

REVIEW

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# Breeding for water-logging tolerance in pigeonpea: current status and future prospects

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## Abstract

Pigeonpea is grown in semi-arid tropics where the annual precipitation ranges from 200 to 800 mm and soil orders comprising of Inceptisols, Entisols, Alfisols, Vertisols, Mixed soils, and Aridisols. During monsoons, the semi-arid tropics also receive up to 140–180 mm/day rainfall for a span of 5–10 days, highlighting the chances of waterlogging in an early vegetative stage of pigeonpea, causing 25–30% yield loss in the Indian subcontinent. Waterlogging is a state where soil reaches saturation at submergence, creating an anaerobic condition in the root zone of the plants. As a result, plant withering, leaf chlorosis, stunted growth, lowered photosynthetic rate and plant mortality is evidenced widely. In response to waterlogging, the formation of aerenchyma cells, lenticels and adventitious roots were noticed as morphological adaptations. Whereas, the production of proline, peroxidase, superoxide dismutase, ethylene and alcohol dehydrogenase (ADH) as biochemical modifications. The minimal breeding efforts for waterlogging tolerance in pigeonpea may be the reason for the susceptibility of current varieties to waterlogging stress. This review emphasized the importance of breeding for waterlogging tolerance in pigeonpea. It focused on the morphological, physiological and biochemical adaptations of a plant when subjected to waterlogging stress. It accentuated the need for a standard screening protocol for waterlogging tolerance. Breeding strategies inclusive of novel single pod descent method, marker-assisted selection and rapid generation advancement techniques are discussed in detail.

**Keywords** Breeding, Marker assisted selection, Pigeonpea, Tolerance mechanisms, Waterlogging

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## Introduction

Pigeonpea is one of the important grain legumes, serving as a lifeline for the small and marginal farmers of Asia and Africa. It is mainly cultivated for seeds and consumed as split dal in Asian sub-continent and as whole seed in African nations. It is used as food, feed, fodder, fuel and as a soil ameliorant. This protein-rich pulse crop holds a significant position in the rainfed eco-system covering an area of 6.03 Mha, with the production of about 5.3 MT and productivity of 883 kg/ha globally (Food and Agriculture Organization of United Nations 2023). Pigeonpea is cultivated in more than 25 tropical and sub-tropical countries, both in well drained red loamy soils as well as deep vertisols (Choudhary et al. 2011). This crop is best suited to those areas having moderate rainfall and temperature not below 15 °C. India is the major producer of pigeonpea contributing to 78.8% of global production, covering an area of 5.00 Mha with 4.2 MT production and productivity of 861 kg/ha (Project Coordinator's report, 2023–24). Maharashtra, Karnataka, Madhya Pradesh, Uttar Pradesh and Telangana accounts for 82% of pigeonpea production in the country (Project Coordinator's report, 2023–24). However, pigeonpea grown in deep vertisols in these states are highly prone to waterlogging.

Waterlogging stress occurs during the monsoon season which can last for about five to ten consecutive days. The early-seedling and vegetative stages of pigeonpea (until 40 days after sowing) coincide with waterlogging for a shorter span of 5–10 days. During this period, the plant reaches a state of hypoxia or anoxia in the rhizosphere region. The oxygen supply at anoxia state is nearly 10,000 times lower in the soil than air (Jackson 1985; Crawford and Brändle 1996). The water level subsides from the soil surface in first 5 days, while it takes almost another 3–5 days for the soil to be well aerated. This state of minimal aeration necessitates the plant to rapidly shift its metabolism from aerobic to anaerobic dependency. Consequently, the ATP and NADP production becomes limited, eventually altering the reserve energy (Kumutha et al. 2009). Thus, the fermentation process not only deprives the plant of stored energy but also releases products such as alcohols, aldehydes, and reactive oxygen species (ROS), which are detrimental to plant growth as reported in mungbean (Sairam et al. 2011).

Another reason for plant mortality is the susceptibility for microbial infection triggered by waterlogging in rhizosphere. The rhizosphere region is highly inimical to anaerobic conditions, in-turn supporting microbial community resulting in a severe nutrient imbalance in the plant (Laanbroek 1990; Levitt 1980; Ponnampereuma 1972). It has been reported in maize that a plant faces N, Mg, and Mn deficiency under waterlogged conditions

due to increased denitrification and nitrate leaching from the topsoil (Srivastava et al. 2007). This shift in nutrient balance results in chlorosis, a decrease in leaf area, dry matter, relative water content and degradation of chlorophyll, posing a direct effect on the photosynthetic ability of the plant (Drew and Sisworo 1979; Kumutha et al. 2008). A notable impact on the reduction of seminal root growth and root dry mass due to hypoxic conditions constricting the growth in pigeonpea is also noticed (Chauhan et al. 1997; Dubey and Asthana 1987). The combined effects of these conditions negatively impact the pigeonpea grain yield and quality (Kumutha et al. 2008). These episodes of stagnant water film over the upper soil also promotes the infestation of saprophytic fungi, namely *Phytophthora* species aiding zoospore production, spread and plant mortality (Duncan and Kennedy 1989; Saxena et al. 2018).

The increasing susceptibility to waterlogging in major pigeonpea producing states of India has compelled the urgency of breeding for its tolerance. Earlier breeding efforts mainly focused on identification of genotypes tolerant to waterlogging stress based on morphological modifications and plant mortality (Sultana et al. 2013; Hingane et al. 2015). The screening for tolerant genotypes involved invitro seed wetting, pot and field submergence method. However, no standard protocol was followed for waterlogging stress screening. With the advancement of technology, the breeding strategies have also evolved. The single pod descent method, marker-assisted breeding and rapid generation advancement techniques embedded in breeding pipeline, enhances the selection efficiency. Cost effective screening protocols and breeding pipelines with the faster product delivery is the current lookout of the breeding programs. This review summarizes the cost-effective screening techniques strategized to breed for waterlogging tolerant varieties and hybrids in pigeonpea.

## Current status of pigeonpea to waterlogging tolerance

Waterlogging tolerance has become a priority trait in pigeonpea from past five years in India. Earlier studies gave information on genetic variability for waterlogging tolerance and the traits associated with it. The widespread damage of the waterlogging susceptibility trait required further study on the genetics and mechanisms underlying it.

## Traits specific to water-logging tolerance

Waterlogging tolerance encompasses morphological, biochemical, physiological or a blend of these adaptations when exposed to stress. The plant survival mechanism depends on the plasticity of these adaptations.

### **Morphological features**

The morphology of a plant is the first visible defense line to sustain hypoxia or anoxia situations. The modifications as a response to stress are reported majorly in three areas: aerenchyma, lenticels and adventitious roots. These typical changes aid in maintaining the oxygen diffusion rates in the plant by supplementing the rootzone function. The tolerant genotypes indicated the presence of either of the aspect or in a combination to adapt to the waterlogging stress (Armstrong 1980).

**Aerenchyma Cells:** These are large intercellular gas spaces in the leaves, stem and root tissues spreading from the cortex to medulla or pith appearing as “a disorganized cartwheel” (Jackson and Armstrong 1999). They are of two types, namely primary and secondary aerenchyma. Primary aerenchyma is cortical aerenchyma and is formed in primary tissue, while secondary aerenchyma is formed from phellogen, cambium or pericycle and is a secondary tissue. Based on the process underlying its formation, primary aerenchyma is further distinguished as lysigenous and shizogenous which include cell death and cell separation as the root cause for the gas space formation respectively (Seago et al. 2005; Sou et al. 2021). These spaces provide a barrier for the transport of oxygen from stem to the roots and expel gases such as methane (CH<sub>4</sub>), carbon dioxide (CO<sub>2</sub>), nitrogen (N<sub>2</sub>), and ethylene (C<sub>2</sub>H<sub>2</sub>) thus, enabling the plant to survive the stress better (Colmer 2003). The oxygen transported would also tip-off from the root zone creating an oxygenated atmosphere around the rhizosphere which would abet the aerobic microbes around. These microbes can prevent the influx of toxic soil compounds such as nitrates and sulfates of Fe, Al, Cu, and Mn thus, maintaining plant health (Armstrong and Armstrong 1988).

**Lenticels:** Waterlogging causes an increase in ethylene production in plant tissues resulting in cellulase activity. Cellulase softens the cell walls causing stem hypertrophy (enlargement) at the root-shoot junction and enhances the formation of large cracks referred to as hypertrophic lenticels. These cracks expose aerenchyma to the atmosphere, facilitating oxygen entry into aerenchyma, which enhances oxygen diffusion along the stem (Yang 1980; Tang and Kozlowski 1984; Jackson et al. 2009).

**Adventitious roots:** Adventitious roots are porous roots capable of gas transport, water, and nutrient uptake during flooding and generally formed from the primary root or the stem near the water line (Havens 1996). Generally, adventitious roots emerge upon the death of primary roots due to flooding (Kozlowski 1984). Earlier studies in *Arabidopsis*, tomato, and rice report that flooding conditions induce the formation of adventitious roots (Vidoz et al. 2010; Steffens and Rasmussen 2016). Moreover, ethylene regulates adventitious root

formation by controlling the localization and transcription of several auxin-efflux and influx carriers, notably while regulating the PIN-FORMED (PIN) protein expression pattern in plant (Negi et al. 2010). Pigeonpea has a tap root system, mainly consisting of seminal roots. Under complete or partial submergence, seminal roots completely fail to absorb atmospheric oxygen, at times leading to death. Whereas the tolerant plants exhibit a defense mechanism by producing adventitious roots at a root-shoot junction, just above the submergence layer in pigeonpea, acting as a substitute to the primary roots (Armstrong 1980; Shimamura et al. 2010). They have also been reported to maintain nodule activity in pigeonpea (Matsunaga et al. 1992). These roots help in absorbing atmospheric oxygen/nitrogen enabling the survival of plants until the water drastically reduces and seminal roots start functioning. However, the number of adventitious roots varies from genotype to genotype. Besides these attributes, germination percentage, radicle and plumule growth, seed coat color and seed size have also been noted for imparting tolerance. Considerable variation was observed in the survival percentage in various pigeonpea genotypes (Hingane et al. 2015). The higher survival is related to the seed reserve and ease of imbibition through the seed layers (Kumar et al. 2020). Healthy growth of radicle and plumule naturally permits tolerance in pigeonpea. The darker seed color corroborated with higher tolerance in the genotypes was also tested (Khare et al. 2002). It was substantiated that higher phenolic and tannin compounds in the seed coat decelerated the imbibition rate which in turn enhanced the survival period (Matsunaga et al. 1992). Results from studies depicted that the small size of the seed holds the larger surface area, which facilitates the rapid imbibition through the micropyle compared to the larger seed (Jabrun et al. 1980). Thus, pigmented seed coats and smaller seed sizes are expected to resist waterlogging in pigeonpea (Sultana et al. 2013; Hingane et al. 2015).

### **Biochemical features**

**Reactive Oxygen species (ROS)** Under anoxia, the plant shifts its metabolism to anaerobic conditions enhancing the reactive oxygen species (ROS). These toxic compounds would damage the DNA, RNA, proteins, and lipids in the cells leading to accelerated senescence in the plant (Bansal and Srivastava 2012). As a defense mechanism, the tolerant genotypes of pigeonpea indicated an accumulation of proline, sugars and antioxidant enzymes in the leaves and roots to handle the redox potential differences. The results justified enhanced sugar content is the product of accelerated hydrolysis of starch (Duhan et al. 2017). The increase in antioxidants such as peroxidase, catalase and superoxide dismutase conferred

to their scavenging activity in the plant (Srivastava et al. 2007; Vinodh Kumar et al. 2023). They tend to protect the plant from oxidative damage and maintain membrane stability.

**Plant hormone signaling** In pigeonpea, ethylene regulates plant growth or senescence under submergence. The presence of ethylene also exhibited a significant effect in anoxia conditions (Jackson 1985). ACC (1-amino cyclopropane 1-carboxylic acid) is the immediate precursor to the ethylene synthesis which accumulates to a larger extent at the root tips under anaerobic conditions. The entire progress of ethylene synthesis needs obligatory oxygen in the last step of conversion from ACC to ethylene. Thus, the anoxic situation creates a higher imbalance of ACC: ethylene forming an upward flux of ACC to the oxygenated zone of plants (Bradford and Yang 1980; Cohen and Kende 1987). It is well-recognized that the generation of ethylene is a key factor in the stimulation of genes related to the fermentation pathway, glycolysis, and aerenchyma formation (Hingane et al. 2015; Mergemann and Sauter 2000).

#### **Physiological features**

Notable physiological reactions in pigeonpea upon waterlogging are the altered redox potential, decreased photosynthetic capacity, chlorophyll development, nutrient and water uptake (Bansal and Srivastava 2015; Meena et al. 2015).

The oxygen-deprived situations tend to disrupt energy production as oxygen serves as the terminal electron acceptor in the mitochondrial electron transport. This situation blocks the NADH production bringing up the adenylate complex (ADP/ATP) to be the aid for the plant's survival. Thus, the needed supplementation of ATP occurs through the alternative glycolysis and fermentation processes. These processes are certainly ineffective compared to mitochondrial respiration (Johnson et al. 1989; Tsai et al. 1997; Pradet and Bomsel 1978). The gap created in the available reserve, leads to breakdown of the chlorophyll components in the plant. Thus, high chlorophyll content is correlated with waterlogging tolerance (Kumutha et al. 2008). The reports suggested delayed senescence in pigeonpea is associated with better nutrient mobilization under anoxia conditions (Kumar et al. 2020).

The anaerobic respiration forms ethanol, lactic acid, and carbon dioxide as the by-products to recycle the nicotine amide adenine dinucleotide (NADH) which eventually becomes hazardous to a plant. Furthermore, the hypoxia situations enhance the reactive oxygen species such as superoxide dismutase and hydrogen peroxide leading to lipid peroxidation in the plant. The plant enhances the production of alcohol dehydrogenase

(ADH) for recycling the nicotine amide adenine dinucleotide (NADH) to maintain the carbohydrate reserve. Thus, the spiked ADH activity is reflected in the tolerance for waterlogging stress in the pigeonpea genotypes (Kumutha et al. 2008; Kumar et al. 2020).

#### **Screening protocols for waterlogging tolerance**

The precise assessment of the waterlogging tolerance mechanism and related traits can be achieved through the development of a screening protocol. The plants' ability to tolerate prolonged waterlogged periods could be tested in the laboratory, glasshouse as well as field conditions.

Accordingly, a study with a diverse panel of accessions (272) was subjected to screening. The seeds of 272 accessions, were soaked in water for 120, 144, 168 and 192 h assessing for its survival. The tolerant genotypes under seed submergence method were advanced to pot submergence for further screening. The pots were subjected to stress for 11 days and survivability was assessed 8 days after ceasing the stress. The selected accessions were forwarded to field submergence resulting in the identification of waterlogging tolerant genotypes. The deep vertisols with no drainage facilities was selected as a site for field screening under natural conditions. The earlier followed screening protocols were purely based on plant mortality. However, very limited study on morphological, physiological, and biochemical modification of a plant while enduring the stress is discussed. Thus, there is a dire need for a standardized and validated protocol to screen for the stress (Sultana et al. 2013).

The field screening technique would be challenging to achieve uniform stress spatially and temporally. Therefore, to maintain the practicality of the objective, initially laboratory and glass house screenings are to be preferred over the *in vivo* experiments. The selected lines could be further assessed in artificial ponds and hotspots as a real-time analysis for confirmation at a large scale. The efficiency of screening would be based on the indicators selected for evaluation. As mentioned, the prime attribute to be targeted is plant survival and recovery in the early stages of plant growth due to its high waterlogging vulnerability. The second line of characters to be considered are morphological, physiological, and biochemical traits. Finally, yield forms the most important trait to couple along with stress tolerance in selecting the best genotype.

#### **Conventional breeding**

A considerable amount of variation has been documented for tolerance and exploiting the available diversity is one of the established ways to withstand losses (Krishnamurthy et al. 2012). Numerous donors

contributing the morpho-physiological traits for tolerance have been well documented in pigeonpea (Table 1). They could be directly released as varieties or added in the breeding programs as a donors to impart the genes. Crosses made using the tolerant lines into the elite background would be successful through backcrossing as the genetic studies revealed the effect of a single dominant gene controlling the trait (Sarode et al. 2007). Another attempt recorded a partial dominance of susceptibility over waterlogging tolerance. In this aspect, their work on lenticel formation, plant height and adventitious root development showed to be controlled by additive and dominance effects (Perera et al. 2001).

Pigeonpea is the only pulse where hybrid technology has been developed. There has been an interesting effort to identify the waterlogging tolerant hybrid parents which hold the highest possibility of developing tolerant hybrids. Sterile, maintainer and restorer lines were identified in early, medium, and long duration groups providing an opportunity for variable crosses (Saxena et al. 2015). Earlier reports recorded a higher resistance in hybrids even after a prolonged waterlogging due to the greater biomass of hybrid seed which in-turn derailed the oxygen deprivation rate (Sultana et al. 2013).

Pigeonpea has a vast diversity pertaining to the maturity durations. In the recent past, there has been a shift of interest and expertise into developing extra early and early lines to widen its horizons. But comparatively extra early and early lines would suffer higher losses under waterlogging stress over medium and long duration genotypes due to their narrow recovery period (Matsunaga

et al. 1992). Thus, the efforts to screen and identify the tolerance mechanism in extra early and early maturing lines including hybrid parents is underway.

### Pre-breeding

Pre-breeding provides an opportunity to broaden the genetic base by adding novel genes from crop wild relatives. It aims to identify and characterize the tolerant genotype to introgress from the wild to the cultivated gene pool (Sharma 2017). Few successful attempts identified *C.sericeus*, *C.lineatus* from the secondary gene pool and *C.crassus* from the tertiary gene pool holding the potential for waterlogging tolerance (Khoury et al. 2015). Studies involving interspecific derivatives of *C.acutifolius* also displayed tolerance and verified it to be due to the development of aerenchyma in the root tissue (Hingane et al. 2015).

### Breeding strategies for developing waterlogging tolerant genotypes

The enhanced threat of waterlogging is driving the needed impetus to find operational solutions. Numerous agronomic management suggestions such as change in irrigation potentials, broad bed and furrow, ridge and furrow and seedling transplantation based on farm type and soil conditions are recommended (Meena et al. 2014; Abebe et al. 1992). However, these interventions would merely act as a cushion but cannot provide the expected laser-focused remedies dealing with the submerged conditions. Knowledge of the traits and genes governing tolerance is thus, essential for a breeder to set the course for

**Table 1** List of traits conferring waterlogging tolerance in specific pigeonpea genotypes

Trait conferring tolerance	Lines/hybrids	References
Aerenchyma development	ICPH 2431, PARAS, ICP 5028, ICPL 87119, ICPH 2740, ICPL 149 and ICPL 20241	Kumutha et al. (2009), Duhan et al. (2017)
Lenticels	ICP 5028, ICPH 2431, ICPL 87119 (Asha), ICPH 2740, ICPL 84023, and MAL 15	Sarode et al. (2007)
Adventitious roots	ICPH 2431, ICPL 87119, ICPH 2740, ICPL 149, and ICPL 20241	Hingane et al. (2015)
Higher chlorophyll content	KPBR 80-2-1 and ICPL 84023	Bansal and Srivastava (2012), Meena et al. (2014)
Increased antioxidant enzymes	ICP 301	Kumutha et al. (2009)
Increased root length	ICPB 2039	Meena et al. (2014)
Dark seed colour and Increased survival	ICP 5028, ICPH 2431, ICPH 2671, ICPH 2740 ICPH 4187, Asha (ICPL 87119), LRG 30, Maruti (ICP 8863), MAL 9, MAL 15, ICPL 332, ICPL 20092, ICPL 20117, ICPL 20125, ICPL 20128, ICPL 20237, ICPL 20238 and ICPL 99050	Sultana et al. (2013)
Decreased mortality	ICP 8743 and ICP 13562	Chauhan et al. (1997)
Seedling length	ICP 4903, ICP 7148, ICP 7869, ICP 7507 and ICP 10397	Basavaraj et al. (2024)
High PS-II efficiency under waterlogging stress	ICP 10397, ICP 7375, ICP 10228, ICP 7869, ICP 4903, ICP 6370, ICP 7148, ICP 8255, ICP 6845, and ICP 7426	Basavaraj et al. (2024)
High waterlogging tolerance coefficient	ICP 10397, ICP 7507, ICP 7869, ICP 7148, ICP 4903, ICP 16309, ICP 7375, ICP 6815, ICP 7507 and ICP 6128	Basavaraj et al. (2024)

improvement. The major intricacy here is due to several biochemical, physiological, and molecular factors influencing stress tolerance and the lack of precise screening techniques. Thus, programs should be devised to unravel the underlying behavior of the tolerance mechanisms. The complete cycle of breeding for waterlogging screening is elaborated under the following subheadings.

**Standardizing the screening protocol**

The protocol for waterlogging screening is unclear and varies from publication to publication. Aiming the avoidance of ambiguity in trait specificity as response to stress tolerance, Pigeonpea breeding at ICRISAT had initiated standardizing the screening protocol with well-defined trait association. Five leaf stage (7–10 DAS) and knee height stage (4045 DAS) of plants are more prone to waterlogging and the survival rate is found from less to nil. Henceforth, an early-stage screening protocol has been set up at ICRISAT under glasshouse conditions. A glass house capacity of housing 5000 plants at a time when sown in 4-inch plot was turned into a make-shift screening facility. The pots placed in a tray of size 246 cm×117 cm×5 cm (L×B×W) formed a perfect screening platform. Subjecting both the five leaf as well as knee height stage for fully submergence and partial submergence for complete four days, plant survival was examined. An excellent result of tolerant plants’ survival with the formation of adventitious roots and aerenchyma cells was clearly observed, while leaf chlorosis, leaf senescence, plant drooping and mortality were noted in susceptible plants. Therefore, the five-leaf stage of plant

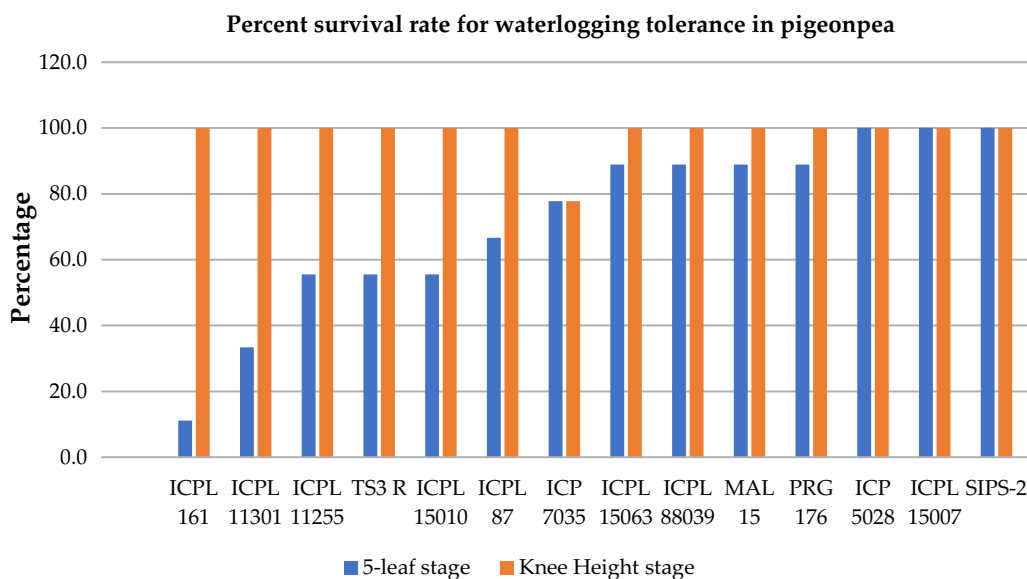
growth was found to be the most susceptible stage (Fig. 1 and Supplementary Table 1). The presence of adventitious roots, aerenchyma cells, leaf chlorosis, and senescence were confirmed to be the traits associated with waterlogging tolerance in pigeonpea. The glass house-based screening is efficient in screening large set of genotypes in one lot and identifying tolerant genotypes in a short span of time (Fig. 2).

The next line of work will be screening the wild germplasm along with breeding stocks claimed to be waterlogging tolerant collected across the globe. ICRISAT gene bank houses 13,632 germplasm collection with a core collection of 1290 germplasm and 146 germplasm in mini-core collection. Earlier studies identified tolerant accessions from the germplasm (Kumutha et al. 2008). However, no clarity exists on the underlying mechanism. Screening of wild lines along with currently available breeding stocks and landraces will give the best donors for waterlogging tolerance.

**Breeding for waterlogging tolerance**

The breeding pipeline has evolved from time to time and is modernized as per the technology update. Conventional breeding though being the core is well supported by genomic selections, rapid generation advancement by deploying single pod descent method leading to efficient selection and genetic gains. Donor identification followed by deployment in breeding after an extensive field screening is a traditional method.

However, the availability of quality control (QC) markers has improved the selection efficiency. Since



**Fig. 1** Percent survival rate for waterlogging tolerance in pigeonpea



**Fig. 2** Early-stage waterlogging screening facility at ICRISAT. **A** Partial Submergence facility; **B** Complete submergence facility; **C** Aerenchyma in tolerant lines; **D** Susceptible plant at Knee height stage; **E** Tolerant plant at Knee height stage

waterlogging is a serious threat evidenced of-late, no trait-specific markers pertaining to it are identified till date. Due to its widespread, efforts have been taken to identify markers. Fortunately, the whole genome resequencing data and reference genome availability in pigeonpea are an added advantage for developing markers specifically for waterlogging tolerance (Varshney et al. 2012). Earlier screening of pigeonpea lines have identified few donors for waterlogging stress and are successfully deployed in crossing well confirmed using QC markers, to identify the true  $F_1$ s. The developed mapping population is advanced to  $F_2$  and then  $F_2:F_3$  using single pod descent as well as rapid generation advancement techniques. At  $F_2:F_3$  both susceptible and resistant pool of lines will be identified through the glasshouse-based screening. Further, the development of linkage maps and markers associated with waterlogging is the next course of action anticipated.

#### Way forward

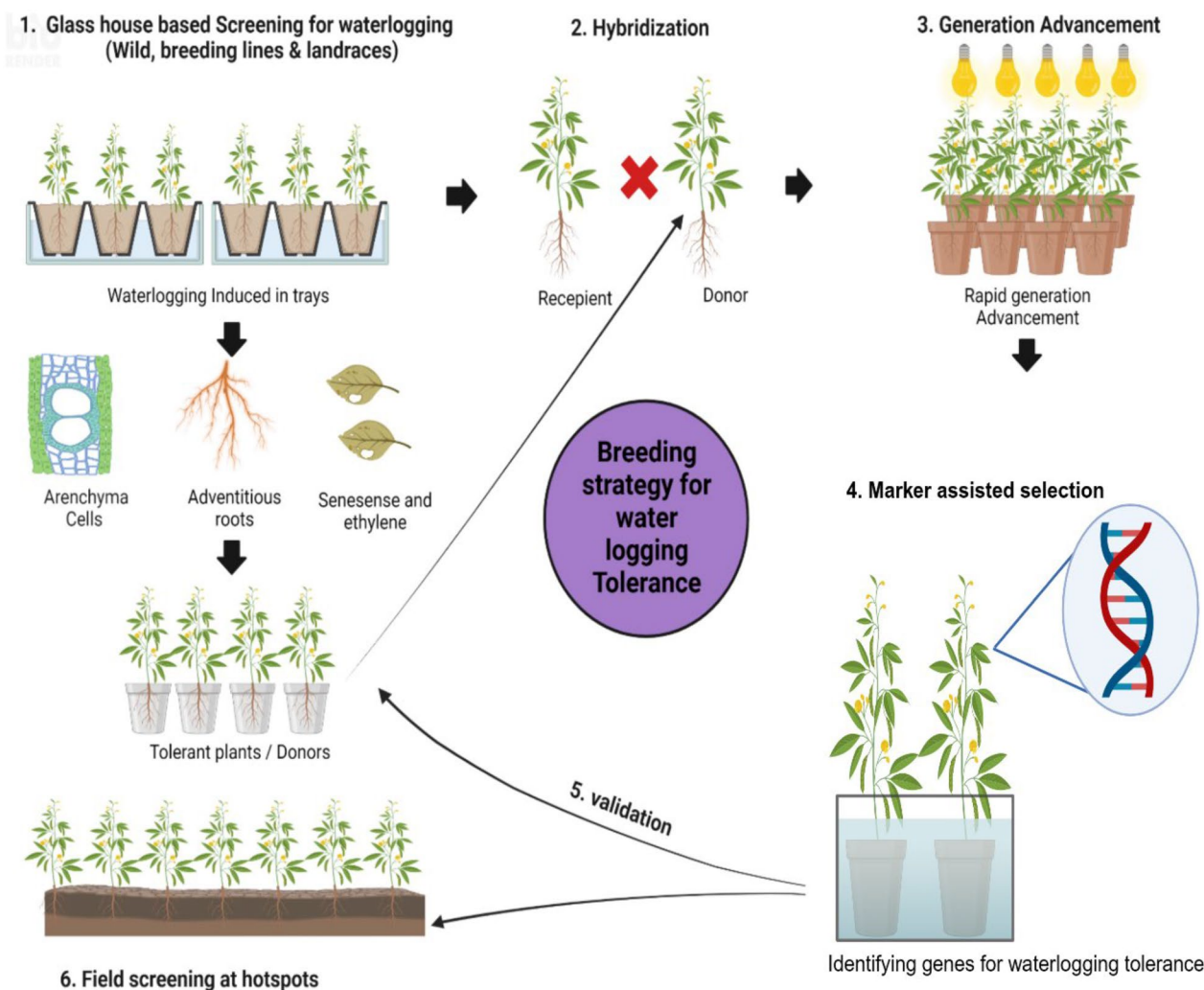
The markers developed for waterlogging tolerance will be a part of a mid-density array and could be used for early-generation screening. The mid-density array of pigeonpea consists of 2000 SNPs distributed over 11

chromosomes, inclusive of QC markers and trait specific markers for fusarium wilt, sterility mosaic disease (SMD), hybrid purity and fertility restoration. This mid-density panel will be a powerful tool for waterlogging screening in pigeonpea. Thoughtful use of whole genome resequencing data with phenotyping of training population will help in genomic selections in pigeonpea. However, the efficiency of genomic selection depends upon population size, trait heritability and marker efficiency (Fig. 3).

CRISPR Cas based genome editing technique is seen as other alternative for developing waterlogging tolerance (Tong et al. 2021). The integration of CRISPR Cas based genome editing is assumed to modify the targeted sequences, such as loss-of-function/ gain-of-function or altering the expression. This system can be deployed for improvement in pigeonpea only after the functional characterization of waterlogging genes.

Rapid generation advancement/ speed breeding is a powerful technology fastening the generation advancement in pigeonpea. This technique could be integrated into breeding pipeline for developing waterlogging tolerant cultivars.

Once the markers associated with waterlogging are identified, the training population will be validated



**Fig. 3** Breeding strategy for waterlogging tolerance in pigeonpea

through glasshouse-based screening confirming the introgression of tolerant genes. This measures the marker efficiency and trait heritability in the population. Completion of glass house-based screening leads to field screening at hotspots to authenticate the waterlogging tolerance. Field screening is a crucial step in verifying our findings. The genotype performing exceptional for yield and its attributes under submergence (8–10 days) will be proceeded for multi-environmental testing and released as a waterlogging tolerant variety of pigeonpea.

**Conclusion**

Waterlogging is a trait of concern in pigeonpea cultivated in deep vertisols of Indian subcontinent. With the widespread yield losses reported, there is an urgent need to develop tolerant genetic material. The

standard protocol for waterlogging screening, and the traits specific for tolerance have been documented in this review. The breeding strategy inclusive of precise screening, marker assisted selection and rapid generation advancement are key to develop waterlogging tolerant varieties. However, emphasis on the identification of genes imparting tolerance and QTLs associated with waterlogging is critical at this point of time. Genomic selection and gene-editing are further needed to be employed to incorporate waterlogging tolerance. Wild relatives being the reservoir of resistance traits, must be thoroughly studied and characterized for identifying new sources of resistance. The identified donors should be gradually deployed in breeding tolerant cultivars of pigeonpea.



## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s43170-024-00299-y>.

Supplementary material 1.

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### Author contributions

SHB: Conceptualizing, drafting, and editing. NB: Provided data on GH based screening. JP: Conceptualizing, drafting, and editing. CDS: Editing. AJH: Contributed on earlier screening techniques and findings. BPS: Drafting and reviewing. SN: Editing. LHC: Editing. MS: Editing. HM: Editing. SCV: Editing. PIG: Conceptualizing and Editing.

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### Consent for publication

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### Competing interests

The authors declare that they have no competing interests.

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