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REVIEW ARTICLE

Advancements in breeding for waterlogging tolerance in sesame: Challenges and strategies

C Parameswari[1], Madhan Mohan M[1], M Jayaramachandran[2], M P Kavitha[1], G Sudhakar[1*], P Geetharani[1], & R Amutha[3]

[1]Agricultural Research Station, Tamil Nadu Agricultural University, Vaigai Dam 625 562, Tamil Nadu, India

[2]Department of Plant Breeding and Genetics, Agricultural College and Research Institute, Tamil Nadu Agricultural University, Chettinad 630 103, Tamil Nadu, India

[3]Department of Crop Physiology, Agricultural College and Research Institute, Tamil Nadu Agricultural University, Madurai 625 104, Tamil Nadu, India

*Correspondence email - sudhkargagron@gmail.com

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Abstract

Sesame, the queen of oilseed crops, exhibits drought tolerance and has evolved to thrive in dry tracts. It is susceptible to waterlogging; even two to three days of waterlogging results in a sharp decline in yield. Evolving waterlogging-tolerant sesame varieties is the most cost-effective approach to sustain sesame production under changing climatic conditions. Breeding for waterlogging tolerance in sesame is gaining momentum due to its significant impact on crop yield and quality. Recent studies have identified genotypes with varying tolerance levels, highlighting the importance of genetic diversity and selection methods. In conventional breeding, the selection of waterlogging-tolerant genotypes is an important step. No standard screening procedures are available to identify waterlogging-tolerant genotypes in sesame. High throughput screening techniques that combine fully automated robotic systems for imaging and data processing are required for in-depth research. Though appreciable improvement has been made in genomics and candidate genes / QTLs identified for waterlogging tolerance in sesame, integration of traditional breeding with molecular techniques is lacking. A multidisciplinary approach is required to develop waterlogging-tolerant sesame varieties. In this mini-review, an attempt has been made to document the physiological, morphological and biochemical response of sesame to waterlogging and the challenges of screening and breeding sesame cultivars that are tolerant to waterlogging.

Keywords : breeding; climate change; sesame; waterlogging

Introduction

Sesame (*Sesamum indicum* L.), popularly referred to as the "Queen of oilseed crops," is one of the ancient oilseed crops. Sesame seeds contain higher oil content in the range of 48 to 55 % than other oilseeds like soybean (~20 %), groundnut (~45 %), sunflower (~40 %) and rapeseed (~40 %). Sesame oil contains up to 80 % polyunsaturated fatty acids, mainly oleic and linoleic acid(1, 2), palmitic and stearic acid, with trace amounts of linolenic acid (3). Due to its higher content of unsaturated fatty acids, its consumption is linked to various health benefits, including anticancer, antihypertensive, anti-ageing and cholesterol-lowering properties. Sesame seeds are rich in phosphorous, iron, magnesium, calcium, manganese, copper and zinc and contain high protein, vitamin B1 and dietary fibre. Sesame oil contains natural antioxidants, sesamin, sesamolin and tocopherol homologs (4). Sesame consumption has steadily increased due to its high nutritive value.

Globally, 12.81 million ha was under sesame cultivation in 2022, producing 6.55 MMT (5). Sudan is the largest producer of sesame, followed by Myanmar and India (5). Sesame is a tropical crop grown in various soils, but it thrives best in well-drained soils with light to medium textures. Sesame has a lower yield among oilseed crops and shows a poor response to inputs; therefore, it is an unattractive option for farmers (6). Sesame crops naturally adapted to dry conditions are highly vulnerable to waterlogging stress (7, 8, 9). Waterlogging may result from heavy rainfall, poor soil drainage, or inadequate irrigation management. Many tropical and subtropical zones have recently faced waterlogging due to global warming. Waterlogging has become a global issue due to unpredictable climatic changes, resulting in increasing incidences of heavy rainfall and flooding(10). Waterlogging affects over 17 million km^2 of agricultural land annually resulting in annual losses of more than $74 USD billion(11, 12). Under changing climatic conditions, the frequency and intensity of heavy precipitation are projected to increase, further worsening waterlogging stress (13). Sesame is a very waterlogging-sensitive crop (14). Most sesame germplasm is susceptible to waterlogging at different crop developmental stages (15).

Morphological Adaptations of Sesame to Waterlogging

When soil becomes saturated with water, oxygen availability for plant roots is significantly reduced, leading to root damage (16, 17). Flooding stress reduces the number of roots and the length and volume of roots in sesame (7). In sesame, waterlogging stress adversely affected crop growth by limiting oxygen availability in the soil, leading to hypoxic and subsequently anoxic conditions (18). Under waterlogging stress, some plants form specialized morphological structures called adventitious roots, which enhance oxygen absorption and help plants overcome hypoxia (19). Under waterlogged conditions, primary roots cannot absorb water and nutrients, a function replaced by newly formed adventitious roots (20). The formation of adventitious roots was reported to be associated with the production of auxin, nitric oxide, ethylene and hydrogen peroxide (21).

In sesame, adventitious roots were developed in the water-logging resistant cultivars ZZM2541 and Rajshahi Khoyeri (15, 22, 16). Another study reported adventitious root development above flooding levels in both tolerant and susceptible sesame cultivars, with the tolerant cultivars exhibiting more rapid and vigorous root development (23). Under hypoxic stress, primary roots perish and adventitious roots partially replace primary roots, further preserving the metabolic cycles and promoting healthy growth and development (24, 25). Aerenchyma formation is another mechanism by which plants adapt to waterlogging stress. Aerenchyma is a specialized tissue formed under waterlogged conditions and contains gas-filled channels to transfer oxygen from the shoots to the roots (26). Aerenchyma forms within 5 to 7 days of waterlogging (27). Two forms of aerenchyma tissues, schizogenous aerenchyma and lysigenous aerenchyma are reported in plants (28). In wetland species, schizogenous aerenchyma was observed in roots without cell death and lysigenous aerenchyma developed from programmed cell death and cell wall autolysis in response to flooding (29). The waterlogging tolerant sesame genotype ZZM2541 synthesized vast lysigenous aerenchyma tissues in the roots and aerenchymatous cells in the leaf vein epidermis under waterlogging conditions (15).

Physiological and Biochemical Response of Sesame to Waterlogging

Waterlogging leads to decreased oxygen levels in the rhizosphere, significantly impairing normal biochemical and physiological functioning. The photosynthetic rate gets reduced by waterlogging stress. In the early stage of waterlogging, there is a decrease in transpiration rate and stomatal conductance and an increase in CO_2 diffusion resistance, affecting photosynthesis. In later stages of waterlogging, chlorophyll synthesis is reduced, leading to reduced light absorption and reduction in photosynthetic rate (30). Hence, the photosynthetic rate frequently indicates waterlogging tolerance (31).

Waterlogging at the seedling stage in sesame significantly increased the relative electric conductivity of the leaf while decreasing leaf water content and water-holding capacity (32). Waterlogging changed the photosynthetic pigment content and composition, directly affecting the photosynthetic rate. Waterlogging-tolerant sesame genotypes exhibited the highest chlorophyll under waterlogging, while genotypes poor in chlorophyll content were sensitive to waterlogging and had poor yields (3, 23). The content of the photosynthetic pigments, chlorophyll A, chlorophyll B and carotenoids, reduced appreciably under waterlogged conditions. This reduction in pigments decreases the photosynthetic capacity (33). Total chlorophyll content with increasing waterlogging duration was decreased in all 142 diverse sesame genotypes screened (23). The reduction was more pronounced in Chlorophyll B and was more significant in waterlogging-susceptible genotypes than intolerant ones.

In plants under normal conditions, there is a dynamic balance between producing Reactive oxygen species (ROS) and scavenging ROS (34). Waterlogging stress leads to insufficient oxygen, causing a rise in intracellular ROS (35, 36). This results in lipid peroxidation, protein degradation and enzyme inactivation, with excess ROS acting as signalling molecules in stressed plant cells. Hence, the ability of the plants to scavenge ROS and reduce harmful effects can be related to waterlogging tolerance (37, 38, 39). The ROS scavenging system is of two types: enzymatic and non-enzymatic. The enzymatic system includes catalase, peroxidase and superoxide dismutase and the non-enzymatic system comprises ascorbic acid, glutathione peptides and carotenoids (40). Under waterlogging conditions in sesame, there is a sharp decline in superoxide dismutase, peroxidase and catalase activities (7). As a result, ROS cannot be effectively removed, disrupting the balance between ROS production and scavenging. This leads to free radical accumulation, increased cell permeability and eventual cell death (41, 42, 43).

Waterlogging-tolerant sesame genotypes exhibited the highest enzymatic antioxidant activities under waterlogging, while genotypes with poor enzymatic antioxidant activities were sensitive to waterlogging and had poor yields (3, 23). Higher enzymatic and non-enzymatic antioxidant activities were observed in the waterlogging tolerant sesame genotype EC377024, compared to the susceptible genotype IC129289 (18). Enzymatic antioxidants are crucial in plant survival during flooding and in preventing cell damage (38, 44, 45, 46). Waterlogging leads to a reduction in ascorbate in sesame (33). Activities of ascorbate peroxidase, which scavenges H_2O_2, monodehydroascorbate reductase and glutathione peroxidase, responsible for Reactive Oxygen Species detoxification increased with increased stress duration. The coordinated interaction of the antioxidant defence system and glyoxalase systems plays a significant role in detoxifying Reactive Oxygen Species and methylglyoxal, which protect plants from oxidative stress and cell damage(33). Waterlogging -tolerant genotypes also showed increased proline, where proline acts as an osmolyte for osmotic adjustment and contributes to stabilizing cell structures and protecting membranes and proteins against ROS (46, 47).

Effect of Waterlogging on Growth and Yield Attributes of Sesame

Waterlogging reduces growth and yield attributes in sesame and even two to three days of waterlogging caused a decline in output (48). Waterlogging in sesame reduced plant height, number of leaves, leaf area, biomass production, SPAD values, net photosynthesis, yield contributing parameters *viz*., capsule number per plant, seed number per capsule, 1000-seed weight and seed yield. Poor drainage in sesame resulted in more than 44 percent yield loss (53), which can go up to 50-90 percent in severe cases (14, 15,16, 48-52). In sesame, the duration of waterlogging stress was reported to be more critical than the crop stage (33). It was reported that 72 hrs of waterlogging was detrimental (3) and 48 hrs of water logging was commonly used for screening purposes (3, 54) in pot culture experiments.

Sesame is affected by waterlogging at different developmental stages. Clear-cut evidence is unavailable regarding which stage of Sesamum, *viz*., early stage, flowering stage or maturity stage, is more sensitive to waterlogging. Many studies report waterlogging at early stages to destructively affect physiological, developmental and agronomical traits as plants cannot follow adaptive mechanisms, making them unfit for flooding. In contrast, another study reported the flowering stage as the most sensitive stage, which hardly withstand waterlogging (18, 51, 55, 56).

Screening for Waterlogging Tolerance in Sesame

It is universally agreed that breeding for waterlogging tolerance and evolving waterlogging tolerant varieties is the most convenient method to cope with climate change (3, 17, 57). In conventional plant breeding, screening and identifying parents with water-logging tolerance mechanisms is essential for utilizing them in hybridization programs. There are no standard phenotyping protocols for screening for waterlogging tolerance due to the variability of water logging stress and its compounding factors in plant response. Less effort has been made to screen, identify waterlogging-tolerant sesame germplasm and develop sesame varieties tolerant to waterlogging (58). Most of the studies used pots in the tank, while others used field assays for screening for waterlogging.

In sesame, the length and weight of seedlings grown in petridishes under waterlogging and optimal conditions were used in laboratory assays to screen for waterlogging tolerance (3). When waterlogging is screened using pot culture experiments, seedling mortality, survival percentage and crop damage indices are used to assess the flooding-tolerant genotypes. Other parameters like chlorophyll content, proline content and enzymatic antioxidant activities (SOD, POD, CAT) have been used in the early stages of the crop. At maturity, plant height, leaf number, fresh and dry weight of shoot, branch number, pod number per plant, seed number per pod, 1000 seed weight and seed yield have been used as indices in sesame for screening (3). Since the number of branches per plant and thousand seed weights positively correlate with seed yield, these traits can serve as indirect indices to seed yield under waterlogging stress (3).

In a pot culture experiment on 20-day-old sesame seedlings, 30 genotypes were screened for waterlogging stress. Seedlings were subjected to waterlogging for 24, 48 and 72 hrs and survival percentage was worked out. The wild species, *Sesamum malabaricum* recorded 100 percent seedling survival even after 72 hrs of waterlogging and was reported to be waterlogging tolerant (59). A new concept for evaluating sesame genotypes for waterlogging tolerance based on the ideotype concept following the MGIDI index was put forth (60). In the study, 40 sesame genotypes raised in pots were subjected to 72 hrs of waterlogging during the pre-flowering stage and data on survival status was recorded, followed by calculation of stress tolerance and susceptibility indices along with grain yield to rank the 12 genotypes that survived 72 hrs of waterlogging.

Challenges in Screening for Waterlogging

Phenotyping for waterlogging tolerance is done in pot culture experiments or field studies. Very often, the experiments conducted under controlled conditions only simulate to some extent what happens initially in the field due to the intricacies of field trials (60, 61). Further, in later stages of crop growth, root growth and development get restricted in pots and pot culture studies become unfit for yield-related studies at later crop growth stages. Under field conditions, waterlogging tolerance is evaluated based on morphological and physiological traits or grain yield, which is simple and requires no specialized equipment. However, environmental factors can influence the precision and efficiency of field experiments and are difficult to control (62). Trained labourers usually do classical phenotypic scoring, which is time-consuming and subjective (63). Traditional phenotypic scoring during waterlogging stress is performed by visual scoring in greenhouses or field conditions, which is laborious, time-consuming and subject to errors, making phenotyping for waterlogging tolerance a big challenge. Accurate phenotyping is essential for breeders to identify and select parents/plants with improved waterlogging tolerance to accelerate the development of waterlogging-tolerant sesame varieties through conventional breeding.

Using high-throughput phenotyping and AI tools can help get accurate results. A detailed review of different phenotyping methods for waterlogging tolerance and the associated challenges was provided by (61). High-throughput phenotyping platforms use fully automatic robotic systems integrating high-throughput imaging systems, high-precision sensors and powerful data processing to collect and analyze phenotypic data (64). Such high throughput phenotyping provides new opportunities for in-depth research. High throughput phenotyping using imaging sensors that can be mounted on ground, aerial or even orbiting platforms and satellite imaging are the most popular choices of imaging in field conditions (3, 65). However, specialized platforms which are technically complex and costly are required. Throughput phenotyping platforms can detect and analyze plant traits such as root morphology, leaf morphology, dynamic growth, biomass and yield (66). Though its application to waterlogging tolerance is limited, high throughput phenotyping will likely become the future development trend.

Breeding for Waterlogging Tolerance in Sesame

Minimal information is available on the breeding of waterlogging tolerance in sesame. As mentioned above, attempts have been made to screen sesame genotypes and identify waterlogging-tolerant ones based on the plants' morphological, physiological, anatomical, molecular and biochemical responses. Development of adventitious roots, aerenchymatous cells, chlorophyll content, proline content, survival under waterlogging, yield and its related parameters, enzymatic antioxidant levels, etc., have been used to screen and identify waterlogging sesame genotypes.

Selection of parents for waterlogging tolerance

Cluster analysis of 24 Chinese sesame genotypes based on physiological parameters grouped *Sesamum schinzianum*, Zhushanbai, Zhongzhi No. 13 and Ganzhi No. 13 as waterlogging-tolerant (32). Another study reported that the sesame cultivar Zhongzhi No. 13 is waterlogging tolerant and can be used in breeding programs to enhance sesame production under waterlogging stress (9). In pot culture-based screening for physiological parameters like root volume, root length, root weight, leaf area per plant, SPAD value and antioxidant enzyme activities, the sesame genotype BD6980 demonstrated higher resistance to waterlogging (53).

Thirty sesame genotypes were screened for waterlogging tolerance in a pot culture experiment at the seedling stage by flooding for 24, 48 and 72 hrs. While all the genotypes survived 24 and 48 hrs of waterlogging, only 17 genotypes survived 72 hrs of waterlogging. Ten best genotypes *viz*., Ayali, *S. malabaricum*, SC 207, Thilarani, Thilak, GT10, SV2, TKG 308, TKG 22 and Rama with the highest survival percentages were forwarded to field trials. Flooding continued in the field for 72 hrs and biometrical traits were recorded. Among the ten genotypes, the native variety, Ayali, recorded the highest single-plant yield (67). Based on survival, the wild sesame, *S. malabaricum* was reported as flood-tolerant out of 30 different sesame genotypes screened at the seedling stage (20 days after sowing) in a pot culture experiment (59). Through conventional breeding, these tolerant genotypes could serve as donor parents in developing waterlogging-tolerant sesame varieties.

Recent Developments in Waterlogging Tolerance Studies in Sesame

In recent years, there has been an upsurge in data generation using genomics, transcriptomics, metabolomics and proteomics under waterlogging stress. RNA-seq-based analysis on samples collected at different periods post 15 hrs of water logging during flowering from tolerant and susceptible sesame cultivars found 9 hrs as the critical time point for the response of sesame to waterlogging stress and 66 candidate genes were explicitly identified for improving waterlogging tolerance in sesame (9).

The MYB gene family is one of the most significant transcription factors (TFs) influencing various biological processes within the plant kingdom. Five SIMYB genes were reported to be up-regulated in sesame under waterlogging. The gene *SIMYB107* was the most induced one and had more than 22-fold increased gene expression, while SIMYB166, SIMYB155 and SIMYB 174 were down-regulated under waterlogging. Nearly 40 % of SIMYBs were linked to waterlogging stress responses, indicating their potential utility in augmenting the resilience of sesame plants under such waterlogging stress (68). The observation that more SIMYBs were modulated under waterlogging compared to drought underscores sesames' heightened vulnerability to waterlogging stress (9). By integrating RNA-seq data alongside quantitative reverse transcription polymerase chain reaction (qRT-PCR) analysis, it was established that SIMYBs function as crucial transcription factors orchestrating sesames' adaptive responses to both drought and waterlogging stresses (68).

Upregulation of genes in the bZIP family (e.g., SibZIP03, SibZIP04, SibZIP30, SibZIP44 and SibZIP62) has been shown to play a crucial role in the metabolic reprogramming processes that occur under waterlogging stress conditions in sesame (69). A study mapped six QTLs (qEZ10CHL07, qEZ10ZCL07, qWH10CHL09, qWH10ZCL09, qEZ09ZCL13 and qWH09CHL15) for waterlogging stress tolerance with one QTL (qWH10CHL09) linked to the SSR marker (ZM428) being used in marker-assisted selection (MAS) for waterlogging stress tolerance(14). Sesame WRKY TFs were explored to understand the structure and function of WRKY genes and it was concluded that manipulating these genes could help improve waterlogging tolerance (70).

The role of the ethylene response factor (ERF) in waterlogging stress has been well documented. In rice, overexpression of *SUB1A,* an ERF family member, increases submergence tolerance (71). Gene expression profile analysis in sesame revealed 26 *SiERFs* to be highly stimulated under waterlogging stress (57). Among the 26 *SiERFs*, *SiERF23* and *SiERF54* were the most induced by waterlogging stress, suggesting their potential for targeted improvement of sesame to waterlogging stress. Metabolomics study in the water logging tolerant sesame cultivar EC377024 at control and 48 h of waterlogging stress indicated significant accumulation of metabolites in fatty acid (decanoate), carbohydrate, amino acid, Shikimate, MEP (5-enolpyruvoylshikimate-3-phosphate) Krebs cycle and Xanthophyll pathways (18).

These multiomics studies were carried out independently and an integrated understanding of the complex features of waterlogging stress has not been attained (72). Convention breeding in sesame for waterlogging tolerance is not known. QTL mapping studies in sesame using bi-parental mapping populations or genome-wide association studies (GWAS) (13, 73) have identified several QTLs and candidate genes associated with waterlogging tolerance, providing valuable resources for Marker Assisted Selection in sesame breeding programs. Integrating traditional breeding with molecular techniques like MAS can accelerate the development of waterlogging-tolerant sesame varieties by improving selection precision for waterlogging tolerance traits (23, 74). Gene editing technologies such as CRISPR/Cas9 enable targeted modifications in specific genes associated with waterlogging tolerance. Deploying them in sesame can result in the development of sesame varieties with enhanced tolerance to waterlogging stress.

Conclusion

Sesame, though often referred to as Queen of Oilseeds, has been an orphan crop with hardly any support from science and industry and hence lags behind other oilseed crops regarding genetic improvement. In India, sesame is mainly cultivated as a rainfed crop. Climate change can lead to no rainfall, followed by heavy and prolonged precipitation, resulting in devastating floods. Developing waterlogging tolerant sesame cultivars is urgently needed to cope with the situation. The waterlogging signalling mechanism is not fully understood in plants. However, appreciable progress has been achieved in understanding the morphological/ physiological/and biochemical basis of waterlogging tolerance in sesame and identifying QTLs and candidate genes for waterlogging tolerance. Further, sesame is primarily cultivated in developing countries where resources are poor and access to advanced techniques is scarce. Hence, there is a need for international collaboration to exploit the full potential of sesame. Climate-smart sesame cultivars can ensure the sustainability of the crop in the face of climate change. A multidisciplinary approach that combines traditional plant breeding, molecular techniques and advanced agronomic practices is needed to address the complexity of waterlogging stress and evolve water-logging-tolerant sesame to sustain sesame production during unpredictable climatic conditions.

Authors' contributions

CP, MMM, MJ, GS conceived the idea and prepared the manuscript. CP, MPK, PG, RA reviewed and revised the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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