Chapter 15
Impact of Flooding on Agricultural Crops—An Overview

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Abstract Water is an important ecological factor for plants and the soil water is a critical factor determining the distributional pattern of plant species on earth. Different plant species are adapted to different degrees of water or moisture availability prevailing in their habitats and are categorized either as xerophytes, mesophytes or hydrophytes. Majority of the wild and crop plants belong to the ecological group mesophytes and are adapted to moderate soil water content. This group of plants performs better under this moderate availability of soil water. Whenever the soil water availability increases to higher degrees during water logging, such plants face the water stress with consequences of decreased growth and survival. Flooding is an environmental stress which negatively influences the growth and biomass production in crop plants. The impact of flooding on growth and survival may be direct on the plant, or it may modify the habitat conditions of the plant and thus bring about its impact on the plants indirectly. Some plants are tolerant to water logging, and in them, the impact of flooding is significantly little as compared to the nontolerant species. The flooding is known to affect and modify the conditions and habitat features of plants as well as directly impacting their survival, growth and reproduction.

Keywords Flooding · Phytotoxins · Crops · Water logging

15.1 Impact of Flooding on Soil Properties

Soil redox potential and Elemental profile: In waterlogged soils, soil pores get completely filled with water, and consequently, the movement of gases through these soil pores is immensely inhibited by their water content, making the path of oxygen diffusion resistant by ten thousand times as that in air (Armstrong et al. 2002).

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Under such circumstances, the little and slow influx of oxygen to roots does not match the demand or need of the growing roots, resulting in insufficient and limited availability of oxygen to the submerged roots. This inadequate or slowing oxygen supply to roots is the primary cause of root injury as well as of shoots which rely on roots (Vartapetian and Jackson 1997). The dissolved oxygen concentration in flood water is little, and this little amount gets consumed rapidly during the initial event of flooding by both plant roots and aerobic microorganisms. This way roots are exposed to complete absence of oxygen and thus suffer from anoxia (Gambrell and Patrick 1978). Besides anoxia, the flooding also hampers the outward diffusion as well as oxidative breakdown of important gases like ethylene (Arshad and Frankenberger 1990) and carbon dioxide that are produced by microorganisms and roots. These accumulated gases are known to inhibit the growth or damage the roots of many crop plants such as soyabean (Boru et al. 2003).

Since oxygen molecule acts as the ultimate acceptor of electrons in cellular respiration (Gibbs and Greenway 2003), its absence shuts off the oxidative phosphorylation in plant root cells (Moller 2001) causing huge reduction in ATP content of root cells. This inactivation of oxidative phosphorylation owing to anoxia results in reduced ATP: ADP ratio (Drew et al. 2000) as roots switch to anaerobic or fermentative pathways for energy generation. The low generation and supply of ATP in root cells do not match their ATP demand resulting in arrest of vital processes and eventually causing the death of root cells, root tips and root. The low supply of ATP also negatively impacts membrane integrity (Rawyler et al. 1999), and when this membrane organization is compromised, it causes irrecoverable damage to cells leading to their death (Zhang and Davies 1987). Absence of oxygen in root cells for non-respiratory reactions such as synthesis of important structural lipids used in membrane formation is also accounted as reason leading to cell death (Vartapetian et al. 1978). Roots in anoxia, which are commonly referred to as anaerobic roots, may also die because of accumulation of products of their fermentation metabolism (Gerendás et al. 2002). The acidification of cytoplasm and vacuole owing to accumulation of protons, acetaldehydes, etc., as a result of fermentative metabolism are thought to trigger early death of root cells and root tips. Long-standing water logging damages crops and incurs huge economic losses as it initially results in root death which in most crops is followed by shoot death and thus destruction of the whole crop.

Water logging causes phytotoxin mediated root death: It has been seen that even if root tips may survive anoxia of their own, it is the surrounding soil biochemistry which may injure or kill them (Ponnamperuma 1972). Flooding or water logging causes the conversion of an oxidizing soil environment into a reducing environment, with soil redox potential values sharply decreasing from +800 mV which can go up to −300 mV. A soil with positive redox potential of 800 mV has an aerobic environment with oxygen available for aerobic respiration. Once water logging sets in, the availability of oxygen decreases, and as soon as free oxygen depletes completely, facultative anaerobic microorganisms start using nutrient ions such as nitrates as electron acceptors in respiration as alternatives to oxygen. This way nitrates are reduced to nitrite and nitrous oxides, leading to release of molecular nitrogen, process referred to as denitrification. This way nitrates are made unavailable for roots. As the soil environment becomes more strongly reducing, obligate anaerobes use oxides of manganese MnO^{4+} and iron Fe^{3+} as electron acceptors reducing them to more soluble Mn^{2+} and Fe^{2+} ions (Laanbroek 1990). This causes a build up of these soluble Mn and Fe cations in the soil often to toxic concentrations (Marschner 1990), which enter the roots and impact the activity of the enzymes and also damage the membrane systems in root cells. With persistence of water logging stress and further reduction in the value of soil redox potential, anaerobes use sulphates and reduce them to hydrogen sulphide (Ponnamperuma 1972) which is a very toxic for respiratory enzymes and non-respiratory oxidases. The formation of methane from carbon dioxide and organic acids occurs on further depletion of soil redox potential by the activity of methanogenic bacteria.

Uptake of nutrients: Flooding is known to impact plant nutrient uptake negatively. The reduced or non-availability of oxygen for roots tremendously reduces the uptake of nutrients. The endogenous concentrations of nutrients drop to low concentrations in different parts of the plant, thereby drastically affecting the plant growth (Ashraf et al. 2011). Because of water logging, crop plants are known to witness acute deficiencies of many essential nutrients vital for plant growth and development (Smethurst et al. 2005). Hypoxia in the rhizosphere is known to cause a significant reduction in ion selectivity, viz. K+ /Na+ uptake, hampering the flux of K+ to the shoots (Armstrong et al. 2002) besides making membranes less permeable to Na^{+} ions (Barrett-Lennard et al. 1999). In canola, Boem et al. (1996) found that water logging results in reduced ability of roots to absorb elements such as N, P, K and calcium. In maize also, the reduced endogenous levels of critical elements (N, P, K, Ca and Mg) were found to be associated with water logging (Atwell and Steer 1990); the latter is known to bring about adverse effects in crops through reduced elemental concentrations (Sharma and Swarup 1989; Smethurst et al. 2005). In wheat also, water logging brought about decline in tissue levels of P, K and Mg in the shoots (Stieger and Feller 1994). Studies on flooding stress of *Medicago sativa* showed that in leaf and root, there is a significant decrease in the nutrient composition of P, K, B, Cu, Ca, Mg and Zn (Smethurst et al. 2005). The reduced concentrations of N, P, K, Ca and Mg hamper many metabolic processes including efficiency of PSII, which impair plant growth and crop yield (Smethurst et al. 2005). The impeded nutrient uptake in crop plants results in deficiency symptoms such as chlorosis, early senescence and retarded growth which are the adverse effects of elemental efficiencies such as that of N, Mg, Ca, P and K (Kaur et al. 2017).

Water logging affects soil pH: Flooding or water logging is also found to be associated with change in soil pH which influences solubility and availability of plant nutrients. Because of water logging, the pH of soils changes towards neutrality, that limits the solubility and hence availability of many nutrients for plant uptake, thereby impacting plant life negatively. This changed soil chemical property also contributes to diminished plant growth and performance. In flooded soils, changes in redox potential values are also found to be associated with change in soil pH (Kögel-Knabner et al. 2010). In acidic soils, pH increases after flooding on account of consumption of protons while as in alkali soils, flooding causes a decrease in pH because of carbon dioxide build up which is known to reduce the alkalinity (Sahrawat 2005). In response to flooding, the change in soil reaction or soil pH may take place in days to weeks, the duration of change being dictated by an array of factors such as soil microbial population, temperature and other allied physical and chemical properties of soil (Kongchum 2005). According to the Nernst equation, a change of 59 mV in the redox potential of soil is accompanied by one-unit change in pH (Kögel-Knabner et al. 2010). Some studies have shown an increase in pH near soil surface after water logging (Kaur 2016). Besides redox potential and soil pH, water logging also brings a change in the soil temperature. Some studies have shown that water logging brings about an increase in soil temperatures (Kaur 2016; Unger et al. 2009). Soil temperature is an important soil property which besides rate of reactions influences many processes in the roots and rhizosphere. The change in soil pH, soil redox potential and soil temperature is known to influence solubility and availability of plant nutrients, making many nutrients non-available for uptake such as nitrogen which then hampers plant metabolism, chlorophyll synthesis, carbon assimilation, crop growth, yield and survival of plants negatively.

Plant metabolism-shift to anaerobiosis: Soil water logging causes hypoxia which progressively and ultimately leads to anoxia. Under these circumstances, aerobic respiration is compromised, oxidative phosphorylation is drastically reduced, and the plants switch over to anaerobic mode of respiration for energy needs. The plants first switch over to lactic acid formation and then to alcohol formation. The activation of alcohol dehydrogenase enzyme comes in the backdrop of increased formation of lactic acid which acidifies the cell protoplasm. Thus, in order to prevent acidosis which causes necrosis or cell death, the acid fermentation shifts to alcoholic fermentation which helps maintain cell pH and allows cell survival. Under anoxia, the respiratory rate of roots is very low and the availability of energy or ATP is very little; this decreases the metabolic activity of roots leading to reduced root and plant growth.

Water logging induces change in morphological and anatomical features: Flooding or water stress has also been known to bring about many anatomical and morphological changes in the plants. These include development of aerenchyma, suberized epidermis, adventitious roots, hypertrophied lenticels, etc. (Yamamoto et al. 1995). An important change induced in root cortex of plants due to water logging is the development of aerenchyma in it (Arber 1920; Armstrong 1979; Crawford 1982; Jackson 1984; Justin and Armstrong 1987; Konings and Verschuren 1980; Sculthorpe 1967). The formation of aerenchyma is conceived to be an important anatomical modification which helps plants adapt to flooding or water stress (Laan et al. 1989). Under flooding stress in many woody species, an important anatomical change is hypertrophied lenticels. Although lenticels are believed to have role in gaseous exchange, downward diffusion of oxygen during flooding, but, a renewed insight considers them linked to water logging tolerance highlighting their role in water uptake in circumstances of a nonfunctional root system and thus maintenance of water homeostasis of the plant during flooding. They do take over the function of water intake for shoots when roots are decaying and not in action. Furthermore, hypertrophied lenticels occur in more numbers in underwater part of the plant than above water which strengthens the view of their involvement in water uptake and maintenance of plant water homeostasis under waterlogged conditions.

Formation of adventitious roots is conceived to be one more important response of plants to water logging. This is a very important morphological adaptation of plants to water logging as these specialized roots with good amount of aerenchyma help the plant to absorb water and minerals when the absorptive ability of the main root is drastically compromised. The formation of adventitious roots is commonly believed to lend water logging tolerance to plants which bear them (Kozlowski 1997; Malik et al. 2001; Parelle et al. 2006; Dat et al. 2006).

Flooding stress and Diseases: In addition to inducing metabolic stress, flooding may also enhance the occurrence of soil-borne pathogens and thus increases the susceptibility of plants to diseases (Yanar et al. 1997). The poor metabolic or energy status of roots renders them less resistant to pathogen attacks. Water-borne pests such as insects, fungi and bacteria easily damage roots of stressed plants (Urban et al. 2015). Pathogens such as *Pythium* (damping off), *Phytophthora* (wilting) and *Pseudomonas putida* are known for their damaging effects on roots of vegetable crops, trees and other plants under waterlogged conditions (Walker 1991). The symptoms of diseased roots include their discoloration and rotting which causes premature death of the plants. The diseased roots also are not able to uptake nutrients efficiently and perform other functions normally. Pathogens such as *Sclerophthora macrospora* causing crazy top or downy mildew, *Cercospora zeae-maydis* causing grey leaf spot in maize, *Ustilago maydis* causing common smut in corn, *Fusarium graminearum* causing blight in wheat and *Fusarium virguliforme* causing sudden death syndrome in soybeans are also known to damage crops during flooding.

Water logging affects plant photosynthesis: Water logging is known to affect plant photosynthesis negatively, decreasing photosynthetic capacity of plants. There are multiple effects associated with flooding which bring about decrease in photosynthesis. Water logging induces stomatal closure, reduction in transpiration, which impacts gaseous exchange, reduction in internal carbon dioxide concentration for carboxylation reaction and thus reduction in photosynthesis. The water logging is also known to decrease leaf area and chlorophyll content of leaves, both of which affect photosynthesis negatively, reducing photosynthesis and rate of photosynthesis. Water logging is also known to damage the PSII which results in consequent drastic decrease and inhibition of photosynthesis. Water logging also causes a change in the chloroplast form, damage to thylakoid membranes and destruction of chloroplast structure. This is the reason why water logging results in bringing down the photosynthetic capacity of leaves, with consequent decrease in overall growth, survival and yield of plants. In many studies, it has been found that water logging results in damage to the integrity of membrane systems of mesophyll cells, damage to mitochondria, with resultant death of mesophyll cells and reduction of photosynthetic capacity of leaves.

Flooding and Phytotoxins: In waterlogged soils with depleted oxygen or lack of oxygen, anaerobic bacterial activity results in increased concentrations of elemental phytotoxins such as Fe, Mn and H2S and organic phytotoxins like butyric acid, acetic acid and propionic acid especially in acidic soils. These phytotoxins are very harmful and impede root growth as well as cause root death. This way also flooding or water logging modifies plant environment parameters which eventually reduces plant growth, plant productivity and survival.

Submergence reduces plant survival: Most of the terrestrial plants, both wild and crop plants, are highly sensitive or intolerant to submergence. The submergence of aerial parts of the plant severely influences and reduces plant photosynthesis and respiration as the diffusion rates of gases and plant gas exchange are drastically reduced. The muddy or turbid waters with little or no transparency further block the light availability which further adds to the reduction in photosynthesis (Vervuren et al. 2003). These impaired physiological processes result in carbon and energy crisis with resultant reduction in growth and survival of the plant.

Submergence and Oxidative stress in plants: One more negative impact of inundation on crop plants is the generation of reactive oxygen species (ROS) that are known to perturb numerous metabolic processes in cells (Ashraf 2009; Ashraf et al. 2010). Hydrogen peroxide (H_2O_2), superoxide (O^2-) and hydroxyl radicals (OH) are some of the lethal reactive oxygen species generated in plants, and these reactive oxygen species (ROS) being highly reactive trigger damage to a number of biochemical components in cells such as lipids, proteins, DNA and pigments (Ashraf 2009; Ashraf and Akram 2009). In plants, reactive oxygen species are produced under non-stressed conditions as well but their rates of production are much less and are thus easily neutralized by the antioxidant enzyme system of the plants. But under stress full conditions such as flooding, their rate of generation is much higher than rate of their neutralization with resultant elevated concentration levels that prove damaging to the cellular components and cellular processes such as photosynthesis and PSII. Elevated levels of H_2O_2 in plants are known to inhibit Calvin cycle (Kaiser 1976). As water levels after submergence come down, the plant tissues are again exposed to high light environment and oxygen levels which compound the submergence mediated damage. This exposure to high oxygen concentration and high light intensity results in elevation of oxidative stress through a surge in the production of reactive oxygen species. This post-submergence ROS burst causes damage to the photosynthetic apparatus, membranes, DNA and PSII, thereby causing leaf senescence and cell death.

Flooding tolerance: Although majority of plants are sensitive to water logging and submergence, there are many plants which have adaptations to survive water logging or submergence. These plants are either having constitutive adaptations or they can develop these features once they are flooded. There is an array of biochemical, molecular, morphological and anatomical adaptations which lend tolerance to flood tolerant species. It is the outcome of these adaptations that there are plant species which grow and can occupy wetlands. These adaptations include formation of aerenchyma, avoidance of oxygen deficiency, anoxia tolerance, pressurized gas transport from shoot to root, ability to inhibit or reduce oxidative damage during re-aeration, formation of adventitious roots, etc. In plants like rice, submergence is avoided by elongation of stem, leaves and internodes, and this elongation is mediated by hormones such as ethylene and Gibberellic acid. This is commonly referred to as escape strategy for submergence tolerance. The other strategy is called as quiescent strategy where in a submerged plant species is able to tolerate submergence by cutting down energy consumptions, saving energy and remaining quiescent under water (Bailey-Serres and Voesenek 2008). The formation of leaf gas films is yet another important feature that attracts attention owing to its marked role in submergence tolerance in rice (Colmer and Voesenek 2009). The gas films help improve gaseous exchange between submerged shoots and the surrounding water by widening the water–gas interface around the leaves. This way both photosynthesis and internal aeration of roots are maintained. If these gas films are disturbed or removed, both photosynthesis and internal aeration of roots are compromised (Pedersen et al. 2009).

Flooding which includes water logging and submergence is the abiotic stress that is also known to affect species distribution and composition in many plant communities globally (Jackson and Colmer 2005). Species with adaptations for such stresses thrive well in wetlands and flood-prone areas worldwide.

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