

Influence of Waterlogging on Anatomical, Morphological and Physiological Responses of Plants

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Abstract: In the conditions of changing climate, plants are continuously subject to several abiotic stresses. Among these stresses, waterlogging is one of the environmental constraints to plant production and productivity. Plants subjected to waterlogging suffer from substantial yield losses. The plants growing on the waterlogged soil face a stressful environment in terms of hypoxia or anoxia. These oxygen-deficient conditions substantially hamper plant growth, development and survival. Under waterlogged conditions, plants exhibit several responses including hampered stomata conductance, net CO₂-assimilation rate and root hydraulic conductivity. Furthermore, plants grown under waterlogged conditions often face the oxidative damage induced by the generation of reactive oxygen species. These reactive oxygen species in turn affect the integrity of membranes and induce damage to the efficiency of photosystem II, thereby, causing a considerable decrease in net photosynthetic rates. Moreover, these perturbations in physiological mechanisms may affect the carbohydrate reserves and translocations. Waterlogging is also known to induce adverse effects on several physiological processes of plants by creating a deficiency of essential nutrients. Apart from these waterlogging induced alterations in physiological mechanisms, plants growing under waterlogged conditions also exhibit certain anatomical and morphological changes entailing the formation of adventitious roots, initiation of hypertrophied lenticels and/or establishment of aerenchyma. Therefore, this review describes some aspects of waterlogging induced alterations in anatomical, morphological and physiological responses in higher plants.

Key words: Anatomy • Morphology • Physiology • Plant Response • Waterlogging

INTRODUCTION

Under both natural and agricultural conditions plants are often exposed to various environmental stresses. Drought and waterlogging are generally common adverse environmental factors that affect the growth of plants and are considered as the main factors determining the global geographic distribution of vegetation and restriction of crop yields in agriculture [1-3]. Waterlogging or floods can negatively influence agricultural yields by delaying planting, reducing vigor, altering development and increasing susceptibility to diseases. Flooding can lead to waterlogging stress by substituting the soil gas phase with a liquid phase and thus cause a decrease of oxygen in the airspaces (O₂ poor availability or hypoxia with total absence or anoxia), in natural and man-made ecosystems worldwide [4]. The symptoms of waterlogging stresses include photosynthesis decline, protein degradation,

slower leaf expansion, decreases in respiration and biomass production and stomatal closure, among others [5-8].

Under waterlogging or flooding conditions, plant responses also include anatomical, morphological and metabolic alterations [9, 10]. During waterlogging the low oxygen concentration in the rooting medium produces an inadequate oxygen supply to the plant roots [11]. Thus, responses of plants to combined stresses are neither independent nor specific and so they can result in increases and/or overlapping of stress effects. Consequently, to know plant responses to combined stresses can be useful in understanding the mechanisms allowing them to survive in adverse conditions. Under these conditions, oxidative stress, alterations in nutrient levels and anatomical and morphological changes occur in plants [12]. Therefore, the effects of waterlogging induce a reduction in dry mass production

[13], an increase in total root length and a decrease in leaf area [14], alterations in dry matter partitioning in the different organs [15], leaf necrosis [16] and reduction in the rate of photosynthesis, stomatal conductance and chlorophyll content have also been observed [7]. Generally, plant responses to abiotic stresses comprise morphological, physiological and biochemical changes that either decrease plant stress exposure and/or limit damage and facilitate recovery of impaired systems [17]. However, understanding abiotic stress responses in plants is difficult due to the complexity, interrelationship and variability of mechanisms and molecules involved a fact that consists of their evaluation of an important and challenging topic in plant research. Therefore, this review paper was summarized to investigate anatomical, morphological and physiological responses of higher plants to waterlogging stresses.

Anatomical Response of Plants to Waterlogging Stress:

Waterlogging stress is also known to cause some anatomical changes in plants. The presence of hypertrophied lenticels is a common anatomical change observed in many woody species during waterlogging stress conditions (Figure 1 [7, 18]. Hypertrophic growth appears as swelling of tissues at the stem base and is believed to result from radial cell division and expansion. It has long been associated with auxin and ethylene production [7]. The development of hypertrophied lenticels is believed to facilitate the downward diffusion of oxygen as well as the potential venting of compounds produced in the roots as by-products of anaerobic metabolism (ethanol, carbon dioxide and methane). Although the actual physiological role of lenticels is still not established, it seems that lenticels may play a crucial role during adaptation to waterlogging conditions in some species by helping maintain shoot water homeostasis [19, 20]. Also, the number of hypertrophied lenticels is more under the water surface that supports the argument stating their involvement in the maintenance of plant water homeostasis and deviating from the argument that dictates their role as important facilitators of oxygen entry toward the root system. It is thus more probable that lenticels may help maintain plant water homeostasis during waterlogging, by partially replacing the decaying root system and providing a means of water intake for the shoot [21]. In support for such a role, lenticels are permeable to water [22], the tendency for stomatal conductance to return towards control levels after a transient decrease has generally been associated with their development [23-25] and their presence is associated

with maintenance of plant water status during waterlogging stress [21].

Waterlogging stimulates alterations in the roots and shoots of plants. In roots, the emergence of adventitious roots is noticed as a general response of tolerant species which help plants to resume with water and nutrient uptake during waterlogged conditions [26]. Ethylene and auxin interaction is vital for the stimulation of adventitious root development [27]. In sorghum root, cortex and stalk are formed [28] and also the formation of adventitious roots occurs due to waterlogging stress [29, 30]. Some genotypes of wheat possess nodal and adventitious roots that initiate aerenchyma formation. Aerenchyma is gas-filled channels that carry out the transportation of oxygen from leaves to roots under the limited supply of oxygen during the waterlogging condition to carry out root respiration. Aerenchyma formation in the root cortex is the most studied plastic response to waterlogging [31-33]. This aerenchyma tissue provides a continuous system of interconnected aerial spaces (aerenchyma lacunae) of lower resistance for oxygen transport from aerial shoots to submerged roots, allowing root growth and soil exploration under anaerobic conditions [34]. The formation of aerenchyma occurs when the temperature is high or elevated to certain degrees [35]. Waterlogging also causes shrinkage of meta-xylem and proto-xylem vessels of the nodal roots of wheat [36]. All this is accepted to crop up due to adaptive retort to waterlogging stress and is found to be much slammed to the growth of plant shoot and capitulate [30]. The same response i.e. response of shoot, root and capitulate to waterlogging stress are shown by grain sorghum [37, 38]. The aerenchyma in sorghum is recognized by the lysigenous aerenchyma (the gas spaces which occur due to the bursting of the cell wall).

The spatial arrangement of aerenchyma in the root cortex in response to water is variable among species [32, 33, 40]. Aerenchyma formation is a natural characteristic in rice. It serves as a model plant to study the formation of uneven lysigenous aerenchyma amongst the monocot. These are formed as a product of the break down of cortical cells. The existence of aerenchyma in the roots of rice has been accounted for to be a consequence of genetic control. So, the aerenchyma is always found in the roots of rice, apart from environmental situations [41]. Apart from being a constitutive feature, aerenchyma formation has been found to enhance in hypoxic conditions [42]. Conversely, some studies point out that no considerable increase in the percentage of aerenchyma with little oxygen root

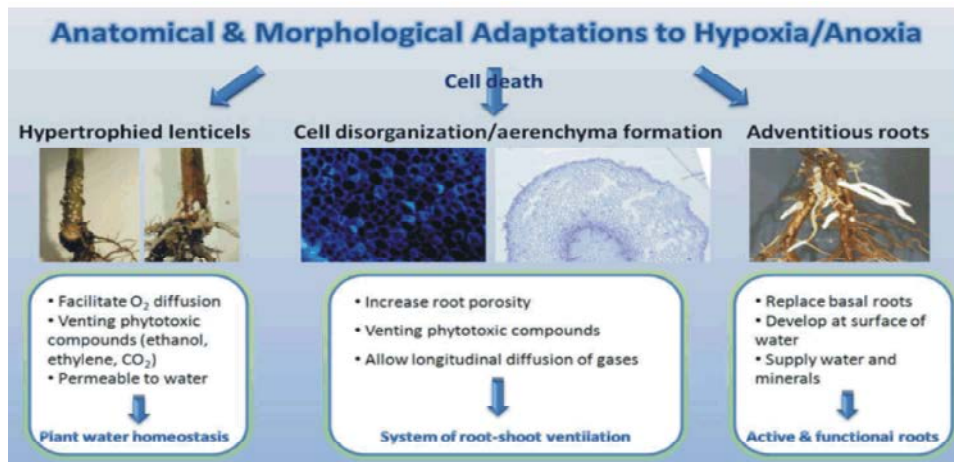


Fig. 1: Anatomical and morphological adaptations taking place during plant waterlogging [39]

region aeration treatment occurs [41]. Consequently, an enhancement in the ratio of aerenchyma is reliant on the rice cultivar and the growth period of the plant [43]. Despite this, the development of air spaces or pore spaces is not limited to the roots only in rice. The cortical aerenchyma extends up roots and in the shoots that are in leaves and tillers and maintain well-organized bidirectional transportation of gases between the roots and the aerial parts, both from the atmosphere and from the oxygen produced by photosynthesis as soon as the shoots are waterlogged, with a few levels of resistance among the root-soil, root-shoot and shoot-atmosphere gas transport [43]. The matter of tillers at the root-shoot transition zone is a chief blockage for smooth inner airing [44]. Different aerenchyma types arise from the combination of four general root structural types [45]. Such four general root structural types - graminaceous, cyperaceous, Apium and Rumex have been described based on the spatial arrangement of the aerenchyma tissue and the packing of the cells in the cortex [45]. The shape of these root types resembles a bicycle wheel (graminaceous), a spider web (cyperaceous), a honeycomb (Rumex) and a non-organized structure with irregular aerenchyma lacunae (Apium) [45].

Cell death and lysis leading to aerenchyma lacunae development are attributed to low pressures of oxygen (hypoxia) and ethylene accumulation [31, 46, 47]. However, aerenchyma development is identical independently of being promoted by hypoxia or by ethylene [48]. This suggests that the cell death program generating aerenchyma is common but it can be triggered by a variety of stimuli [31], also including soil mechanical impedance [49] and phosphorus deficiency [50, 51]. Application of low oxygen or high ethylene

concentrations provoked an increase of the cellulase activity in the root apex, which is likely to contribute to cell wall breaking down [52]. In herbaceous plants, oxygen transport through aerenchyma along relatively short distances (i.e. from shoots to roots) is mostly attributed to diffusive mechanisms. Diffusion of oxygen under waterlogging conditions is established by the generation of a longitudinal gradient towards the root apex. This gradient is produced by oxygen consumption due to respiration along the root and by the radial oxygen loss towards the rhizosphere. Both processes act as a sink of oxygen in the waterlogged soil, determining a low oxygen concentration in the root apex and consequently the generation of the mentioned gradient. It should be noticed that a higher aerenchyma generation by lysogeny (cell death in root cortex) determines a lower respiratory demand, favoring the supply of more oxygen to the root apex, at the same time that it facilitates the oxygen transport due to the lower resistance for oxygen diffusion, associated to the bigger size of the aerenchyma lacunae.

Morphological Response of Plants to Waterlogging Stress: Waterlogging induces morphological changes in roots and shoots. In roots, the formation of adventitious roots is highlighted as a common response of waterlogging-tolerant species (Figure 1). The formation of adventitious roots potentially replacing the basal roots is considered as one of the potential morphological adaptations depicted by plants under waterlogging stress [53, 54]. These adventitious roots, which have high porosity, help plants to continue with water and nutrient uptake under waterlogging conditions, replacing in some way the functions of the older root system [26]. Adventitious roots are commonly formed near the base of

the stem or in the region where lenticels are abundant and their growth is lateral, parallel to the water/soil surface. Their presence at the interface between the water-saturated soil and atmosphere reflects their importance in replacing the normal root system both underwater and following the retreat of the water table. Furthermore, the ability to produce adventitious roots is commonly associated with enhanced tolerance to waterlogging and their development has commonly been associated with ethylene production [55-57].

The formation of these specialized roots takes place when the original root system becomes incapable of supplying the shoot with the required water and minerals [55]. The deterioration of the main root system is taken as the sacrifice of providing energy for the development of a well-adapted root system [58]. Besides, the formation of adventitious roots is associated with the waterlogging tolerance of plants [56]. The formation of adventitious roots could be responsible for the maintenance of root dry matter under vegetative waterlogging, which is one of the adaptation mechanisms. Waterlogging greatly accelerated the development of new adventitious roots in mungbean [59, 60]. Reduction of water loss through decreased leaf area and enhanced adventitious root growth could be adaptive mechanisms against waterlogging [61]. The ultimate lengths of adventitious roots are restricted [42]. Eventually, mutually root and shoot dry weight is decreased [62]. As the hypoxic or anoxic situation continues, impaired membrane integrity, starvation and diffusion of phytotoxic compounds into the root cells combine to hinder root growth and function [63].

The most unpleasant consequence of the waterlogging is hypoxia or anoxia in the soil medium which causes reduced growth, inhibits the metabolic processes and finally reduces the yield [64]. When waterlogging is functional for the duration of seed sowing or on sprouts stage, it causes the fatality of seedling and no further growth take place. Because seeds or seedling root is not adapted to waterlogging at once and it is most vulnerable to certain diseases caused by waterlogging [65]. Mostly the forbearance of wheat plant enhances as it grows older and the adverse effect is that production reduces [66]. Lower nitrogen concentration in the main stem of the wheat plant results in a minimized yield of the tiller and adversely affect relative growth rate [54]. Under the waterlogged condition, the transpiration rate is also affected unless wheat roots regain their normal activity. However, prolonged waterlogging will result in the death of the root. Waterlogging also restricts the

wheat plant's uptake of nutrients by reducing transpiration and restricting root function [67]. The growth of seedlings of sorghum is also affected by short-range waterlogging is pointed by the high death rate of seedlings, decline in net assimilation rate, leaf assimilation rate and relative growth rate. The only crop rice can germinate under conditions of limited or lacking oxygen so, it acts as a representative plant for proper adaptation to anoxia [68]. These adaptations take in coleoptile lengthening, when these are exposed to hypoxic state they develop thick adventitious roots, the number of adventitious roots also increased, in well-oxygenated waterlogged conditions growth of surface roots increased, enhanced leaf area and reduced relative root length and shoot length. Though the rice plants are grown in hypoxic conditions by constant exclusion with nitrogen, it was observed in them that there were no alterations in hypoxic circumstances but there was a decrease in root dry weight in accordance to shortening and enhanced branching of roots [69].

It is predictable that stress from soil waterlogging on roots also alters shoot morphology because of the close functional interdependence between both of them. In this way, waterlogged plants of tolerant species are often taller than their non-waterlogged counterparts as a result of increases in the insertion angles and length of their aerial organs. These responses were well characterized in the dicotyledonous species [70, 71]. The faster response is the increase in the petiole angle, called hyponastic growth, where the maximum angle (70-80°, an almost vertical position) is reached just in four hours [70]. Next to the change in the insertion petiole angle, an increase in petiole length follows [70, 71] to maximize the leaf area above the water level [72]. Such lengthening of petioles is associated with the cell wall loosening due to an increase in the expression and action of expansions [73]. It was proved that both the increase in petiole angle and lengthening, are well mimicked by treating plants with ethylene, so that this hormone appears to be involved in regulating those responses [71, 73]. In graminaceous species, the morphological responses are analogous to those developed by dicotyledonous species. For instance, in the grass *Paspalum dilatatum*, the first morphological response to waterlogging is the increase in the tiller insertion angle [74] followed by the elongation of the leaf sheaths and lastly elongation of leaf blades [74, 75]. The higher leaf sheath length of waterlogged plants is the result of a higher number of longer parenchymatic cells concerning control plants [74].

Plants exposed to waterlogged conditions are affected by gas exchange limitations, nutrient deficiencies and toxicities. The shoot system of plants exhibit wilting, premature yellowing of leaves, epinasty, stem deformation, shoot length and leaf area reduction, among other problems [12]. Waterlogging highly reduces plants' height in sorghum and this effect may be unpleasant with an increase in extent [76]. Waterlogging prevents the growth of sorghum and causes permanent injury. The degree of inclination differs from specie to specie [77]. Waterlogging prevents shoot growth, dry matter accumulation and final yield in plants. Waterlogging decreases the yield rate in maize and the other changes brought about by waterlogging in maize are reduction in leaf growth and root growth [78]. A major developmental feature of rice is an improved rate of rising extension, allowing coleoptiles and shoots to raise contact with oxygen, light and carbon dioxide [79]. This takes place in the presence of ethylene, jointly with an accumulation of carbon dioxide and partial availability, but not an entire deficiency of oxygen [80]. Waterlogging causes leaf peeling, flaccidity, reduced nodulation and leaf epinasty [81]. Leaf lengthening rates and the total size of leaf become decreased under waterlogging stress conditions [54].

Another specific change at shoot level implies stem hypertrophy, which is a white spongy tissue with large volumes of intercellular gas spaces [82]. This tissue is secondary aerenchyma that forms externally from a phellogen and is homologous to cork [83, 84]. Its role seems to be increasing air space which allows for increased movement of gases between water and plant tissues [84]. Some species with the capacity to develop stem hypertrophy are *Lythrum salicaria* [85], *Lotus uliginosus* [86], *Lotus tenuis* [87], *Glycine max* [83] and *Melilotus siculus* [84]. In woody plants, an important morphological trait developed by tolerant species is lenticels hypertrophy at the stem base [7]. It is supposed that these special structures, functionally analogous to hypertrophied stem tissue, allow oxygen entrance into shallow roots through aerenchyma and intercellular spaces [7, 83]. This idea was based on studies where the blocking of lenticels of waterlogged plants with lanolin determined a marked reduction in the root aeration so that lenticels appeared as points of air entrance to the root system [88]. Despite the above discussed, there is controversy about the function of hypertrophied lenticels, because in several cases, they tend to be more developed below water [20]. Hence, this location does not support the idea of enablers of oxygen entry toward the root

system. Some authors proposed that it is more likely that lenticels may help maintain plant water status during waterlogging, by partially supplying water for the shoots and thus replacing the less functional roots [23, 25]. The recovery of stomatal conductance of waterlogged plants matching in time with the appearance of hypertrophied lenticels supports the belief that they contribute to the plant water homeostasis under waterlogging conditions [21, 22].

Another important morphological response of plants is the development of lacunae gas spaces (aerenchyma) in the root cortex. The development of aerenchyma may be a response to waterlogging in both waterlogging-tolerant and waterlogging-intolerant species [89-92]. On the other hand, aerenchyma formation is an adaptive response in waterlogging-tolerant species only, specifically in bottomland woody species [25, 93]. There are two types of processes involved in the development of aerenchyma. The first is the constitutive development of aerenchyma as it is not linked with abiotic stress. It is formed by the cells separated during tissue development. This type of cell death occurring as a result of cell separation is termed as shizogeny, regulated developmentally and independent of external stimulus. It is formed as a result of a highly regulated tissue specific pattern of cell separation. The second type of aerenchyma development is known as Isogeny since it is formed due to a partial breakdown of the cortex that resembles programmed cell death and its formation depends on the external stimulus like abiotic stress [94]. The increase in porosity may enhance venting toward the shoot and the atmosphere of phytotoxic compounds (ethanol, methane), produced in the roots [95, 96] and/or enhance the longitudinal diffusion of gases in the roots, thus increasing their aeration [90, 97].

The proportion of aerenchyma is generally considered as a key discriminating factor between wetland and non-wetland plants [98]. The development of aerenchyma or lacunae tissues is not unique to roots. They are also observed in the leaf sheath following waterlogging, forming an interconnecting system of shoot-root ventilation [99, 100]. Aerenchyma increases tissue porosity which itself can be initiated as a result of osmotic dependent changes in cell shape [23, 45]. The changes in cell shape and assemblage in the root cortex are most likely linked to enhanced cell wall loosening enzyme activity and with suberin deposition in the exodermis [34, 101-103]. The development of a suberized exodermis correlates with the development of aerenchyma in maize [103] and is associated with a decline

in radial loss of root oxygen [40, 101]. Such a barrier on the periphery of the cortex may not only reduce the loss of oxygen to the rhizosphere but could also protect the plant from phytotoxins produced by microorganisms in the environment surrounding the roots [101, 104].

Physiological response of plants to waterlogging stress: In waterlogging intolerant species, a few hours after the soil becomes saturated, the water uptake by roots of most plants is reduced [41, 105]. The reduction of water uptake under water excess of the soil in waterlogging intolerant species shows the paradoxical response of wilting of leaves, as it can be seen under drought [105, 106]. Under waterlogged conditions, plant roots are in a condition of hypoxia (shortage of oxygen), their metabolic activity is suppressed and adenosine triphosphate (ATP) production decreased [107]. The decreased ATP production restricts the supply of energy for root growth, thus reducing growth and development in plants. The greatest oxygen utilization rate in root tips is linked with respiration, which is required for linked metabolic actions. Germinating seeds of sorghum species are severely susceptible to waterlogging because the seedlings do not possess enough oxygen due to the waterlogging problem [37]. Due to insufficient oxygen, respiration and electron transport chain is inhibited, thus the rate of production of ATP reduces in sorghum. Moreover, membrane permeability in sorghum increases when the rate of production of ATP becomes reduce due to the absence of oxygen. In the wheat chief reaction of the root to the waterlogging condition is the decrease of respiration [108]. Low oxygen levels due to the waterlogging problem may reduce hydraulic conductivity consequent to a decrease in root permeability [109, 110]. Oxygen deficiency induces a rapid reduction in the rate of photosynthesis in waterlogging sensitive plants which are generally considered a result of reduced stomatal aperture [54, 111, 112]. Reduced photosynthetic rate and leaf gas exchange are the characteristic features of waterlogging in sorghum and its increase in intensity occurs with an increase in the duration of waterlogging [76]. Waterlogging may stimulate stomatal closure apparently without detectable changes in leaf water potential because oxygen deficiency in roots can induce abscisic acid production which ultimately limits stomatal aperture [113]. High stomatal resistance under waterlogging conditions could be related to the shortage of oxygen availability, which affects the normal root functions of plants.

One of the first plant physiological responses to waterlogging conditions is the reduction in stomatal conductance in plants (Figure 2) [23]. The rapid increase in stomatal resistance and subsequent reduction in transpiration and net photosynthesis rates of waterlogged plants may be an adaptive response to water stress caused either by water deficit or excesses [114]. Fast stomatal closure in barley plants was reported when subjected to waterlogging conditions [115]. Similarly, when pea plants were subjected to waterlogging conditions, prompt closure of stomata was recorded due to abscisic acid transport from older to younger leaves [116]. Moreover, stomatal conductance in mungbean declined under waterlogging conditions irrespective of the growth phase the stress was applied, however, the impact had become more pronounced at later growth phases owing to the natural aging of the leaves (Figure 3) [117]. On the other hand, approximately similar sensitivities of stomatal conductance to waterlogging were recorded in mungbean at vegetative and flowering phases [118]. Soil waterlogging may not only increase stomatal resistance but also limit water uptake, thus intern leading to internal water deficit [21, 23, 119]. Remarkable reduction in stomatal conduction, leaf potential, photosynthesis rate and enhanced leaf and root senescence were recorded in cotton plants when subjected to waterlogging conditions [120]. It has been suggested that the point at which waterlogging down-regulates photosynthetic and stomatal conductance depends on the intrinsic anatomical differences, leaf age and rubisco content of waterlogging tolerant species [121]. However, partial stomatal closure during waterlogging may have a beneficial role in avoiding the upward movement of toxic elements in plants [122].

Waterlogging stress is also known to cause marked perturbation in different chlorophyll fluorescence attributes of plants. The use of chlorophyll fluorescence as an indicator of waterlogging stress is because chlorophyll fluorescence is an excellent physiological factor that determines the primary process involved in photosynthesis such as energy transfer due to excitation, absorption of light and photochemical reactions occurring in the photo-system II [123]. Therefore, changes in chlorophyll fluorescence parameters determine the function and stability of photo-system II [124, 125]. The plants subjected to waterlogged conditions exhibit certain alterations in this physiological marker. For instance, a prominent decrease in maximum quantum efficiency was

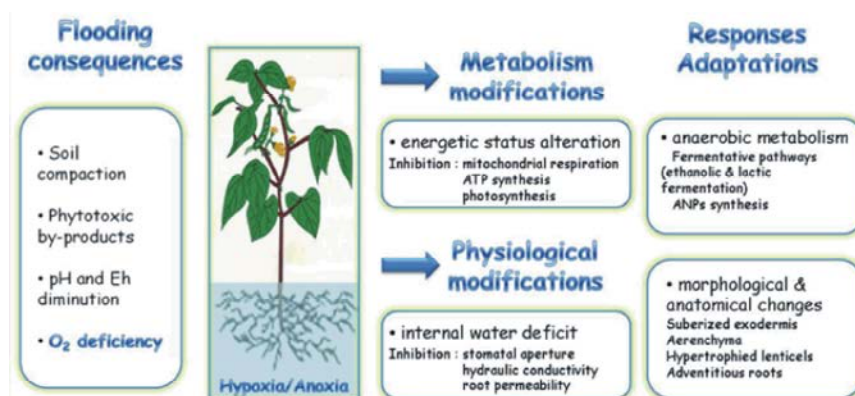


Fig. 2: Main physicochemical events taking place in the rhizosphere during soil waterlogging and the resulting modifications in plant metabolism and physiology followed by the initiation of adaptive responses [39]

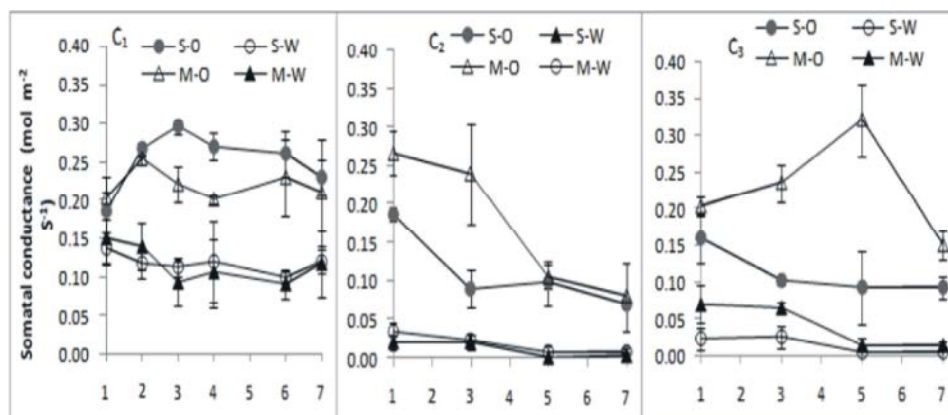


Fig. 3: Waterlogging effects on stomatal conductance (C₁, C₂, C₃); S-O, Sunaina variety with optimum moisture; S-W, Sunaina waterlogged; M-O, MH-97-6 variety with optimum moisture; M-W, MH-97-6 waterlogged; The figure label subscripts 1, 2, 3 designate vegetative, flowering and seed filling phases, respectively [117]

recorded when species of cork oak (*Quercus variabilis*) and china wingnut (*Pterocarya stenoptera*) were subjected to waterlogging conditions [126]. Likewise, a decrease in the maximum quantum yield of photo-system II photochemistry was also recorded in field beans when subjected to varying days of waterlogging stress [127]. Photo-system II photochemistry was also impaired due to waterlogging in alfalfa. The decrease in photochemistry indicated the sensitivity of the photosynthetic apparatus to abiotic stress and also the inability of the plants to regenerate rubisco under stressful conditions [128]. The reductions in chlorophyll content and early leaf senescence are some of the major indicators when the plants are subjected to low levels of nitrogen [9]. Lower nitrogen amount causes loss of chlorophyll content and early senescence of leaves. This loss in chlorophyll content ultimately leads to a reduction in photosynthetic rate. Photosynthesis inhibition initiates many days before the chlorophyll content declined [129]. Nitrogen

concentrations in leaves stems and seminal roots decrease with increasing waterlogging conditions. But nitrogen concentration increases in adventitious roots [54]. The greater amount of nitrogen in adventitious roots as compared to seminal roots is due to upholding of the capability for nutrient uptake in the aerenchyma possessing adventitious roots [130].

The decrease in leaf chlorophyll content, early leaf senescence and a reduction in leaf area may also contribute to the inhibition of photosynthesis at a later stage of plant growth [54, 131]. The increased diffusive resistances decreased in leaf chlorophyll concentration and leaf water potential are some of the major contributing factors for loss of assimilation rate in mungbean due to waterlogging stress [117]. Moreover, the decrease in photosynthetic rate, water use efficiency and intrinsic water use efficiency was reported in okra plants when subjected to waterlogged conditions [111]. Transpiration rate declined in response to waterlogging at any of the

growth phases of plants. The transpiration rate recorded in mungbean was highest at the flowering phase followed by the seed filling and vegetative phases when subjected to waterlogging conditions and the mean losses were 36, 84 and 64% for the vegetative, flowering and seed filling phases, respectively [117]. Similar results have been reported in mungbean [118], in cowpea [132] and in pigeon pea [114, 133]. Reduced transpiration rate during stressful conditions may be considered as a defense/avoidance mechanism against the stress [122]. It is a consensus that stomata regulation controls the carbon dioxide exchange rate of plants under waterlogged conditions [111].

The decline in photosynthesis rate is one of the physiological factors affected by waterlogging stress [60, 118]. Photosynthesis can drop as a result of a restriction of carbon dioxide uptake due to stomata closing [54, 87, 134]. Several works have shown a correlation between stomatal conductance and carbon fixation in waterlogged plants indicating that stomatal aperture can be a limiting factor for photosynthesis [135, 136]. When the waterlogging stress is prolonged, it may lead to the inhibition of the photosynthetic activity of the mesophyll [25, 137, 138], as well as a reduction in the metabolic activity and the translocation of photoassimilates in plants [139, 140]. The outcome of photosynthesis on plant growth and development may be dramatic and it may lead to concurrent physiological dysfunctions such as the inhibition of water transport and changes in hormone balance [48, 110]. Photosynthesis is generally declined by stomatal closure triggered by root hypoxia; however, resistant species might maintain stomatal functioning during exposure to waterlogging [136, 141]. The reduction in assimilation rate could be attributed to increased stomatal resistance [60, 118], drop-in leaf water potential [132] and decline in leaf chlorophyll content [60].

The reductions of photosynthetic rate during long periods of waterlogging could be explained by the reduction of carbon dioxide carboxylation by rubisco. Reduction of mesophyll conductance has been proposed as a phenomenon that limits photosynthesis rate when stomatal closure has not yet occurred and could occur during drought or waterlogging conditions [142]. The photosynthesis rate of mungbean genotypes declined significantly starting from the second day of exposure to early waterlogging and the mean net photosynthesis rate declined by 42, 87 and 73% due to waterlogging at the vegetative, flowering and seed filling phases, respectively (Figure 4) [117]. Reduction in

leaf water potential due to waterlogging was also observed in mungbean after exposure to waterlogging at vegetative and flowering phases. Photosynthesis rate and nutrient uptake also decline in maize plants under waterlogged conditions [78]. Therefore, the effects of waterlogging induce a reduction in dry mass production [13], an increase in total root length and a decrease in leaf area [14], alterations in dry matter partitioning in the different organs [15], leaf necrosis [16] and reduction in the rate of photosynthesis, stomatal conductance and chlorophyll content have also been observed [7].

Like other mechanisms to alleviate waterlogging stress, biochemical adjustments could also occur in herbaceous species, where activation of fermentation pathways has been identified during waterlogging [143]. In swamp forest species tolerant to waterlogging, the production of photoassimilates likely maintains the transport of sugars from the mature leaves (source) to the roots and new leaves (sink) and this likely continues even during waterlogging in opposition to sensitive to waterlogging species, which close their stomata, thereby decreasing carbon gains and halting the transport of sugar to sink organs [144]. Keeping enough levels of fermentable sugars in roots is undeniably vital for the long-standing survival of plants throughout waterlogging conditions. Some studies demonstrated that the starch levels in whole roots of rice and alfalfa did not considerably diverge under enlarged durations of waterlogging, telling that starch of root is not freely activated and transformed to substrates which are fermentable [145]. Germinating seeds of rice could degrade accumulated starch under anoxia (absence of oxygen), while seeds of wheat did not sprout and were not capable to degrade the starch [146]. These separate behaviors are because of the successful introduction of α -amylase in anoxia in rice seeds, however not in wheat seeds. Accumulated starch in roots is believed to be simply assembled all through waterlogging and supply sugars for anaerobic metabolism in roots. Under waterlogged conditions, accumulation of Total non-structural Carbohydrates (TNC) had been well studied in wheat [147]. During waterlogging, TNC accumulated in all parts of plants [129]. Accretion of starch has been found in leaves of a variety of waterlogged plants. During root hypoxia, accumulation of starch in the leaves has been credited to a declined rate of shifting of carbohydrates from leaves to roots [148] and to delayed growth and a lesser level of metabolism of roots, which causes the carbohydrate requirement to reduce [149].

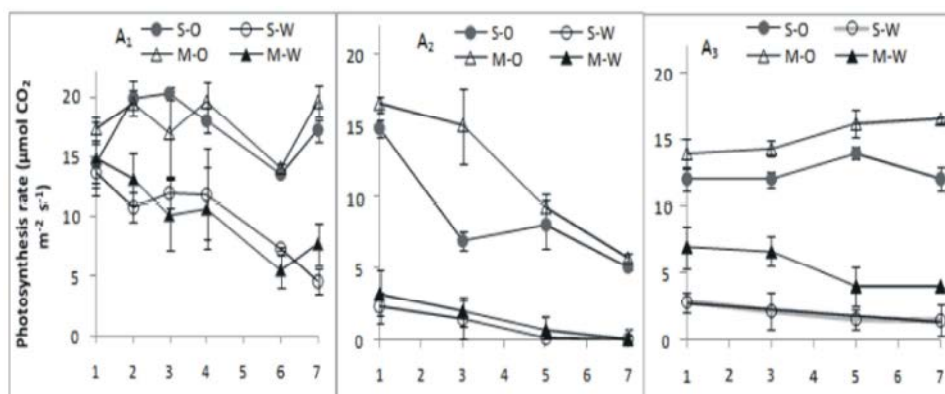


Fig. 4: Waterlogging effects on photosynthesis rate (A₁, A₂, A₃); S-O, Sunaina variety with optimum moisture; S-W, Sunaina waterlogged; M-O, MH-97-6 variety with optimum moisture; M-W, MH-97-6 waterlogged; The figure label subscripts 1, 2, 3 designate vegetative, flowering and seed filling phases, respectively [117]

To maintain its metabolic activity, the plant has to draw on its carbohydrate reserves. As initial carbohydrate supply is correlated with the level of tolerance to hypoxia in many species, presumably through its involvement in providing energy during anaerobic conditions, the level of carbohydrate reserves may be a crucial factor in the tolerance to long-term waterlogging [150, 151]. For instance, an increased capacity to utilize sugars through the glycolytic pathway enables rice seedlings to survive longer periods of waterlogging [152]. Although a plant may have high sugar reserves, these must, however, be available and converted readily through an efficient glycolytic pathway. The availability of photoassimilates to the cells under anaerobiosis has been proposed as one of the limiting steps for survival under waterlogging conditions [139]. Indeed, waterlogged soils tend to reduce the translocation of photosynthetic products from "source" leaves to "sink" roots [153, 154]. As a result, the maintenance of photosynthetic activity and accumulation of soluble sugars to roots is an important adaptation to waterlogging [155]. Hormones regulation is dependent upon an increase in the amount of ethylene, which cooperates with gibberellins and auxins [156]. Auxins and gibberellins are fundamentals for ethylene activity and play activating rather than regulatory roles. The effect of waterlogging is to arouse the production of definite plant hormones in wheat. During anaerobic conditions, these hormones are released out from the roots in a larger amount and most likely affect responses of root and leaf. Roots and microorganisms present in waterlogged soils usually produce ethylene. The hormonal activity of ethylene released during waterlogging is of great interest. Ethylene is known to be a non-promoter or trigger of

senescence of leaf [67]. In sorghum, senescence is delayed by Endogenous cytokinins and promotes protein synthesis to advance plant establishment [81].

CONCLUSION

Waterlogging affects the development, growth and yield in plant crop, but the tolerance crops to this stress vary remarkably. Waterlogging reduces plant growth and development, leading to the production of smaller organs and hampered flower production and grain filling. A diminution in grain filling occurs due to a decrease in the accumulation of sucrose and starch synthesis enzymes. Timing, duration, severity and speed of development undoubtedly have pivotal roles in determining how a plant responds to water stress. Following water stress, stomata close progressively with a parallel decline in net photosynthesis and water-use efficiency. Stomatal conductance is not controlled by soil water availability alone, but by a complex interaction of intrinsic and extrinsic factors. Depending upon the availability of moisture, activities of the enzymes of carbon assimilation and those involved in adenosine triphosphate synthesis are decreased and sometimes inhibited. One of the major factors responsible for impaired plant growth and productivity under water stress is the production of reactive oxygen species in organelles including chloroplasts, mitochondria and peroxisomes. Other features such as higher carbohydrate reserves and/or their efficient use, maintenance of photosynthesis and plant water status through shoot elongation or aquaporin gating may greatly improve plant survival to waterlogging. Morphological changes such as lenticels

formation, aerenchyma development, adventitious roots initiation and/or root suberization can not only ameliorate the rate of O₂ diffusion to the submerged growing parts but also help alleviate water and nutrient deficiencies. Therefore, changes in anatomical, morphological, physiological and biochemical aspects are generally noted in response to waterlogging stress. Understanding these responses to waterlogging is important for screening the tolerance of genotypes to water stress conditions.

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