Surviving the Flood: Pigeon Pea's resilience under Waterlogging

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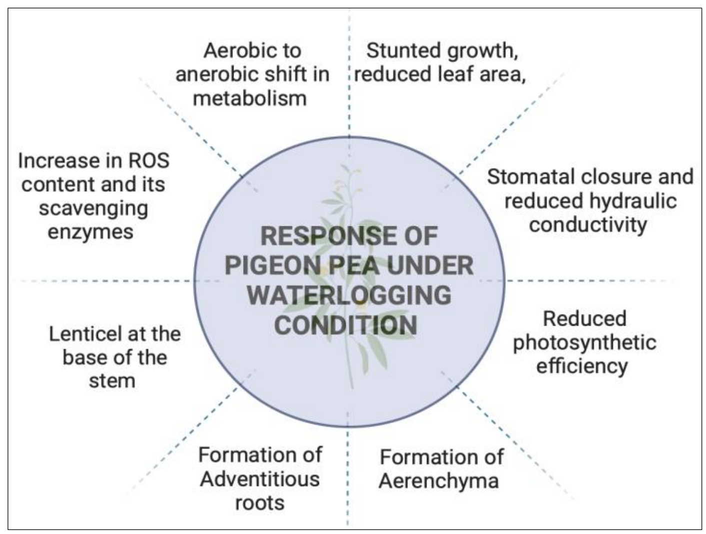
Introduction

Pigeon pea (*Cajanus cajan* L. Millsp.), a sixth most important legume cultivated worldwide is more than just a staple in tropical and subtropical agriculture. As a rainfed crop, it is cultivated on approximately 6.08 million hectares globally, producing 5.32 million metric tons annually (FAOSTAT, 2023). In India, pigeon pea has been grown mainly in areas of deep vertisols with a maximum annual rainfall of 600-1500 mm during monsoon season (Choudhary et al. 2011). Despite its versatility under various climatic conditions, pigeon pea is highly susceptible to waterlogging, which has become a major constraint in recent years due to climate change. Globally, approximately 10% of total arable land is affected by waterlogging, resulting in crop yield losses of nearly 40–80% (Shabala et al., 2014). In India, the annual loss of pigeon pea due to waterlogging is estimated to be about 0.28–1.1 million tons per hectare which reduces production by 25%–30% (Sultana, 2010). Despite waterlogging being a significant yield constraint in pigeon pea, only few focused studies have been done to understand the response of this crop under waterlogging situation which is imperative to develop a climate resilient crop.

Events triggered in the soil due to waterlogging

Waterlogging refers to a condition in which the soil is saturated with water at levels at least 20% higher than its field capacity. It can also occur due to many other reasons including geography, soil type, perched or raised water table, faulty irrigation and poor drainage. Excess water primarily affects soil gas exchange because oxygen diffusivity is 10^4 times slower in water than in air (Parent, 2008), ultimately reducing oxygen availability. This reduction is further exacerbated by increased microbial activity and CO_2 accumulation in the soil, leading to toxic effects. This reduction leads to hypoxic conditions (low oxygen levels) initially, which can progress to anoxic conditions (complete lack of oxygen) over time, disrupting the homeostasis in both soil and plant. In the soil, this shift causes a transition from aerobic to anaerobic microflora, along with the accumulation of toxic compound, leaching and reduced nutrient availability. Several chemical changes occur in soil under waterlogged conditions, including a decline in soil redox potential (Eh), which serves as an indicator of O_2 levels and soil nutrient availability. Soil pH, another crucial chemical characteristic, is severely affected under waterlogging, often increasing towards neutrality. This shift impacts processes such as mineralization, nitrification, and urea hydrolysis (Probert and Keating, 2000). The anaerobic shift in soil environment also leads to accumulation of by-products of fermentative metabolism, methane and volatile fatty acids.

Altered metabolisms of pigeon pea under waterlogging



When a plant is exposed to waterlogged conditions, its initial response is a decline in energy production due to the inhibition of mitochondrial respiration in roots. To adapt to the prevailing conditions, the plant switches to an alternative fermentative pathway for ATP production, yielding only 2 ATP molecules compared to the 36 produced during aerobic respiration. In order to elevate the ATP production glycolysis process is found to be accelerated which is evident by the fact of increased ANPs (Anaerobiosis induced proteins) expression. In pigeon pea, studies have shown that tolerant genotypes express ANPs such as sucrose synthase and alcohol dehydrogenase to enhance ATP production via glycolysis (Kumutha et al., 2008). Since fermentative pathway is a substrate demanding low return pathway, plant based on its resilience alters the carbohydrate metabolism which is evident by changes in amount of total, reducing and non-reducing sugar contents.

Morpho-physiological changes

One of the primary responses of pigeon pea to waterlogging is stomatal closure, which becomes negligible under prolonged exposure. This is accompanied by reduced hydraulic conductance due to decreased root permeability. This reduced hydraulic conductance in turn create the water deficit. Other physiological parameters such as transpiration rate and intercellular CO_2 concentration also found to be reduced under given situation which can be due to stomatal closure. In case of photosynthetic rate, waterlogging condition reduces the rate attributed by stomatal as well as non-stomatal components (Bansal and Srivastava 2015). This may lead to reduced metabolic activity and impaired translocation of assimilates. PS II Quantum yield is a sensitive indicator of photosynthetic yield. It represents the CO_2 assimilation efficiency of a plant which is found to be decreased with increased duration of waterlogging stress duration (Meena et al. 2014). Chlorophyll content, a direct indicator of photosynthetic activity reduced under waterlogging condition as a consequence of reduced soluble protein content influencing carbon assimilation ultimately curbing photosynthesis. Oxygen deficiency also affects pigeon pea morphologically, leading to reduced leaf area, plant height, root length, and root branching.

ROS and its scavenging enzymes

The surge in reactive oxygen species (ROS), triggering oxidative stress, is a significant element of many stress situations, including waterlogging. This occurs as a result of saturated electron components, a highly reduced intracellular environment, and limited energy supply. The effects of ROS formation vary depending on the severity of the stress and the cell's physico-chemical conditions, such as antioxidant levels, redox state, and pH. In pigeon pea several studies have shown that ROS such as superoxide and hydrogen peroxide content increases having detrimental effect on the integrity of the membranes because of lipid peroxidation. Increase in cytoplasmic Ca^{2+} concentration, acidification and change in cell membrane permeability are observed primarily under waterlogged condition (Bansal et al. 2011). This ROS surge acts as a signal not only for synthesis of antioxidant enzymes such as superoxide dismutase, catalase and peroxidase involved on ROS scavenging, but also for alcohol dehydrogenase which involved in regeneration of NAD^+ essential for adenylate energy charge production via glycolysis.

Anatomical and other adaptations

Pigeon pea under hypoxia situation forms hypertrophied lenticels in the forms of cracks in epidermal layers of stem tissue at root-shoot junction (Hingane et al. 2014) as a result of radial cell division and expansion. These cells are believed to promote the movement of oxygen downward and may also assist in expelling compounds generated as byproducts of anaerobic metabolism in the roots. One another adaptations in roots under water saturated situation is the lysigenous aerenchyma formation by partial breakdown of cortical cells, facilitating oxygen supply into the roots and also allows growth of micro-organisms preventing poisonous substances entry. Under waterlogged conditions, the function of the original roots is substituted by adventitious roots near the base of the stem, where lenticels are abundant. All these adaptations confer tolerance to the pigeon pea under waterlogging situation. Plant hormones such as ethylene and auxin are involved in the formation of these adaptations.

Conclusion

Under waterlogged conditions, pigeon pea undergoes several adaptive changes depending on its resilience. These include metabolic adjustments to compensate for reduced adenylate charge production, morphological and physiological changes, enzymatic and non-enzymatic ROS scavenging systems, and anatomical modifications in roots to enhance gas exchange and aeration.

Future Perspectives

Several valuable insights were obtained from the previous work done in pigeon pea under waterlogging situation but there is a pressing need to evaluate a large number of genotypes to identify the tolerant ones as a sustainable measure to adapt to the ever-changing climate conditions. Breeding strategies should be designed to incorporate adaptations conferring tolerance like aerenchyma and adventitious root formation. Deeper understanding into molecular insights of the adaptations is essential to identify the genes responsible for the adaptations and utilizing it to develop resilient cultivars.

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