



Waterlogging: An emerging threat for minor millet cultivation

Kumari Anjani^{*1}

¹Department of Agricultural
Biotechnology and Molecular
Biology
College of Basic Sciences and
Humanities
Dr. Rajendra Prasad Central
Agricultural University, Pusa



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INTRODUCTION

According to the records of the World Bank 2022, by June 2022, there were 345 million individuals in 82 nations who were experiencing acute food insecurity as compared to 135 million in 2019. This increase was caused by the conflict in the Ukraine, supply chain problems, ongoing economic effects of the COVID-19 pandemic and largely due to adverse effects of the climate change. The increasing frequency of bad weather events presents a persistent threat to agriculture worldwide. Since, the distribution of rainfall has been uneven and unexpected, conditions like droughts and floods are arising more often. Because of this, agriculture is facing ongoing difficulties worldwide (Food and Agricultural Organization of the United Nations [FAO], 2017). In Sub-Saharan Africa, South Asia, and Southeast Asia, where agricultural families are extremely poor and vulnerable, roughly 80% of the world's population is most at danger from crop failures and famine brought on by climate change (World Bank, 2022). The situation in India is more alarming, since it has 17.7% of the world's population but only 2.4% of the global land. India's rain-fed agricultural systems further pose a problem for food and nutrition security. The most limiting factor which is greatly impacting agricultural productivity in recent years is waterlogging caused by untimely floods. Due to global climate change, the distribution of rainfall across the country has become highly unpredictable and uneven. Unpredictable rainfall has led to an increase in flood events. In recent years, two or even three floods a year have been observed (Bailey-Serres et al., 2012; Hirabayashi et al., 2013). Agricultural field flooding is typically brought on by heavy rains that fall continuously, but it can also happen when a body of water overflows onto the land. The situation is more troublesome for crops like small/minor millets, which have limited area under production and shallow root systems. Small or minor millets are excellent climate-resilient crops as they can adapt to wide range of ecological conditions, require less nutrient input, less irrigation, have better growth and less dependence on inorganic fertilizers and minimum vulnerability to various stresses (Shankar and Anjani, 2023).

The minor millets require only 12-14 weeks for completing their life-cycle which assists them to escape from stress whereas most cereals require 20-24 weeks. Several stress tolerant traits like small leaf area, short stature, thickened cell wall and deep root system, help them to mitigate prevailing stress conditions. The C₄ photosynthetic behavior of the minor millets made them to adapt any adverse environment (Kumar et al., 2023). These made small millets as a “climate smart” and a good source for genetic traits that can strengthen the crop improvement program towards the adaptation to changing environment (Bandyopadhyay *et al.*, 2017). However, millets especially minor millets are believed to be adapted to drought conditions and are unable to survive under waterlogged conditions. Due to the recent events of erratic rainfall patterns, new problems like waterlogging are thus limiting the production of these millets, which are grown in small patches in the country. Since the growing season of minor millets coincides with the monsoon in India, the untimely rain and floods can expose the plant to waterlogging stress. Waterlogging can also be problem in cultivation of the crop in the lowlands where water stagnation may occur. It is also the main cause of low productivity in regions of high precipitation (Numan *et al.*, 2021). Due to uneven and untimely flooding event, the crop can be exposed to waterlogging during any stage of growth like early seedling stage, vegetative stage, flowering stage or maturity stage. Waterlogging before and after heading particularly affects the grain yield of millet (Matsuura *et al.*, 2016).

MECHANISM OF STRESS DUE TO WATERLOGGING

The flooding causes two types of conditions for plant: waterlogging and submergence. Flooding can be defined as waterlogging or submergence depending on the height of the water column that is formed. Waterlogging occurs when the water merely covers the roots and is superficial while submergence occurs when the entire plant is under water (Sasidharan et al., 2013). Water logging and submergence stress are two common environmental challenges that plants face in their natural habitats which to a large extent leads to crop failure. Both are two significant abiotic stresses that can have detrimental effects on plant growth and development. Water logging leads to the lack of oxygen and the accumulation of toxic compounds in the root zone. On the other hand,

submergence stress deprives the plants of access to oxygen and light. Both types of flooding prevent the plant tissue from receiving oxygen from the air (Lee et al., 2011) giving rise to a condition known as hypoxia which occurs when the oxygen level in the plant goes below 21% (Sasidharan et al., 2013). These stresses can have a significant impact on plant growth and development, including reductions in photosynthesis, root respiration, and nutrient uptake. The waterlogging causes stress due to filling of soil pores with water which leads to the inhibition of gas diffusion and induce anaerobic conditions. The resultant hypoxia (reduced oxygen level) or anoxia (complete absence of oxygen) affects roots, stomatal conductance, and photosynthesis (Numan et al., 2021).

EFFECT OF WATERLOGGING ON PLANTS RESPONSE

The plants exhibit various morphological, transcriptional and metabolic changes to withstand this condition (Bailey-Serres and Colmer, 2014). Induction of anaerobic respiration and nicotinamide adenine dinucleotide (NAD) regeneration to replenish lack of ATP are the first responses of the plant to cope up with low oxygen levels. Additionally, the plants develop spongy tissues called aerenchyma and adventitious root to promote gas diffusion (Colmer and Voesenek, 2009). To offset the negative effects of ROS, endogenous antioxidant enzymes and nonenzymatic compounds are also up-regulated. (Apel and Hirt, 2004; Numan et al., 2021). Some plants show abundance of solubilized sugar, while other show increased nitrogen reductase activity. Some plants show fast growth to escape the stress.

Anaerobic pathway activation: One of the primary responses of plants to water logging and submergence stress is the induction of anaerobic respiration pathways, which allows them to produce energy in the absence of oxygen. A study conducted by Bailey-Serres et al. (2012) investigated the role of alternative respiration pathways in flood-tolerant rice varieties. The researchers found that these varieties had higher levels of alternative respiration enzymes, which helped them to maintain cellular energy levels and survive under water logging conditions. This process involves the conversion of pyruvate to ethanol or lactate, which helps to maintain cellular energy levels.

Changes in Root Structure: The roots are the tissues which are most affected by waterlogging

conditions. Thus, roots undergo morphological changes to cope up with these conditions. The formation of adventitious roots and aerenchyma can be observed in many plant species as a means of improving oxygen transport to the roots under anaerobic conditions (Colmer and Voesenek, 2009). Aerenchyma is useful for improving the diffusion of internal oxygen to the roots from the aerial parts of the plant in order to keep up the aerobic respiration (Armstrong, 1980). Generally, lysigenous aerenchyma are formed due to the selective death of root's cortical cells followed by their disintegration during waterlogged conditions. Additionally, schizogenous aerenchyma may be formed by separation of cell without causing their death. In many plants secondary aerenchyma formation takes place from the phellogen leading to the formation of air-filled sponge-like tissue on the surface of hypocotyl and roots (Fukao et al., 2006).

Activation of ethylene pathway: Ethylene is a plant hormone that regulates several processes, including seed germination, fruit ripening, and responses to environmental stresses. During waterlogging conditions ethylene biosynthesis and signaling pathways are activated which helps the plant to adapt to hypoxia/anoxia conditions. In water logging and submergence stress, ethylene helps to promote the formation of adventitious roots and aerenchyma. Additionally, in a study by Shiono et al. (2017), it was demonstrated that ethylene also helps to regulate plant responses to submergence stress by promoting the expression of genes involved in the formation of aerenchyma and underwater photosynthesis. The induction of ERF-VII group by hypoxia is observed in many plants. These factors are responsible for the elongation of adventitious roots. Ethylene also induces the expression of genes involved in the synthesis of antioxidant enzymes, which helps to reduce oxidative damage caused by the stress.

Activation of antioxidant defense mechanism and other physiological changes: The plants activate antioxidant defenses and osmoprotective mechanisms to reduce the harmful effects of oxidative stress and maintain cellular water balance under waterlogging and submergence stress. An upregulation in the activity of antioxidant enzymes and nonenzymatic molecules is generally observed to counteract the adverse effects of ROS (Apel and Hirt, 2004; Numan et al., 2021). Some plants show

abundance of solubilized sugar, while others show increased nitrogen reductase activity. In wheat, it is observed that waterlogging tolerance mechanism is manifested by increase in the activity of glycolytic and fermentative enzymes to increase levels of sugars to counteract post stress oxidative damages (Hossain et al., 2011). Other parameters like chlorophyll content, peroxidase activity, hormonal balance etc. are also affected by waterlogging (Turhadi et al., 2020; Adegoye et al., 2023).

EFFECT OF WATERLOGGING ON MINOR MILLETS

The minor millets which include foxtail, little, finger, barnyard, kodo and proso millet; are plants with shallow root systems and mostly grown as Kharif crop in India, which coincides with monsoon season. The uneven rainfall throughout the season leads to water stagnation in the fields, causing serious problems of waterlogging for the crops. Thus, they cannot thrive well in waterlogged conditions. The waterlogging at early seedling stage is particularly detrimental for the performance of the millets (Anjani et al., 2022). The crops like little millet and foxtail millet cannot survive waterlogged conditions at germination and early seedling stage (Kumar, 2021). It is observed that the waterlogging conditions for more than 3 days at seedling stage significantly reduced the performance of the foxtail millet genotypes. At seedling establishment stage, even a stress for 12 h affects the growth of the plant (Borah, 2023). The waterlogging stress in millets triggers anaerobic metabolism in roots; lysigenous aerenchyma formation; decrease in content of starch and total soluble sugar; increase in pyruvate kinase activity; enhanced alkaline pyrophosphate; decrease in alpha amylase activity besides other adaptations (Kulkarni and Chavan, 2013; Numan et al., 2021). The minor millets thus show a combination of different stress tolerance mechanisms to cope up with waterlogging stress. Furthermore, the waterlogging stress at pre and post heading stages of four millets i.e., *Panicum miliaceum*, *P. sumatrense*, *Setaria glauca* and *S. italica* was found to decrease the grain yield of the plants. Since, the area under minor millet is very less in India, even a minor decrease in yield is thus aggravated. Thus, waterlogging is emerging as a major stress for the minor millet crops.

In conclusion, water logging stress is an important environmental challenge that plants

face, and their responses involve a complex interplay of physiological and molecular mechanisms. Understanding these mechanisms can help to develop strategies to improve plant growth and productivity under adverse environmental conditions. The minor millets are especially vulnerable to this stress. The waterlogging is thus becoming a limiting factor in large scale adaptation of the minor millet cultivation throughout the country.

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