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Ultrastructure, adaptability, and alleviation mechanisms of photosynthetic apparatus in plants under waterlogging: A review

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Abstract

Photosynthesis is a process highly sensitive to various abiotic and biotic stresses in plants. Among them, the major abiotic stress, waterlogging, affects the crop's growth and productivity. Under waterlogging, the photosynthetic apparatus of plants was destroyed. Waterlogging reduced chlorophyll content and the net photosynthetic rate. Therefore, this updated review summarized the effect of waterlogging on chloroplast ultrastructure, photosynthetic characteristics, and chlorophyll fluorescence attributes of plant species. By studying various research papers, we found that intercellular concentration of available carbon dioxide in mesophyll cells, assimilation of carbon, and the net photosynthetic ratio declined under waterlogging. The chlorophyll fluorescence efficiency of plants decreased under waterlogging. Thus, the study of photosynthesis in plants under waterlogging should be done with respect to changing climate. Moreover, the recognition of photosynthetic characteristics present in tolerant species will be beneficial for designing the waterlogging-tolerant crop plant in changing environments.

Keywords: chlorophyll; PEP carboxylase; photosynthesis; photosynthetic pigments; stomatal conductance; waterlogging.

Introduction

Globally, changes in climatic conditions enhance the unfavourable environmental conditions that generate various abiotic stresses in field-grown plants. One of the severe abiotic stress in many areas worldwide is flooding (either submergence or waterlogging), caused by an increase in occurrence and quantity of precipitation events due to changing climate (Wright *et al.* 2017). Among flooding, waterlogging is the utmost significant stress that limits the development and growth of plants and reduces crop productivity. The main reasons for waterlogging occurrence are poor drainage of the soil and extreme rainfall events. Recently the waterlogging conditions are expected to increase in frequency due to extreme and unpredictable rainfall patterns. The soil texture can also

Highlights

- Photosynthesis in plants is seriously hampered by waterlogging
- Waterlogging drastically affects PSII in plant leaves
- Plants alleviate waterlogging through physiological, biochemical, and molecular adaptations

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Abbreviations: BR – brassinosteroids; C_i – intercellular CO_2 concentration; E – transpiration rate; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; JA – jasmonic acid; MDA – malondialdehyde; P_N – net photosynthetic rate; ROS – reactive oxygen species; SA – salicylic acid; WL – waterlogging.
Conflict of interest: The authors declare that they have no conflict of interest.

be affected by waterlogging because the high amount of clay and compacted soil (as the results of repeated use of agricultural technology) result in poor drainage (Najeeb *et al*. 2015, Ploschuk *et al*. 2018).

Waterlogging is a condition in which soil contains excessive water and limits the flow of gases found in the soil pores (Falakboland *et al.* 2017). The diffusion rate of required gas, *i.e.*, oxygen, is 10^3 times slower in water than that in air and this restriction is the major limiting factor under waterlogged conditions (Najeeb *et al.* 2015). A low concentration of oxygen decreases the hydraulic conductivity of plants because of the hampered permeability of roots. Low oxygen content leads to an extensive decline in transpiration and net photosynthetic rate. This decrease is accredited to stomatal closure under waterlogging. However, some other factors, including leaf senescence and lower leaf area, are also responsible for reduced photosynthetic rate (Ashraf 2012, Bailey-Serres *et al.* 2012a, Azhar *et al.* 2020, Sharma *et al.* 2021). The adaptation strategies under waterlogging have been recognized by many researchers. Under waterlogging, changes in morphological and anatomical characteristics have been observed, for example, in the architecture of root, leaf area, and plant height (Radhakrishnan *et al.* 2012). Plant's adaptation to waterlogging including the development of adventitious roots and aerenchyma is highly regulated by the interaction of plant hormones (Ashraf 2012, Sharma *et al.* 2021). The ACC oxidase 1 (*ACO1*) gene, which is involved in the generation of ethylene, was shown to be upregulated in cotton leaves. Furthermore, under waterlogging stress, 9 out of 13 ethylene-responsive factors (ERFs) were differentially expressed and upregulated, implying that ethylene may be important in cotton's waterlogging response (Christianson *et al.* 2010). Ethylene stimulates shoot elongation in wetland plants and it is believed to have a role in hormone interactions with abscisic acid (ABA) and gibberellic acid (GA) (Musgrave *et al.* 1972, Kende *et al.* 1998, Cox *et al.* 2003, Voesenek *et al.* 2004, Pierik *et al.* 2005). The GA is recognized by its nuclear receptors, GA-INSENSITIVE DWARF1s (*GID1*s), which cause the elimination of downstream repressors DELLAs (Gallego-Giraldo *et al.* 2014). Waterlogging stress increased the expression of GA biosynthetic genes and *GID1* genes. GA has been used to ameliorate rice and *Rumex palustris* waterlogging tolerance in submerged conditions (Hoffmann-Benning and Kende 1992, Benschop *et al.* 2006). GA could promote the lengthening of internode, enabling rice leaves to emerge from the water surface for aerobic respiration (Hoffmann-Benning and Kende 1992, Fukao *et al.* 2006, Bailey-Serres *et al.* 2012b, Gallego-Giraldo *et al.* 2014). Under hypoxic stress, Bai *et al.* (2011) discovered an increase in ABA content in *Malus* leaves, suggesting that ABA is an important signal in modulating responses to waterlogging. Moreover, indole-3-acetic acid (IAA) is also an essential hormone for plant growth and development. Three auxin-related genes (*Auxin induced 15 A*, *Auxin induced 15 B*, *Auxin transporter-like protein 2*) were found to be downregulated in the leaves of waterlogged cotton. These genes were commonly related to changes in the IAA content in the leaves of a 15-d waterlogged cotton plant (Zhang *et al.* 2016). Besides, phytohormones, such as jasmonic acid (JA), salicylic acid (SA), and brassinosteroids (BR), are other effective growth regulators of waterlogging tolerance. They may be implicated in a network of signaling cascades that assist plants to adapt under waterlogging; many different JA, SA, and BR-related genes were upregulated in waterlogging according to Nguyen *et al.* (2016). The understanding of plant adaptation mechanisms to waterlogging helps improve plant tolerance to stress.

Different parts of photosynthesis and PSI are vulnerable to severe conditions of waterlogging (Yan *et al.* 2018). Due to waterlogging the amount of chlorophyll (Chl) in plant leaves (especially Chl *a* and *b*) is also reduced (Li *et al.* 2018, Ma *et al.* 2018), and it indirectly and directly affects the chloroplast photosynthetic machinery of plant leaves (Yu *et al.* 2019a, Azhar *et al.* 2020). The hampered photosynthetic apparatus caused a reduction in photosynthetic rate (P_N) and finally in the yield and productivity of plants (Sharma *et al.* 2021). It was reported in many crops that the production of photosynthetic material, biomass, and other physiological characteristics are seriously influenced by waterlogging stress (Wang *et al.* 2019). Reduced transpiration rate (E), stomatal conductance (g_s), photosynthetic rate (P_N), and other physiological attributes have been reported in many dryland plants, such as winter wheat (*Triticum aestivum* L.) (Abid *et al.* 2018) and maize (*Zea mays* L.) (Zaidi *et al.* 2003). The stomatal closure, decrease in intercellular CO_2 concentration (C_i), and available CO_2 concentration in mesophyll cells can affect the carbon assimilation in plants and ultimately decrease plant yield (Zou *et al.* 2019). The general processes in photosynthesis are illustrated in Fig. 1.

Different Chl fluorescence characteristics are changed by waterlogging in plants. Chl fluorescence is an excellent physiological marker for assessing the primary procedures and mechanisms of photosynthesis, such as absorption of photons and energy transfer owing to excitation, numerous photochemical activities in the PSII can be monitored (Langan *et al*. 2022, León-Burgos *et al*. 2022). The stability and functions of PSII are determined by

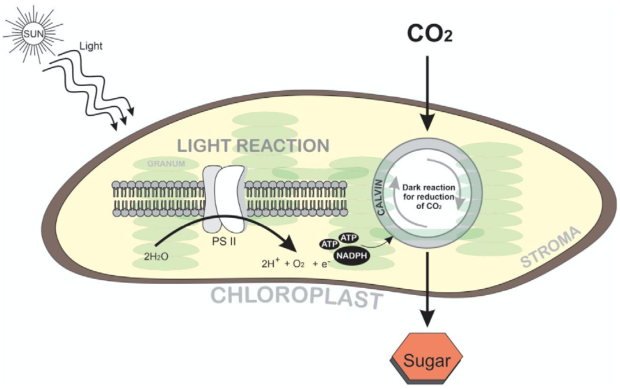

Fig. 1. General mechanism of photosynthesis in plants.

assessing the variations in Chl fluorescence characteristics (Abdeshahian *et al.* 2010, Singh *et al.* 2020, 2021; Soni *et al.* 2021). Chl fluorescence marker shifts in plants growing under the conditions of waterlogging. The susceptibility of the photosynthetic machinery to this stress is shown by a significant drop in Chl fluorescence characteristics (Smethurst *et al.* 2005).

Therefore, to understand the plant photosynthetic performance under waterlogging and other associated stresses, it is necessary to study the various photosynthetic traits and their regulatory mechanism for survival in waterlogged conditions. In the following review, the modification of various photosynthetic parameters in diverse plant species was discussed under the severe conditions of waterlogging. Waterlogging stress has not been fully assessed in photosynthetic apparatus in plants, so it is necessary to determine the photosynthetic characteristics of tolerant plant species under waterlogging. The current review focuses mainly on the activity of the photosynthetic pigments, enzymes, PSI, PSII, and regulatory genes in plant species. In this paper, we emphasize recent advancements in our knowledge of the physiological systems that govern plant waterlogging responses. It also summarizes the mechanism of electron transfer in photosynthesis, functions of the PSI and PSII, and photosynthetic traits associated with waterlogging response involved in metabolite synthesis and carbon assimilation procedures.

The consequences of waterlogging in plants

The exchange of gases between the atmosphere and plant roots is severely hampered under waterlogging (Striker 2012). The oxygen in waterlogged soil is quickly depleted, causing roots to switch from aerobic to anaerobic respiration, whereas CO_2 and ethylene concentrations increase. The reduced ATP production in root cells impacts different metabolic processes in plants (Pampana *et al.* 2016, Kaur *et al.* 2020); for example, stomata closure restricts nutrients and water uptake as shown in Fig. 2. It prevents the carbon dioxide inflows into the leaves and causes a decline in transpiration rate. It also causes senescence and wilting of leaves and photosynthesis inhibition, resulting in a lower accumulation of plant biomass that ultimately reduces kernel mass and grain yield in many crops (Ashraf 2012, Shao *et al.* 2013, Voesenek and Bailey-Serres 2013, Arguello *et al.* 2016).

Oxygen deprivation has a major impact on most stages of plant growth and shifts energy-related metabolic pathways from aerobic to anaerobic fermentation (Xu *et al.* 2015). Due to a lack of energy, toxins such as aldehydes and alcohol begin accumulating excessively in the tissues (Tamang *et al.* 2014). Most plants are susceptible to waterlogging (Bailey-Serres and Colmer 2014), and they have evolved a range of ways to deal with waterlogging (Fukao *et al.* 2019). The activity of enzymes related to anoxic respiration increases significantly as compared to aerobic conditions (Fukao *et al.* 2003). Interestingly, exogenous calcium peroxide (CaO_2) increases the soluble oxygen concentration in water under waterlogging circumstances and decreases the activities of anaerobic enzymes. Because treatment of calcium peroxide enhances oxygen contents, resulting in aerobic respiration, adequate energy is available for seed development or seedling establishment under waterlogging (Mei *et al.* 2017).

Moreover, plants exposed to prolonged waterlogging can suffer from root injuries, which can reduce photosynthetic efficiency by causing biochemical changes within photosynthesis processes. Limited activity of phosphoglycolate, Rubisco, and glycolate oxidase are some of the biochemical changes observed in waterlogged soil (Yordanova and Popova 2001). Flooding tends to decrease the photosynthetic efficacy of many plants, including maize (Qi *et al.* 2021), peanut (Zeng *et al.* 2021), *Lycopersicon esculentum* (Bradford 1983, Jackson 1990), and *Pisum sativum* (Jackson and Kowalewska 1983). Plants, on the other hand, acclimatize to waterlogging to preserve their photosynthetic performance (Li *et al.* 2002).

Waterlogging affects the defensive enzyme system and enhances malondialdehyde (MDA) contents, suggesting that waterlogging affects peroxidation and integrity of membrane lipids. It causes membrane degradation and

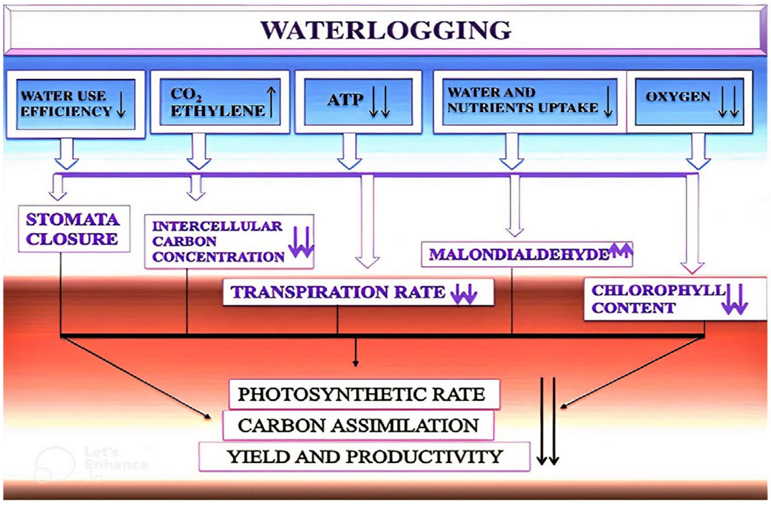

Fig. 2. The effect of waterlogging on plant productivity and photosynthesis.

prolonged leaf senescence (Aarti *et al.* 2006, Irfan *et al.* 2010). Yordanova and Popova (2007) have reported that the chlorophyll concentration, associated photosynthetic enzymes (Irfan *et al.* 2010), and PSII photochemical efficiency were lowered when waterlogging frequency increased (Smethurst *et al.* 2005), leading to a significant decrease of plant yield (Ren *et al.* 2014).

Chlorophylls (Chl) are the magnesium-containing tetrapyrroles necessary for light capturing and energy transmission in plants (Ohmiya *et al.* 2014). In shade conditions, *Lilium auratum* absorbs light energy by synthesizing large amounts of Chl and increasing net photosynthesis, which can assure plant development, however, the influence of light intensity and waterlogging stress on Chl content has no consistent conclusion (Zhang *et al.* 2015). The Chl concentration of *Zea mays* was reduced as shade increased, limiting photosynthetic and organic synthesis (Chen *et al.* 2013). The Chl synthesis, the Chl cycle, and the degradation of the Chl molecule into a nonfluorescent Chl catabolite are the three different stages of Chl metabolism (Aarti *et al.* 2006, Hörtensteiner 2013). The gene activities involved in Chl biosynthesis are influenced not only by environmental variables (light, temperature, and nutrition) but also by enzymes involved in Chl production. In *Arabidopsis*, 15 enzymes and 27 genes essential for Chl metabolism have been discovered so far (Nagata *et al.* 2005, Chen *et al.* 2013). Seasonal, developmental, and tissue-specific variables influence the enzyme activity and the expression of enzyme-encoding genes (Ohmiya *et al.* 2014). Chls are associated with Chl-binding proteins of the PSI and PSII complexes and accumulate in tissues where PSI and PSII are synthesized (Mullet *et al.* 1990, Croce 2012). A lot of research has been reported on the genetic elements that determine chlorophyll accumulation in photosynthetic tissues (Eckhardt *et al.* 2004, Croce 2012). The Chl molecules are the magnesium-containing tetrapyrroles that is necessary for light capturing and energy transmission in plants (Ohmiya *et al.* 2014). In waterlogged sesame, the expression of a gene for Chl-*a*/*b*-binding protein 4 (*LHCB4*), which is involved in the PSII light-harvesting complex, was specifically reduced (Wang *et al.* 2012) (Table 1). Waterlogging stress was also shown to drastically lower the expression of *GhLHCB* in a prior study on cotton (Zhang *et al.* 2016). The damage is caused due to the upregulation of genes involved in Chl degradation and downregulation of genes involved in Chl synthesis (Araki *et al.* 2012, Ding *et al.* 2020, Gan *et al.* 2020, Qi *et al.* 2020). The gene expression linked with Chl degradation alters under waterlogging. The upregulation of *CLH* and *PaO* genes was reported under waterlogging; they encode hydroxymethyl chlorophyll *a* reductase and pheophorbide *a* oxygenase, respectively. The genes of Chl synthesis were downregulated under waterlogging including *HEMF* (translating coproporphyrinogen III oxidase), *HEMD* (translating uroporphyrinogen III synthase), and *HEMB* (translating 5-aminolevulinate dehydrogenase) (Yu *et al.* 2019b). Moreover, cotton research revealed that waterlogging stress dramatically reduced the expression of four Chl *a*/*b*-binding (LHCBs) genes that are involved in the light-harvesting complex of PSII (Zhang *et al.* 2017).

Maize production is becoming more restricted by waterlogging. *ZmCAO1* was extracted from a maize *ygl* mutant. *ZmCAO1* is a master regulator in the Chls biosynthesis pathway, converting Chl *a* to Chl *b*. The *zmcao1* mutants have smaller ears, shorter plants, heavier kernels, and lower grain production. Waterlogging is a problem for the *zmcao1* mutants. As a result, the *ZmCAO1* gene might be an excellent target for increasing agricultural production and waterlogging resistance (Li *et al.* 2021).

Carbon assimilation and photosynthate distribution are both directly connected to the yield of the plant. Previous research found that under waterlogging, the photosynthetic procedure in plant leaves was disturbed due to reduced Chl content and the net photosynthetic rate (Dubey 2016). However, the study has demonstrated that waterlogging would activate an increase in the net photosynthetic rate (P_N), which might be associated with an increase in the ethylene concentration in leaves as a result of waterlogging. Furthermore, ethylene caused an increase in the stomata number and width in plant leaves, which facilitated carbon dioxide absorption, followed by an elevation of the P_N and dry mass accumulation (Wang *et al.* 2016a, Ceusters and Van de Poel 2018).

Photosynthetic efficiency in plants is controlled by the structure of chloroplasts and the mesophyll cells' internal structure. All organelles in mesophyll cells are sensitive to the external quantity of light but mitochondria (Xu *et al.* 2008) and chloroplasts (Weston *et al.* 2000) are the most susceptible and their morphological and internal structure modifies in response to environmental change (Pessarakli 2016). Therefore, it is necessary to investigate the effects of waterlogging at the cellular level on leaf photosynthetic properties.

Chloroplast and cell: morphology and ultrastructure under waterlogging

Chloroplasts are organelles where photosynthesis occurs and PSI or PSII are located. In chloroplasts, during light-dependent electron transport, ATP synthase catalyzes ATP synthesis from ADP and Pi at the expense of the electrochemical proton gradient generated (Buckley *et al.* 1999). It is also the major site of generation of reactive oxygen species (ROS) such as superoxide anion radicals and hydrogen peroxide (H_2O_2) during the electron transfer along the electron chain (Foyer *et al.* 1994, Asada 1999). Thus, chloroplasts are easy to be attacked by various oxidants. Zheng *et al.* (2008) found severe oxidation damage to spinach leaf chloroplasts by increased O_2 and H_2O_2 content under UV-B radiation. The accumulation of ROS in chloroplast during photosynthesis could further lead to oxidative damage to PSII under severe stresses (Hideg *et al.* 1999). The scavenging system is composed of antioxidant enzymes, such as superoxide dismutase (SOD, EC 1.15.1.1), ascorbate peroxidase (APX, EC 1.11.1.11), catalase (CAT, EC 1.11.1.6), peroxide (POD, EC1.11.1.7), and glutathione reductase (GR) that can minimize the cellular damage caused by ROS (Khatun

Table 1. The regulatory photosynthetic genes and their mode of action under waterlogging in different plants.

Waterlogging-induced genes	Activities regulated by genes	Plant	Reference
Sucrose synthase 1 (*SUS1*)	Sucrose metabolism	*Arabidopsis*	Zhang *et al.* (2017)
Sucrose synthase 4 (*SUS4*)	Sucrose metabolism	*Arabidopsis*	Zhang *et al.* (2017)
Alcohol dehydrogenase (*ADH*)	The ethanolic fermentation gene	*Arabidopsis*	Zhang *et al.* (2017)
Chlorophyll *a-b* binding protein 4 (*LHCB4*)	A gene involved in the light-harvesting complex of PSII	Sesame	Wang *et al.* (2012)
GhLHCB	A gene involved in the light-harvesting complex of PSII	Cotton	Zhang *et al.* (2016)
JcERFVII-2, *JcERFVII-3*	Ethylene response factors (ERFs)	*Jatropha*	Juntawong *et al.* (2014)
Snorkel (*SK*), Submergence-1A (*Sub-1A*)	Both genes encode ethylene-responsive factor type transcription factors, they function in opposite ways	Rice	Hattori *et al.* (2009)
HRE1, *HRE2*, *RAP2.2*, *RAP2.12*	Four members of group-VII ERFs; overexpression of these four genes significantly improved low oxygen survival by promoting the expression of genes involved in low oxygen adaptation	*Arabidopsis*	Hinz *et al.* (2010)
COX	Inhibition of root respiration	Watermelon	Zheng *et al.* (2021)
RbcL, *RbcS*, *Rac*	A decrease in the photosynthetic rate	*Cucumis sativus*	Sun *et al.* (2014), Zhang *et al.* (2013)
Sucrose phosphate synthase (*SPS*), Sucrose synthase (*SuSy*)	Sucrose metabolism under anaerobic respiration	*Potamogeton distinctus*	Harada and Ishizawa (2003)
ZmCAO1	Leads to reduced concentrations of Chl *a* and Chl *b*	Maize	Li *et al.* (2021)

et al. 2008). The antioxidant enzyme activities are reported to decrease, along with increased ROS accumulation in plants under salinity or waterlogging stress (Lin *et al.* 2004, Jebara *et al.* 2005, Duan *et al.* 2008, Xie *et al.* 2008). Previous research has demonstrated that ROS generated due to waterlogging stress in chloroplasts cause the majority of damage to chloroplast structure (Mei *et al.* 2017, Ren *et al.* 2018a, Zhou *et al.* 2020). Waterlogging damages the ultrastructure of mesophyll cells and reduces the leaf photosynthetic capacity. The breakdown of membrane systems caused by waterlogging on mesophyll cells resulted in apoptosis and the loss of photosynthetic potential (Bertamini *et al.* 2006, Burkey and Wells 1991).

Under waterlogging, the chloroplast arrangement was scattered, the ultrastructure of chloroplasts was damaged, and their membranes and thylakoids became disintegrated. Hence, the photosynthetic mechanism was hindered (Shao *et al.* 2014) and the content of Chl pigments and different fluorescence parameters were lowered (Xu *et al.* 2006), finally leading to leaf photosynthetic efficiency deterioration. Furthermore, certain mitochondria grew longer and became dysfunctional with time, and their membranes disintegrated. These modifications would suppress leaf respiration that is associated with photosynthesis (Ren *et al.* 2016).

In waterlogged plants, cells may die because of a shortage of ATP in the cell membrane, which causes reduced stability of the membrane system and structure (Pfister-Sieber and Brändle 1994, Crawford and Braendle 1996). Moreover, MDA concentration began to increase after waterlogging at different phases, suggesting that waterlogging has a detrimental effect on membrane integrity and, eventually, membrane degradation. Such modifications would have an impact on the plasma membrane's ion exchange capacity as well as several physiological processes connected to membrane function (Chaoui *et al.* 1997). According to research, waterlogging destroys the ultrastructure of mesophyll cells in functioning leaves and decreases photosynthetic performance. Plants might decrease photosynthetic product consumption by limiting leaf development and decreasing the number of blades to adapt to the anoxic environment induced by waterlogging stress (Liu *et al.* 2015).

Chloroplast ultrastructure studies in two cultivars of sorghum leaves under waterlogging as well as control were revealed (Zhang *et al.* 2019). Both cultivars of sorghum exhibited chloroplasts with normal structure as in control. The chloroplasts appeared oval with a distinct border, with integrated grana and stroma lamellae, and the lamellae were folded in an organized manner. The stroma lamellae and granum were surrounded by an exterior envelope with an easily visible and integrated double membrane. The chloroplasts altered their exterior and internal morphology in response to waterlogging stress, and these alterations differed considerably across the two sorghum cultivars. The chloroplasts were inflated and spherical after waterlogging, the membrane, external capsule, and grana lamellae were ambiguous and disorganized, and the plastoglobuli were more prominent and bigger. The exterior grana lamellae and membrane structure of chloroplasts of sorghum genotypes were damaged after continuous waterlogging, while the interior spaces of the chloroplasts were occupied with plastoglobuli. Researchers assessed the quantity and structure of chloroplasts in sorghum to measure alterations in chloroplasts during waterlogging. The number of chloroplasts was likewise reported to be lower under the waterlogging than in the control. The waterlogging treatment reduced the length-to-width ratio of chloroplasts considerably. Chloroplast size and cell area occupied by chloroplasts both decreased after the waterlogging treatment. Under waterlogging stress in sorghum, the chloroplast membrane disintegrated and the basal layer border became unclear (Zhang *et al.* 2019). Transmission electron microscopy revealed alterations in the ultrastructure of leaf cells in waterlogged Virginia saltmarsh mallow (*Kosteletzkya virginica)* seedlings. The chloroplasts became spherical and their volume decreased under waterlogging. Moreover, thylakoids' lamellae swelled, and chloroplast inclusions decreased. Starch granules changed their form significantly, but their numbers and volume were reduced, and they eventually disappeared. Plastoglobules enlarged in size and number with time. The mitochondrial membrane and inner cristae eventually became unclear, as the mitochondria enlarged in size at first but then disappeared. The cell nuclei decreased progressively, concentrated, and tended to a spherical form, similar to the chloroplast. In addition, the annulate lamellae and multivesicular body appeared in the waterlogging, and the cell wall was distorted and bent towards the end. As a result, under long-term waterlogging, these organelle abnormalities were indicative of total cell death in *Kosteletzkya virginica* (Zhou *et al.* 2011).

Photosynthesis is directly influenced by the morphology and ultrastructure of chloroplasts, which causes a significant decrease in productivity and dry mass accumulation in maize crops. It was observed in two cultivars of maize that chloroplasts had complete outer membrane with distinct borders and well-developed thylakoids and both stroma lamellae and grana were organized densely and visible in control plants. Under waterlogged circumstances, however, chloroplast arrangment became irregular. Condensed grana lamellae, disordered stroma lamellae, and deformed thylakoid were seen in maize seedlings chloroplasts under waterlogging. Furthermore, the quantity of grana lamellae and grana was significantly reduced to varying levels. However, as indicated in waterlogged maize seedlings, γ-aminobutyric acid (a small signaling molecule) stimulates chloroplast ultrastructure (Salah *et al.* 2019). A foliar spray of 6-benzyladenine had a similar outcome in waterlogged maize (Ren *et al.* 2017).

Thus, significant modifications have been detected in the plant chloroplasts under waterlogging. The condensed grana lamellae, disordered stroma lamellae, and deformed thylakoid of chloroplast can reduce the light-harvesting mechanism and ultimately lead to decreased plant photosynthetic performance and plant yield. The modification in chloroplast structure impacts PSI and PSII structure and affects the electron transport system.

Effect of waterlogging on PSII and Chl fluorescence parameters

The use of chlorophyll fluorescence imaging technology to determine the link between photosynthesis and the plant environment has been identified as a nondestructive and noninvasive technique (Kalaji and Guo 2008, Henriques 2009, Gameiro *et al.* 2016, Singh *et al.* 2019). The Chl fluorescence parameters (Table 2) are a particularly sensitive marker for investigating photodamage under stressful circumstances (Maxwell and Johnson 2000, Kalaji *et al.* 2011, 2016; Sharma *et al.* 2021). The Chl fluorescence characteristic changes are used to assess a plant's adaptation and resistance to environmental changes. Plants' dynamic fluctuations in Chl fluorescence evaluate local modifications in photosynthetic apparatus function (Rolfe and Scholes 2002).

Plants' photosynthetic reaction centers are more functional under nonstress conditions than under stress, according to many studies. Therefore, plants grown in non-stressed environments demonstrate higher fluorescence characteristics, *e.g.*, maximum photochemical efficiency (F_v/F_m) and photochemical quenching (q_P) (Kong *et al.* 2010). The minimum fluorescence (F_0) is a suitable tool for assessing plant stress damage, and the maximum fluorescence (F_m) after dark adaptation can indicate PSII electron transport efficiency. The shift in F_v/F_0 shows that the light energy received by PSII was used to lower the efficiency of quinone A (Q_A), which might indicate plant tolerance level to extreme conditions (Rao *et al.* 2021). The adversity of waterlogging stress on fluorescence characteristics has been the subject of significant investigation in plants, such as *Pterocarya stenoptera*, *Salix integra*, *Hemarthria altissima*, *Phragmites australis*, and *Distylium chinense* (Rao *et al.* 2021).

Chl fluorescence is a useful tool for analyzing the functioning and photosynthetic system changes, which can be harmed by waterlogging (Mielke *et al.* 2003, Wang *et al.* 2019, Minhas *et al.* 2020). During the early phase of waterlogging, a rapid reduction in photosynthetic rate and water-use efficiency was observed. Some negligible changes were observed in transpiration rate or stomatal conductance, suggesting that diminished photosynthetic rate may be caused by a mechanism other than stomatal closure. The early decline in photosynthetic rate is associated with photoinhibition of PSII, as revealed by the decrease of the value of F_v/F_m due to waterlogging. Water-use efficiency and stomatal conductance significantly decreased under prolonged waterlogging, whereas leaf water potential (ψ_L) remained constant, indicating stomatal closure in the absence of water stress (Ahmed *et al.* 2002). Several ROS were generated due to oxidative damage associated with the excessive decrease in the electron transport chain (ETC) during waterlogging/flooding circumstances (Lal *et al.* 2019).

The OJIP transient curve obtained from Chl fluorescence experiments is extremely sensitive to environmental stressors (Calatayud and Barreno 2001, Sayed 2003, Van Heerden *et al.* 2003, Govindachary *et al.* 2004, Badr and Brüggemann 2020, Khan *et al.* 2021). The shape of the OJIP transient changed over the first hours of hypoxia resulting in a significant decline in the variable fluorescence of all phases (Kumar *et al.* 2020, 2021; Soni *et al.* 2021, Bhatt *et al.* 2022a,b). The fast O to J increase is the phase regulated by photochemical mechanisms, whereas J to I is entirely a thermal phase (Neubauer and Schreiber 1987, dos Santos Junior *et al.* 2015, Khan *et al.* 2021). The process that occurs on the donor site of the

Table 2. Different chlorophyll parameters affected by waterlogging in plants (Kumar *et al.* 2020, Gorbunov and Falkowski 2021).

Fluorescence parameter	Definition
F_0, F_m	Minimum and maximum yields of Chl *a* fluorescence measured in a dark-adapted state
F_v	Variable fluorescence ($F_m - F_0$)
F_v/F_m	Maximum quantum yield of photochemistry in PSII, measured in a dark-adapted state
σ_{PSII}	Functional absorption cross-section of photosystem II (PSII)
ABS/RC	Absorption flux (of antenna Chls) per reaction center (RC)
ETR_{Fv}	Electron transport rate from amplitude-based variable fluorescence analysis
ETRτ	Electron transport rate from kinetic fluorescence analysis
TR_0/RC	Trapped energy flux (leading to Q_A reduction) per RC
ET_0/RC	Electron transport flux (further than Q_A^-) per RC
ϕP_0	Maximum quantum yield for primary photochemistry
ψE_0	Efficiency/probability for electron transport (ET)
ϕE_0	Quantum yield for ET
PI_{ABS}	Performance index (potential) for energy conservation from excitation to the reduction of intersystem electron acceptors
RC/ABS	Q_A-reducing RCs per PSII antenna Chl (reciprocal of ABS/RC)
S_m	Normalized total area above the OJIP curve
DI_0/RC	Total energy dissipated per RC
ET_0/CSm	Electron transport flux (further than Q_A^-) per RC
TR_0/CSm	Trapped energy flux (leading to Q_A reduction) per RC
ABS/CSm	Absorption flux (of antenna Chls) per RC
k_N	Nonphotochemical rate constant
k_P	Photochemical rate constant

PSII regulates the release of fluorescence from this phase. Every abiotic stress that disrupts the structure and function of the oxygen-evolving complexes (OECs) affects the rate of oxygen evolution, therefore enhancing fluorescence quenching in the J–I phase (Panda *et al.* 2006). The increase in the O–J phase is driven by a net photochemical decline in the PSII quinone pool (Prakash *et al.* 2003). Whenever the donor (J–I) and acceptor (O–J) PSII sides were compared, the first was more greatly affected during the hypoxia owing to the inactivation of the OEC and consequent deterioration of the ETC (Panda *et al.* 2006).

Chl fluorescence is used for detecting the changes in damaged photosynthetic apparatus functions under waterlogging (Mielke *et al.* 2003, Wang *et al.* 2019, Minhas *et al.* 2020). A rapid decline in the photosynthetic rate and water-use efficiency has been observed after waterlogging, however, stomatal conductance and transpiration rate are not affected during the early waterlogging time. These results indicate that the photosynthetic rate was reduced, and this might be caused by a process other than the closing of stomata. The value of F_v/F_m of chlorophyll fluorescence declines early within waterlogging, which suggested photoinhibition of PSII. At the time of chronic waterlogging, the water potential of leaves remains unchanged but water-use efficiency and stomatal conductance declined significantly indicating closing of stomata under no water stress (Ahmed *et al.* 2002). The adverse effect of waterlogging/flooding on the leaf area index and Chl content resulted in a reduction in the photosynthetic rate of leaves. This decreased photosynthetic rate is connected to reduced g_s, E, and C_i. It indicates the declined photosynthetic rate is coupled with stomatal factors (Mielke *et al.* 2003, Wang *et al.* 2019, Minhas *et al.* 2020). Under the circumstances of waterlogging/flooding/hypoxia due to excessive reduction of electron transport chain (ETC), oxidative damage and production of ROS have been taking place (Lal *et al.* 2019).

The reductions in maximum quantum yield for primary photochemistry (Φ_{PSII}) and F_v/F_m after waterlogging indicate damage of PSII in summer maize, which causes a decline in PSII photosynthetic potential energy and photosynthetic rate along with other characteristics of photosynthesis (Irfan *et al.* 2010).

The physiological responses were recognized at various growth rates in common buckwheat (*Fagopyrum esculentum*) (Choi *et al.* 2021). In this work, the Chl fluorescence parameters of leaves at the early stage showed the lower values as compared to maximum vegetative growth. The study revealed that at the time of recovery, treated plants showed maximum Chl fluorescence (Choi *et al.* 2021).

The physiological data of peanut genotypes HY 39 and ZKH 1 under control and waterlogging conditions were studied by Zeng *et al.* (2021). The waterlogging treatment was given at flowering stage for 10 d. Increased stem diameter and dry mass accumulation under waterlogging was associated with the increased soil and plant analysis development (SPAD) along with net photosynthetic rate (P_N) and upregulation of Chl and porphyrin metabolism related genes have been reported in both genotypes.

The Chl fluorescence analyses and the characteristics of photosynthetic gas exchange studied in two ninebark species, *Physocarpus amurensis* and *Physocarpus opulifolius*, under hypoxia conditions evaluated the stomatal limitation differences in both species (Zhang *et al.* 2018). In *P. amurensis*, the nonstomatal limitation played the main role under severe stress conditions. The Chl fluorescence variables, such as F_v/F_m and actual photochemical efficiency, were analyzed in *P. opulifolius*. The increased value of both parameters has been reported in *P. opulifolius*. The decline rate during the stress was lower in *P. opulifolius* than in *P. amurensis*. Moreover, nonphotochemical quenching in the leaves of *P. opulifolius* increased on the 10th day of stress while the variation of nonphotochemical quenching was lower in *P. amurensis* leaves. This implies that *P. opulifolius* had not only improved tolerance to waterlogging stress but showed also higher PSII photochemical activity that may be caused by its higher ability of nonphotochemical quenching. The performance index (PI_{ABS}) was reduced significantly with the reduction in F_v/F_m in both ninebark species leaves. Under subsequent waterlogging, the fluorescence curve has been altered in both species. In *P. amurensis*, at J and I points (V_J and V_I), the fluorescence was significantly higher. The degree of growth in V_J was significantly higher than that of V_I. In *P. opulifolius*, the alterations of V_J and V_I in the leaves were smaller. However, the maximum quantum yield of nonphotochemical quenching increased. The other fluorescence parameters, such as electron transport and trapped energy per reaction centers (ET_0/RC and TR_0/RC), in the *P. amurensis* leaves decreased along with a drastic increase of dissipation energy in the reaction center (DI_0/RC). This also suggests that the PSII reaction center function in *P. opulifolius* leaves was significantly greater than that in *P. amurensis* (Zhang *et al.* 2018).

The study of post-anthesis photosynthetic rates and grain-filling capacity of wheat (waterlogged frequently at the elongation stage of the stem) indicated that waterlogging significantly limits grain filling and ultimately causes yield loss. The decline in the grain mass is due to the early drop in the P_N at post-anthesis. This decrease was compensated by external potassium (K) application. The decline in C_i and g_s after 7–21 d after anthesis was reported during the study and these reductions were aggravated due to waterlogging treatment. The nonstomatal factors constrained photosynthesis in wheat as observed by increased C_i and g_s after 21–28 d after anthesis but the photosynthetic rate was reduced significantly. On 21 d after anthesis, the P_N declined by waterlogging in wheat. The fluorescence parameter of photochemical efficiency (Φ_{PSII}) remained unchanged under waterlogging; it suggested the decrease in dissipation of the energy absorbed by PSII. The decline of energy dissipation elevated the danger of photodamage (early reductions in photochemical efficiency) in plants waterlogged for 28 d after anthesis. Hence, the treatment by potassium can enhance the growth of roots and nutrient availability under waterlogging, thus improving post-anthesis photosynthesis (Gao *et al.* 2021).

Carbon assimilation and photosynthate distribution under waterlogging stress

Waterlogging stress, based on the most of research, inhibits plant photosynthesis and is not favorable to carbon assimilation in plants. Chl content and several other factors of photosynthesis are affected by water stress (Aarti *et al.* 2006). The photoassimilation process is also associated to chlorophyll concentration, which might alter the net photosynthetic rates in angiosperms. Carbon assimilation and photosynthate distribution are both directly associated with crop productivity. Previous research suggests that during waterlogging, the photosynthetic apparatus was destroyed and thus reduced P_N in leaf tissue.

The major photosynthetic product is triose phosphate, while the main prominent storage form of photosynthates in plants is starch. Photosynthates are mostly transported from the carbon source to sink in the form of sucrose (Vu 2005, Gupta *et al.* 2017, Ohara and Satake 2017, Mizuno *et al.* 2018). Plant efficiency relies upon the efficient transfer of photosynthates from carbon source to sink (Julius *et al.* 2018). Besides, waterlogging causes an imbalance in the plant source–sink interaction. First of all, waterlogging stress may disrupt the metabolism of starch and sucrose. According to a prior study, waterlogging stress reduced the storage of dissolved sugar in the leaf of the main stem, which was associated with lower expression of sucrose metabolism-related genes (Zhang *et al.* 2017). Furthermore, root disruption has been reported in plants under the stress of waterlogging and soluble carbohydrates also accumulated in the phloem of certain waterlogged plants. However, the carbohydrate content in the waterlogged plant roots significantly declined (Kogawara *et al.* 2006, Merchant *et al.* 2010). Similarly, it was discovered that this treatment decreased the distribution rate of assimilation products in the grain because of starch assimilation in the waterlogged rice stem (Lee *et al.* 2019).

Photosynthates are stored mostly as starch, whereas sucrose is used to transfer them from the vegetative to reproductive parts (Lunn and Hatch 1995). Various crops and organs with different sucrose and starch concentrations respond differently to waterlogging. After waterlogging, the aboveground glucose content was generally reduced, but the carbohydrate content in roots varied significantly across different varieties. The carbohydrate content decreased in sensitive cultivars but increased in tolerant cultivars of plants. The reason behind this is blocked transportation of leaf photosynthates, reduced transportation of photosynthates to the root system, and accumulation of starch and sucrose in the plant leaves (Castonguay *et al.* 1993, Sairam *et al.* 2009).

Waterlogging causes productivity loss in rapeseed (*Brassica napus* L.) at various levels depending on the duration of stress occurrence (Zhou and Lin 1995, Zou *et al.* 2014, Wollmer *et al.* 2018, Ploschuk *et al.* 2020), along with photosynthesis inhibition being the major causative factor for yield. At the initiation of waterlogging, stomatal closure is the principal cause of the decline in P_N, but as the waterlogging persisted, decreased enzyme activity for photosynthesis and Chl breakdown had become the main limiting factors of photosynthesis (Ashraf and

Habib-ur-Rehman 1999, Araki *et al.* 2012, He *et al.* 2018). Rapeseed leaves have a higher photosynthesis capability than silique husks, and the area and photosynthesis of leaves during the flowering stage are proportional to seed yield and oil content (Wang *et al.* 2016b). Waterlogging has a substantial impact on barley, wheat, and maize leaf growth (de San Celedonio *et al.* 2016, Ren *et al.* 2018b).

In wheat, the decline in grain yield capacity was reported due to waterlogging during the grain-filling stage. The losses were associated with reduced rearrangement of stored photosynthates to the grain and grain conversion capacity of carbohydrate to starch (Jiang *et al.* 2008). In conclusion, waterlogging caused an imbalance in source–sink connection and diminished the efficient assimilation of photosynthates to sink, causing a reduction in yield.

Due to waterlogging, cotton production declined as a result of decreased photosynthesis, which is a general physiological reaction to waterlogging stress (Li *et al.* 2011). Waterlogged cotton leaves had significantly lower Chl content, Rubisco activity, and finally P_N, which caused severe loss of yield and early senescence (Pandey *et al.* 2000, Dong *et al.* 2003, Liu *et al.* 2010). In cotton, waterlogging sensitivity has been linked to photosynthetic inhibition. Waterlogging drastically reduced the stability of the leaf thylakoids, perhaps accounting for a substantial decrease in P_N during waterlogging (Luo *et al.* 2008). Similarly, stomatal closure and reduced leaf Chl concentration also resulted in lower photosynthesis during waterlogging (Bradford 1983, Yordanova *et al.* 2005). The finding was confirmed by Luo *et al.* (2008) and Meyer *et al.* (1987), who discovered that waterlogging stress reduced leaf water potential, stomatal conductance, and transpiration rate in cotton.

In star magnolia (*Magnolia stellata*), C_i increased with the decreased stomatal conductance and P_N under waterlogging treatments, showing that the nonstomatal factors are the main reason for the decline in photosynthetic activity (Farquhar and von Caemmerer 1982). It may rely upon several factors, such as reduced Rubisco enzyme carboxylase activity in mesophyll cells, diminished ribulose bisphosphate (RuBP) regeneration potential, and degradation of photosynthetic regions (Salvucci and Crafts-Brandner 2004). According to an analysis of several photosynthetic parameters, the lowest value of C_i was likewise comparable with the higher P_N value observed after waterlogging treatment. P_N was observed increasing in *M. sinostellata* after waterlogging, perhaps due to a higher rate of CO_2 assimilation.

In *Calophyllum brasiliense*, the growth characters (biomass production, leaf expansion, shoot height, new leaf development, stem diameter, CO_2 assimilation rate, stomatal conductance, chlorophyll content, and fluorescence) were examined in controls and waterlogged plants. Although waterlogged plants continued to incorporate carbon throughout the experiment, their assimilation and growth rates were lower than that of control plants. Reduced CO_2 assimilation rates were most likely related to decrease in total chlorophyll content (de Oliveira and Joly 2010).

Research on the photosynthetic properties of vulnerable shade-grown plants, such as *Lauraceae*, *Mosla hangchowensis*, and *Heptacodium miconioides*, found that P_N and g_s decrease when irradiance falls (Aleric and Kirkman 2005, Liao *et al.* 2006, Liu *et al.* 2006). Plants grown under water stress have also similar results to shade grown plants, *i.e.*, P_N and g_s decrease as waterlogging increases (Ge *et al.* 2004, Zhang *et al.* 2004).

The Calvin cycle and the formation of cytoplasmic sucrose are the two main processes involved in sucrose loading. The limiting enzyme of photosynthesis is ribulose-1,5-bisphosphate carboxylase/oxygenase (EC 4.1.1.39) and is the main enzyme of the Calvin cycle for regulating photosynthetic carbon metabolism. The drop in cotton photosynthesis developed by waterlogging is mostly due to the Rubisco activity decline (Kuai *et al.* 2014). The plant resistance to external stress is influenced by the Calvin cycle's susceptibility; hence, the Calvin cycle and photosynthesis are interconnected (Takahashi and Murata 2005). Rubisco contains eight big subunits and eight small subunits. The P_N is determined by the activity of Rubisco (Suzuki *et al.* 2007). Rubisco activase is a chloroplast enzyme expressed by a nuclear gene that separates and activates Rubisco through the carbon assimilation process (Yin *et al.* 2014). Downregulation of genes such as *RbcS*, *Rac*, and *RbcL* causes a reduction in photosynthetic rate. Under low light as well as water stress, Rubisco enzyme-encoding genes in cucumber (*Cucumis sativus*) are downregulated, resulting in a lower P_N (Zhang *et al.* 2013, Sun *et al.* 2014). Photosynthesis is a complex network that is based on the activities and control of many genes.

Other enzymes of the Calvin cycle, which are affected by waterlogging, are: (*1*) adenosine diphosphate glucose pyrophosphorylase (AGPase, EC 2.7.7.21), which is involved in starch synthesis regulation. (*2*) sucrose phosphate synthase (SPS, EC 2.4.1.14), a crucial enzyme in carbon metabolism that regulates the carbon distribution of sucrose and starch in the presence of light. The SPS enzyme activity is associated with the formation, accumulation, and output rates of sucrose, carbon-fixation rate, and transportation of photosynthates to the seed. (*3*) Sucrose synthase (SuSy, EC 2.4.1.13), is a cytoplasmic enzyme that breaks down sucrose and releases energy.

The sucrose metabolism of leaves in Mokara Yellow orchid (Li *et al.* 2002) and yield in chickpea are both affected by the activities of the latter two enzymes (Kaur *et al.* 2005). Both SPS and SuSy activities in pondweed (*Potamogeton distinctus*) increased after waterlogging, with SuSy activity increasing more, indicating that SuSy plays a significant role in sucrose metabolism in anaerobic or hypoxic conditions (Harada and Ishizawa 2003). In the waterlogging conditions, SuSy instead of invertase catalyzes the breakdown of sucrose in the roots, resulting in an increase in SuSy concentration in the waterlogged plants (Kreuzwieser *et al.* 2009, Narsai *et al.* 2011). Under low-oxygen stress, in the soil induced by waterlogging, sucrose breakdown by SuSy has greater benefits than sucrose decomposition *via* invertase. Sucrose increases the

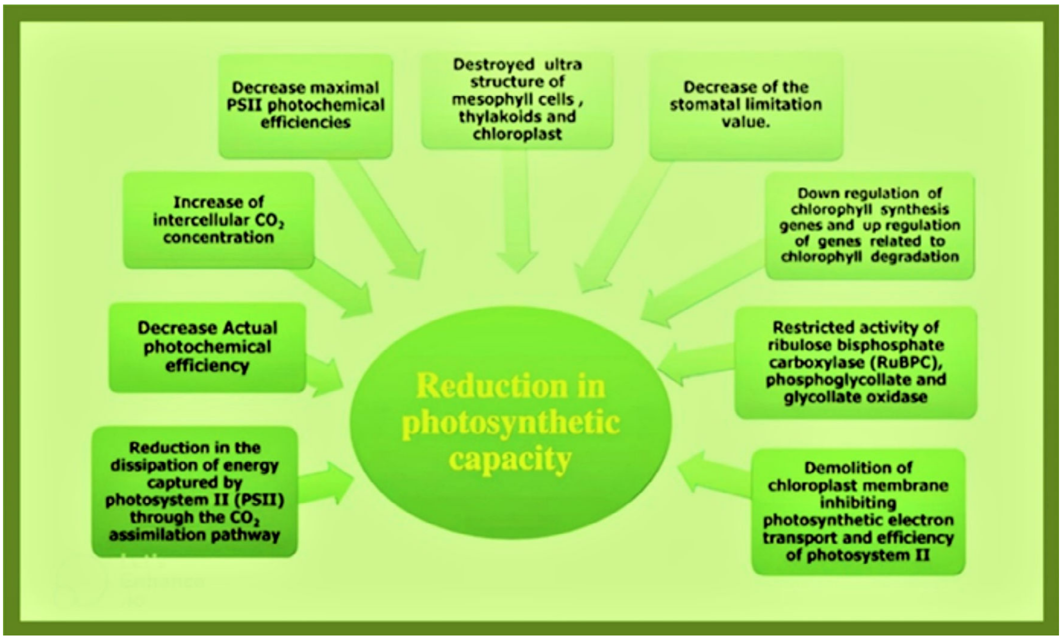

Fig. 3. Factors affecting photosynthesis in plants under waterlogging.

root system's capacity to commence anaerobic respiration by maintaining glycolysis through SuSy breakdown.

In this review article, the reasons for the reduction of plant yield instigated by waterlogging were analyzed from the aspects of photosynthesis, Chl fluorescence, chloroplast ultrastructure, Chl metabolism, and carbohydrates metabolism. This has some significance for increasing the cultivation yield of plants and waterlogging-tolerant breeding. Waterlogging leads to the decreased rate of photosynthesis, damaged photosynthetic apparatus, imbalance in the relationship between source and sink, which causes plant yield loss. The photosynthesis of plants is affected by many other factors (effect of waterlogging on photosynthetic rate in plants are given in Fig. 3). Hence, it is necessary to describe the photosynthetic performance of leaves, photoassimilate output from leaves, and transportation in stems. Furthermore, the balance of the chlorophyll fluorescence parameters, chlorophyll contents, source–sink relationship, and the photosynthetic rate is the key point for waterlogging-tolerant breeding and cultivation methods.

Concluding remarks

Waterlogging causes slower CO_2 diffusion, chlorophyll degradation, declines photosynthetic rate, causes peroxidation of membrane lipid along with MDA accumulation. It also damages the endogenous protective enzyme system, chloroplast structure, electron transport mechanism of photosystem II and limits the production of photoassimilates and organic carbohydrates, *etc.* To acclimatize under waterlogging, plants develop various effective molecular and physiological mechanisms to sustain normal development. We summarized the research advances in the effects of waterlogging on photosynthesis, respiration, hormones, physiological metabolism, and gene regulation, the modification of plant physiological characteristics, chlorophyll fluorescence parameters after waterlogging. We suggest that studying the photosynthetic processes of plants in response to waterlogging and the effects would be an important research aspect in the future. Despite all the technological advancements, the data on the photosynthetic mechanism of plants under waterlogging is quite limited. Rigorous research must be done to elaborate the functions of each component of the photosynthetic system by taking a more mechanistic approach. The photosynthetic enzyme activities are seen to modify in response to waterlogging which further needs optimization of their kinetics. Therefore, by using omics and system biology techniques, several research groups have considerably improved pure physiological or biological approaches.

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