different compounds in soil. Under severe conditions, these crops can survive by adopting tolerance strategies such as aerenchyma, and adventitious root formation occurs in plants as a morphological adaptation. Some species can tolerate this water stress, but most of them are sensitive to it. Plants that can survive under water stress conditions do so because they have an adaptation mechanism.

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