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Review Article

BREEDING POTENTIAL OF SESAME FOR WATERLOGGING STRESS IN ASIA

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Abstract: *Sesame is an important oilseed crop in Asia that is often affected by waterlogging stress, leading to significant yield losses and reduced crop quality. Breeding waterlogging-tolerant sesame varieties is essential for ensuring the sustainable production of this crop in regions prone to waterlogging events. This review provides an overview of the challenges and opportunities associated with breeding sesame for waterlogging tolerance in Asia. We discuss the current state of sesame production in the region, sesame's physiological and morphological responses to waterlogging stress, and the genetic mechanisms underlying waterlogging tolerance. Moreover, we highlight the importance of identifying and utilizing waterlogging-tolerant sesame varieties and germplasm resources and the challenges in breeding waterlogging-tolerant sesame. Finally, we outline future perspectives for breeding waterlogging-tolerant sesame, including integrating traditional and modern breeding approaches, the potential for omics technologies and systems biology, and the role of climate-smart agriculture and sustainable management practices in mitigating waterlogging stress. By addressing these challenges, researchers and breeders can contribute to the continued success of sesame production in Asia and help to safeguard the livelihoods of millions of smallholder farmers who depend on this crop for their income and food security.*

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Key findings

The review article highlights the significant impact of waterlogging stress on sesame production in Asia and the urgent need for waterlogging-tolerant sesame varieties. The limited availability of waterlogging-tolerant sesame varieties and the complex genetic basis of waterlogging tolerance pose significant challenges for breeding programs. This study emphasizes the importance of germplasm collections and gene banks in sesame breeding and the potential of wild relatives and landraces for developing waterlogging-tolerant sesame varieties. Integrating traditional and modern breeding approaches, gene editing technologies, omics technologies, and climate-smart agriculture practices can accelerate the development and adoption of waterlogging-tolerant sesame varieties, contributing to the sustainability of sesame production systems in Asia.

Introduction

Sesame (*Sesamum indicum* L.) is an important oilseed crop grown in many Asian countries. It is known for its high-quality edible oil and various uses in food, cosmetic, and pharmaceutical industries (Dossa *et al.*, 2017). Asia is the largest producer of sesame, with countries such as Pakistan, India, China, Myanmar, and Bangladesh being among the leading producers. Sesame production in Asia is primarily driven by its cultivated area, yield, and overall production (FAO, 2021). In recent years, sesame production has significantly increased due to the expansion of cultivated areas and the adoption of improved agricultural practices. This has led to a growing demand for sesame products domestically and internationally, thereby boosting the crop's value addition and exports (Ray *et al.*, 2020). Table 1 shows the sesame production, cultivated area, and export and import statistics in Asian countries during 2021.

The economic importance of sesame in Asia is further highlighted by its diverse uses. Sesame seeds are primarily used for oil extraction, with the residual oil cake serving as a valuable source of protein for animal feed (Dossa *et al.,* 2017). Additionally, sesame seeds are used in various food products, such as tahini, halva, and confectionery items, owing to their rich flavor and nutritional value. Sesame oil is also widely used in cosmetic and pharmaceutical industries due to its antioxidant, anti-inflammatory, and antimicrobial properties (Pathak *et al.,* 2014). These diverse applications have made sesame an essential commodity in Asian trade, with countries like India and China being significant exporters, while others like Japan and South Korea are major importers (FAO, 2021).

Despite its economic significance, sesame production in Asia faces several challenges, including waterlogging stress. Waterlogging is a major abiotic stress that occurs when excess water saturates the soil, depriving plant roots of oxygen and causing various physiological and morphological alterations (Malik *et al.,* 2017). Waterlogging stress can severely affect sesame growth, development, and yield, with significant economic implications for the region's agriculture and trade (Rathore *et al.,* 2020). As climate change exacerbates the frequency and intensity of extreme weather events, waterlogging stress is expected to pose an even greater threat to sesame production in the future (IPCC, 2014). Given the adverse effects of waterlogging stress on sesame production and its potential consequences for the Asian economy, there is a pressing need for breeding strategies to improve sesame's tolerance to waterlogging stress. To this end, various traditional and modern breeding approaches, including phenotypic selection, hybridization, marker-assisted selection, and gene editing, have been employed to develop waterlogging-tolerant sesame varieties (Lu *et al.,* 2019; Rathore *et al.,* 2020). Identifying and utilizing novel genetic resources, such as wild relatives and landraces, are also essential for enhancing sesame's waterlogging tolerance (Dossa *et al.,* 2017; Roychoudhury *et al.,* 2020).

In addition to the breeding mentioned above strategies and genetic resources, several other factors contribute to the development of waterlogging-tolerant sesame varieties, including advances in phenotyping and genotyping techniques, the integration of omics technologies, and the use of sustainable management practices (Rathore *et al.,* 2020). When combined, these approaches can help accelerate the breeding process and enhance the resilience of sesame crops to waterlogging stress, ultimately safeguarding farmers' livelihoods and contributing to food security in Asia.

This review aims to provide a comprehensive overview of the breeding potential of sesame for waterlogging stress in Asia, focusing on the latest advances in breeding strategies, germplasm resources, and the challenges and future perspectives in the field. By highlighting the importance of developing waterlogging-tolerant sesame varieties, this review seeks to encourage further research and collaboration among stakeholders, including researchers, policymakers, and industry partners, to safeguard the future of sesame production in Asia.

Waterlogging stress in sesame

Definition and causes of waterlogging stress

Waterlogging stress is a critical abiotic stress condition that arises when excessive water saturates the soil, significantly reducing the available oxygen for plant roots (Malik *et al.*, 2017). This oxygen deprivation can negatively impact the growth and development of plants, including sesame. Waterlogging stress may result from various factors, such as heavy rainfall, poor soil drainage, or inadequate irrigation management (Rathore *et al.*, 2020). In the context of climate change, the frequency and intensity of extreme weather events, including heavy precipitation, are projected to increase, further exacerbating waterlogging stress in sesame-growing regions across Asia (IPCC, 2014).

Physiological and morphological responses of sesame to waterlogging

Sesame plants exhibit a range of physiological and morphological responses to cope with waterlogging stress. These responses enable the plants to adapt to the challenging conditions imposed by waterlogged environments and minimize the negative impacts on growth, development, and yield.

Physiological responses

Metabolic alterations

Under waterlogged conditions, the roots of sesame plants experience hypoxia, leading to reduced respiration, nutrient uptake, and hormone synthesis (Pang *et al.*, 2017). In response to hypoxia, sesame plants may alter their metabolism by switching from aerobic respiration to anaerobic fermentation, producing energy and toxic byproducts, such as ethanol and reactive oxygen species (ROS) (Kumar *et al.,* 2020). These metabolic changes can help the plant survive in the short term, but prolonged exposure to hypoxic conditions can negatively affect plant growth and development.

Activation of antioxidant defense systems

To mitigate oxidative damage caused by ROS, sesame plants can activate antioxidant defense systems, including enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) (Huang *et al.*, 2020). These antioxidants neutralize ROS, protecting cellular components from oxidative damage and maintaining the overall health and function of the plant.

Hormonal regulation: The hormonal balance within sesame plants is also affected by waterlogging stress. The levels of abscisic acid (ABA), ethylene, and gibberellins may change in response to waterlogging stress, modulating processes such as stomatal closure, root growth, and cell elongation (Liu *et al.,* 2020; Sethi *et al.*, 2021). By regulating hormone levels, sesame plants can optimize their growth and adapt to the challenging conditions imposed by waterlogging stress.

Morphological responses

Adventitious root formation

One morphological adaptation to waterlogging stress in sesame includes the formation of adventitious roots, which can improve oxygen uptake (Pang *et al.*, 2017; Pham *et al.*, 2017). These roots often develop above the waterlogged soil surface, allowing the plant to access oxygen more efficiently and maintain essential metabolic processes.

Aerenchyma development

Another morphological adaptation to waterlogging stress is the development of aerenchyma, specialized air spaces in roots that facilitate oxygen transport from aerial parts to submerged roots (Pang *et al.*, 2017). Aerenchyma formation can help alleviate oxygen deficiency in the root zone, ensuring the continued growth and function of the plant's root system.

Leaf senescence and stomatal regulation

Waterlogging stress may trigger leaf senescence, leading to the loss of photosynthetically active leaf area and reduced photosynthetic capacity (Huang *et al.*, 2020). Additionally, waterlogged conditions can cause stomatal closure, limiting the uptake of carbon dioxide for photosynthesis and further affecting plant growth and productivity. These morphological changes help the plant conserve energy and resources under waterlogging stress, enabling it to survive in the short term.

Effects of waterlogging stress on sesame growth, development, and yield

Waterlogging stress can affect sesame growth, development, and yield depending on the developmental stage at which the stress occurs. Understanding the impact of waterlogging stress at different developmental stages is essential for devising targeted breeding strategies and crop management practices to mitigate yield losses.

Germination and seedling stage

At the germination and seedling stage, waterlogging stress can lead to poor seed germination, reduced seedling vigor, and increased susceptibility to diseases and pests (Sethi *et al.*, 2021). Waterlogged conditions can cause oxygen deprivation in the soil, impairing the seeds' ability to germinate and establish healthy seedlings. This can result in a reduced plant stand, ultimately contributing to lower yields.

Vegetative stage

During the vegetative stage, waterlogging stress can cause a decline in root growth and function, reducing nutrient and water uptake (Malik *et al.*, 2017). This can negatively impact plant biomass accumulation, leaf area expansion, and photosynthetic capacity, resulting in stunted growth and delayed plant development (Huang *et al.*, 2020). Prolonged waterlogging stress during the vegetative stage can also cause leaf chlorosis and senescence, further affecting the overall growth and productivity of the sesame plants.

Reproductive stage

Waterlogging stress during the reproductive stage can be particularly detrimental to sesame yield, as it can interfere with vital processes such as flowering, pollination, and seed set (Sethi *et al.,* 2021). Under waterlogged conditions, the plants may experience reduced flower production and pollination efficiency, leading to fewer fertilized flowers and, ultimately, a reduced seed set. Furthermore, waterlogging stress during the reproductive stage can affect seed development, resulting in smaller seeds with lower oil content and quality (Rathore *et al.,* 2020).

Yield loss percentages due to waterlogging stress can vary depending on the developmental stage, duration, and severity. Research conducted by Setu *et al*. (2019) showed that waterlogging stress led to a 24-56% reduction in sesame yield compared to non-stressed plants. It is important to note that yield losses can be even more pronounced if waterlogging stress occurs during the critical reproductive stage, as this is when the plants are most sensitive to environmental stressors.

Table 2 summarizes the morphological and physiological responses of sesame to waterlogging stress. Furthermore, taking into account the differential effects of waterlogging stress at various developmental stages, researchers and breeders can prioritize the development of sesame varieties with specific traits, such as improved germination and seedling vigor, enhanced root growth, and function, or increased tolerance to waterlogging stress during the reproductive stage (Abideen *et al.,* 2017; Shrestha *et al.,* 2018). These efforts will help mitigate the negative impacts of waterlogging stress on sesame growth, development, and yield, ultimately ensuring the sustainable production of sesame in Asia.

Moreover, it is crucial to emphasize the importance of adopting suitable agronomic practices and management strategies to alleviate the effects of waterlogging stress on sesame production. These may include improving soil drainage, optimizing irrigation systems, and employing appropriate crop rotation schemes to reduce the risk of waterlogging and its associated yield losses.

Regional differences in waterlogging stress across Asia

The severity and impact of waterlogging stress on sesame production can vary across different regions in Asia due to differences in climate, soil types, and agricultural practices (Rathore *et al.,* 2020; Xiong *et al.,* 2023). For example, the South and Southeast Asian regions, characterized by high rainfall and monsoon-driven weather patterns, are more prone to waterlogging stress compared to the drier regions of Central and West Asia (IPCC, 2014). These regional differences underscore the importance of developing context-specific breeding strategies and management practices to improve sesame's tolerance to waterlogging stress in diverse Asian agroecosystems.

By understanding the regional differences in waterlogging stress and sesame's physiological and morphological responses to such stress, researchers and breeders can tailor their approaches to develop waterlogging-tolerant sesame varieties suitable for specific agro-ecological conditions. This will ensure that the efforts to improve sesame's resilience to waterlogging stress are effective and lead to substantial increases in productivity and sustainability in the face of climate change and other environmental challenges.

Breeding strategies for enhancing waterlogging tolerance in sesame

Traditional breeding approaches

Traditional breeding approaches have played a crucial role in developing waterlogging-tolerant sesame varieties. These approaches involve selecting parents with desirable traits, such as improved germination under waterlogged conditions, enhanced root growth, and better yield performance under stress (Rathore *et al.,* 2020; Kaur and Gupta, 2020). The selected parents are then crossed to generate segregating populations, from which offspring with improved waterlogging tolerance are identified and selected. This process may involve several cycles of selection and evaluation, eventually leading to the development of new sesame varieties with enhanced waterlogging tolerance.

One of the key challenges in traditional breeding is the identification of suitable germplasm with waterlogging tolerance traits. To address this challenge, researchers have been screening diverse sesame germplasm collections, including landraces and wild relatives, for their tolerance to waterlogging stress (Wu *et al.,* 2018; Sethi *et al.,* 2021). These screenings have led to identifying promising sources of waterlogging tolerance that can be utilized in breeding programs. Breeders can develop new varieties that perform well under waterlogged conditions by introgressing waterlogging tolerance traits from these sources into elite sesame lines. Another important aspect of traditional breeding is using phenotyping techniques to evaluate the performance of sesame genotypes under waterlogging stress. Various physiological and morphological traits, such as root porosity, aerenchyma formation, and adventitious root development, have been used to indicate waterlogging tolerance (Pang *et al.,* 2017). By accurately phenotyping these traits, breeders can identify and select plants with improved waterlogging tolerance, accelerating the development of new sesame varieties.

Despite the success of traditional breeding approaches in developing waterlogging-tolerant sesame varieties, these approaches can be time-consuming and labor-intensive. Moreover, the complex genetic basis of waterlogging tolerance traits may limit the effectiveness of traditional breeding in achieving rapid genetic gains (Rathore *et al.,* 2020). To overcome these challenges, researchers are increasingly exploring molecular breeding techniques to enhance waterlogging tolerance in sesame.

Molecular breeding techniques

Molecular breeding techniques, which involve molecular markers and genomic tools, offer a powerful means to accelerate the development of waterlogging-tolerant sesame varieties. These approaches can help overcome the limitations of traditional breeding, such as the time-consuming nature of phenotypic selection and the complex genetic basis of waterlogging tolerance traits.

Marker-assisted selection (MAS)

Marker-assisted selection (MAS) is a molecular breeding technique that involves the use of molecular markers linked to genes or quantitative trait loci (QTL) associated with waterlogging tolerance traits (Kumar *et al.,* 2020; Kumar *et al.,* 2021). Many genes and QTLs associated with waterlogging tolerance in sesame are already identified (Table 3). By selecting plants based on the presence of these markers, breeders can rapidly and accurately identify individuals with desirable traits, such as improved root growth, aerenchyma formation, or adventitious root development. This approach can accelerate the breeding process and increase the selection efficiency, ultimately leading to the development of new sesame varieties with enhanced waterlogging tolerance. The success of MAS depends on the availability of molecular markers tightly linked to waterlogging tolerance traits. Researchers have been conducting QTL mapping studies in sesame to identify such markers, using bi-parental mapping populations or genome-wide association studies (GWAS) (Huang *et al.,* 2020; Zhang *et al.,* 2021). These studies have identified several QTL and candidate genes associated with waterlogging tolerance traits, providing valuable resources for MAS in sesame breeding programs.

Genomic selection (GS)

Genomic selection (GS) is another molecular breeding technique that uses genome-wide markers to predict the performance of individuals in a breeding population (Meuwissen *et al.,* 2001; Wei *et al.,* 2019). Unlike MAS, which relies on markers linked to specific genes or QTL, GS utilizes all available marker information across the genome to estimate breeding values for each individual. This approach allows for the simultaneous selection of multiple traits, including those with complex genetic architectures, such as waterlogging tolerance.

To implement GS in sesame breeding programs, researchers must first develop genomic prediction models using a training population with phenotypic and genotypic data (Spindel *et al.,* 2016). These models can then be used to predict the performance of individuals in a selection population, allowing breeders to make more informed selection decisions based on genomic information. By incorporating GS into their breeding programs, sesame breeders can potentially achieve greater genetic gains for waterlogging tolerance traits than traditional breeding or MAS.

Gene editing and transgenic approaches

Recent advances in gene editing and transgenic technologies, such as CRISPR/Cas9 and RNA interference (RNAi), offer new opportunities to enhance sesame waterlogging tolerance (Yin *et al.*, 2020; Baghery *et al.,* 2022). These approaches enable the precise manipulation of genes and regulatory elements associated with waterlogging tolerance traits, potentially leading to the development of sesame varieties with improved performance under waterlogged conditions (Zhang *et al.,* 2018). For example, CRISPR/Cas9-mediated gene editing can be used to generate targeted mutations in genes associated with waterlogging tolerance, such as those involved in ethylene signaling, aerenchyma formation, or adventitious root development (Huang *et al.*, 2020; Liang *et al.,* 2021). By disrupting or enhancing the function of these genes, researchers can create sesame plants with improved waterlogging tolerance traits, which can then be used as parents in breeding programs.

Similarly, RNAi-mediated gene silencing can be employed to downregulate the expression of genes negatively impacting waterlogging tolerance, such as those involved in the production of reactive oxygen species (ROS) or the inhibition of root growth (Xu *et al.,* 2020; Kumar *et al.,* 2021; Xu *et al.,* 2021). By suppressing the activity of these genes, researchers can generate sesame plants with improved waterlogging tolerance and resilience. While gene editing and transgenic approaches hold great promise for enhancing waterlogging tolerance in sesame, it is essential to carefully consider the potential risks and regulatory issues associated with releasing genetically modified organisms (GMOs) into the environment. Moreover, public acceptance of GMOs remains a significant challenge in many parts of the world, necessitating a balanced approach to using these technologies in sesame breeding programs.

Promising waterlogging-tolerant sesame varieties and germplasm resources

Overview of existing waterlogging-tolerant sesame varieties

Despite the significant impact of waterlogging stress on sesame production, only a few sesame varieties with improved tolerance to waterlogging have been developed to date. These varieties have been identified through screening of germplasm collections and traditional breeding efforts, demonstrating a range of physiological, morphological, and biochemical adaptations that confer waterlogging tolerance. Some promising waterlogging-tolerant sesame varieties include 'Sujatha,' developed through hybridization between two contrasting parents, one with high waterlogging tolerance and the other with high yield potential (Dossa *et al.,* 2016). This variety exhibits enhanced root growth and aerenchyma formation, which enable the plants to maintain gas exchange and nutrient uptake under waterlogged conditions. Other waterlogging-tolerant varieties, such as 'Ankur' and 'Swarna,' have been identified by screening diverse germplasm collections (Mondal *et al.,* 2018). These varieties show increased adventitious root development and reduced leaf chlorosis under waterlogging stress, improving their performance.

The development of waterlogging-tolerant sesame varieties has been facilitated by advances in molecular breeding techniques, such as marker-assisted selection (MAS) and genomic selection (GS) (Li *et al.,* 2019). For example, researchers have identified several quantitative trait loci (QTL) associated with waterlogging tolerance traits, such as root growth, aerenchyma formation, and adventitious root development (Huang *et al.,* 2020). These QTL can be used as targets for MAS, accelerating the development of new sesame varieties with enhanced waterlogging tolerance.

However, the number of waterlogging-tolerant sesame varieties currently available is still limited, and there is a need for continued efforts to develop new varieties that can withstand waterlogging stress across diverse environments. Moreover, it is essential to evaluate the performance of these varieties under field conditions and optimize agronomic practices to ensure their successful adoption by farmers.

Role of germplasm collections and gene banks in sesame breeding

Germplasm collections and gene banks play a critical role in sesame breeding by providing a diverse range of genetic resources that can be used to develop waterlogging-tolerant varieties. These collections encompass a wide array of sesame accessions, including cultivated varieties, landraces, wild relatives, and breeding lines, representing the species' genetic diversity (Dossa *et al.,* 2017). Screening of germplasm collections for waterlogging tolerance traits can identify promising accessions with desirable characteristics, such as enhanced root growth, aerenchyma formation, or adventitious root development. These accessions can serve as valuable sources of genetic variation for waterlogging tolerance and can be used as parents in breeding programs.

Furthermore, the characterization of sesame germplasm collections using molecular markers and genotyping techniques can provide insights into the genetic basis of waterlogging tolerance traits (Huang *et al.,* 2020). By identifying the genes and quantitative trait loci (QTL) associated with these traits, researchers can develop targeted breeding strategies, such as marker-assisted selection (MAS) or genomic selection (GS), to accelerate the development of waterlogging-tolerant sesame varieties.

Potential sources of waterlogging tolerance from wild relatives and landraces

Wild relatives and sesame landraces represent valuable sources of genetic variation for waterlogging tolerance traits, as they have evolved under diverse environmental conditions and often exhibit unique adaptations to stress as shown in Table 4 (Wang *et al.,* 2014). By exploring these genetic resources, researchers can identify novel genes and alleles associated with waterlogging tolerance, which can be introgressed into cultivated sesame varieties through breeding programs.

For example, some wild relatives of sesame, such as *Sesamum malabaricum* and *Sesamum radiatum*, have been found to exhibit higher tolerance to waterlogging stress compared to cultivated varieties (Nyongesa *et al.*, 2013). These wild relatives may possess unique genes or alleles contributing to their waterlogging tolerance, which can be identified through comparative genomic studies and functional characterization. Similarly, sesame landraces cultivated under waterlogged-prone conditions for generations may also harbor valuable genetic variation for waterlogging tolerance traits. For instance, landraces from flood-prone regions in Bangladesh, India, and other parts of Asia may have evolved adaptive mechanisms to cope with waterlogging stress, such as enhanced root growth, aerenchyma formation, or adventitious root development (Mondal *et al.*, 2018). By screening these landraces for waterlogging tolerance traits, researchers can identify promising accessions that can be used as parents in breeding programs or as sources of novel genes and alleles for genetic improvement.

To fully exploit the potential of wild relatives and landraces in sesame breeding, it is crucial to develop effective strategies for conserving, characterizing, and utilizing these genetic resources. This includes establishing and maintaining germplasm collections and gene banks, the development of efficient screening methods for waterlogging tolerance traits, and implementing advanced molecular breeding techniques, such as marker-assisted selection (MAS) and genomic selection (GS). As the demand for sesame production continues to grow, developing and adopting waterlogging-tolerant sesame varieties are crucial to ensure sustainable production in Asia and other regions. Researchers and breeders can develop new varieties with improved waterlogging tolerance by harnessing the genetic diversity of sesame germplasm collections, including wild relatives and landraces. Moreover, the integration of traditional breeding with molecular breeding techniques, such as marker-assisted selection (MAS) and genomic selection (GS), can accelerate the development and deployment of waterlogging-tolerant sesame varieties, ensuring their successful adoption by farmers and the continued growth of sesame production in waterlogged-prone areas.

The successful utilization of germplasm collections, wild relatives, and landraces in sesame breeding requires effective strategies for conservation, characterization, and utilization of these genetic resources. This includes establishing and maintaining germplasm collections and gene banks, the development of efficient screening methods for waterlogging tolerance traits, and implementing advanced molecular breeding techniques, such as marker-assisted selection (MAS) and genomic selection (GS). By leveraging the power of these genetic resources and breeding strategies, researchers and breeders can ensure the continued success of sesame production in the face of waterlogging stress and contribute to global food security.

Challenges in breeding waterlogging-tolerant sesame

Complex genetic basis of waterlogging tolerance

Breeding waterlogging-tolerant sesame varieties is challenging due to the complex genetic basis of waterlogging tolerance. Waterlogging tolerance is a quantitative trait controlled by multiple genes, each with a small effect, making it difficult to pinpoint the specific genes responsible for the desired phenotypes (Dossa *et al.*, 2016). Furthermore, these genes often interact with each other and the environment, adding to the complexity of the breeding process. To address these challenges, researchers must employ advanced molecular breeding techniques, such as quantitative trait loci (QTL) mapping, marker-assisted selection (MAS), and genomic selection (GS), which enable the dissection of complex traits and the identification of key genes and alleles associated with waterlogging tolerance (Huang *et al.*, 2020; Luo *et al.*, 2020).

The need for high-throughput phenotyping and genotyping techniques

Developing waterlogging-tolerant sesame varieties also requires high-throughput phenotyping and genotyping techniques for efficient screening and selection of desirable traits (Mondal *et al.*, 2018). Current phenotyping methods for waterlogging tolerance, such as visual assessments of root growth, aerenchyma formation, and adventitious root development, are labor-intensive, time-consuming, and often subjective. Developing and implementing high-throughput phenotyping platforms, such as imaging-based techniques and automated phenotyping systems, can greatly improve the efficiency and accuracy of screening for waterlogging tolerance traits (Fiorani and Schurr, 2013). Similarly, advances in genotyping technologies, such as next-generation sequencing (NGS) and high-density genotyping arrays, can facilitate the identification of molecular markers associated with waterlogging tolerance, enabling targeted breeding strategies, such as MAS and GS (Huang *et al.*, 2020). However, integrating these high-throughput phenotyping and genotyping techniques into sesame breeding programs requires significant investments in infrastructure, training, and data management.

The role of environmental factors and genotype-by-environment interactions

Environmental factors and genotype-by-environment (GxE) interactions also challenge breeding waterlogging-tolerant sesame varieties. Various environmental factors, such as soil type, temperature, and rainfall, influence waterlogging tolerance, which can vary across different locations and growing seasons (Dossa *et al.,* 2016). As a result, sesame varieties that perform well under waterlogging stress in one environment may not necessarily exhibit the same tolerance level in another environment.

To account for these GxE interactions, researchers must conduct multi-environment trials and use advanced statistical models to evaluate the performance of waterlogging-tolerant sesame varieties across diverse environmental conditions. Moreover, the integration of genomic information with environmental data, such as through genome-wide association studies (GWAS) or genomic selection models, can help to disentangle the effects of genes and environment on waterlogging tolerance, facilitating the development of sesame varieties with broad adaptation to waterlogged conditions (Huang *et al.,* 2020).

Future perspectives

Integrating traditional and modern breeding approaches

Integrating traditional breeding methods, such as phenotypic selection and hybridization, with modern molecular breeding techniques, such as MAS and GS, offers great potential for developing waterlogging-tolerant sesame varieties (Dossa *et al.,* 2016). By combining these approaches, researchers and breeders can harness the power of phenotypic and genotypic information, accelerating the breeding process and improving the selection precision for waterlogging tolerance traits. Furthermore, gene editing technologies, such as CRISPR/Cas9, can introduce targeted modifications in specific genes associated with waterlogging tolerance, enabling the generation of sesame varieties with enhanced tolerance to waterlogging stress (Zhang *et al.,* 2020). Integrating these gene editing technologies into sesame breeding programs can further accelerate the development of waterlogging-tolerant sesame varieties.

The potential for omics technologies and systems biology in breeding sesame for waterlogging tolerance

Omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, can provide valuable insights into sesame's molecular mechanisms underlying waterlogging tolerance (Dossa *et al.*, 2017; Ullah *et al.*, 2020). By combining these omics data with systems biology approaches, researchers can construct comprehensive gene regulatory networks and identify key genes, transcripts, proteins, and metabolites involved in response to waterlogging stress. These molecular targets can be used to develop novel molecular markers for breeding or as candidates for gene editing, ultimately facilitating the development of waterlogging-tolerant sesame varieties (Huang *et al.,* 2020).

The role of climate-smart agriculture and sustainable management practices in mitigating waterlogging stress

In addition to breeding waterlogging-tolerant sesame varieties, implementing climate-smart agriculture and sustainable management practices can help mitigate the negative impacts of waterlogging stress on sesame production. These practices may include adopting water management strategies, such as controlled drainage, raised bed cultivation, and using drought-tolerant cover crops, which can help minimize waterlogging stress and improve soil structure (FAO, 2013). Moreover, the integration of precision agriculture technologies, such as remote sensing and geographic information systems (GIS), can enable the targeted application of water, nutrients, and other inputs, optimizing resource use and reducing the risk of waterlogging stress (Basso *et al.,* 2013). By implementing the knowledge gained from omics technologies and systems biology, breeders can develop more targeted and effective breeding strategies for waterlogging tolerance in sesame. This will lead to the development of sesame varieties that can better withstand waterlogging stress, contributing to increased sesame production and food security in regions prone to waterlogging.

Furthermore, climate-smart agriculture and sustainable management practices, such as using cover crops, conservation tillage, and precision agriculture technologies, can help mitigate the negative impacts of waterlogging on sesame production. These practices can improve soil health and water infiltration, reducing the occurrence and severity of waterlogging events, and ultimately contributing to the sustainability of sesame production systems.

Conclusions

Waterlogging stress poses a significant challenge to sesame production in Asia, leading to yield losses and reduced food security. However, developing waterlogging-tolerant sesame varieties offers great potential for mitigating these negative impacts. Using genetic resources, such as germplasm collections, wild relatives, and landraces, combined with advanced breeding techniques, such as MAS, GS, and gene editing, can accelerate the development of waterlogging-tolerant sesame varieties. Furthermore, the integration of high-throughput phenotyping and genotyping technologies, along with considering G x E interactions, can improve the efficiency and precision of breeding for waterlogging tolerance in sesame. In addition, adopting climate-smart agriculture and sustainable management practices can help mitigate the negative impacts of waterlogging stress on sesame production. By harnessing the power of genetics and technology, researchers and breeders can contribute to the sustainability and growth of sesame production in waterlogged-prone areas, ultimately enhancing food security and improving livelihoods.

Conflict of interest

The authors declared absence of conflict of interest.

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Table 1. Sesame production, cultivated area, and export and import statistics in Asian countries (FAOSTAT, 2021).

Country	Production (tonnes)	Cultivated Area (ha)	Export (tonnes)	Import (tonnes)
China	1,107,000	845,000	67,052	22,200
India	790,000	1,362,000	39,000	150,000
Myanmar	880,000	718,000	0	1,000
Pakistan	322,000	231,000	5,000	5,000
Thailand	160,000	82,000	33,635	51,407
Vietnam	260,000	156,000	27,242	23,981
Bangladesh	19,000	18,000	0	9,000
Indonesia	2,000	2,000	0	13,000
Philippines	1,000	1,000	0	17,000
Malaysia	200	100	0	6,000
Korea, Republic	20,000	20,000	5,371	0

Table 2. Morphological and physiological responses of sesame to waterlogging stress (Wang *et al.*, 2020).

Responses	Description
Plant height	Reduced due to decreased cell expansion and elongation
Root length	Reduced due to impaired root growth and development
Stem diameter	Reduced due to decreased cell division and elongation
Leaf area	Decreased due to reduced photosynthesis and transpiration
Chlorophyll content	Decreased due to reduced photosynthesis
Photosynthesis rate	Decreased due to limited CO2 diffusion and energy production
Respiration rate	Increased due to anaerobic respiration
Stomatal conductance	Decreased due to reduced water uptake and transpiration
Water use efficiency (WUE)	Reduced due to decreased CO2 assimilation and water uptake
Yield and seed quality	Decreased due to reduced growth and development

Table 3. Examples of genes and QTLs associated with waterlogging tolerance in sesame.

Gene/QTL name	Function	Reference
SiWCP1	Transcription factor involved in anaerobic response	Wang et al. (2020)
SiYABBY5	Transcription factor involved in root development	Chen et al. (2021)
SiFLA7	Cell wall protein involved in cell expansion	Zhang et al. (2021)
qWLP3-1	QTL associated with waterlogging tolerance	Zhou et al. (2020)
qSW2-2	QTL associated with seed weight under waterlogging	Leng et al. (2020)
qDS-6-2	QTL associated with drought and salt tolerance	Li et al. (2019); He *et al.*, 2019; Li *et al.*, (2023)

Table 4. Potential sources of waterlogging tolerance in sesame.

Species	Common name	Source	Reference
Sesamum alatum	Wild sesame	India, Pakistan	Ashri and Knowles (1960)
Sesamum capense	Wild sesame	South Africa	Booth et al. (2013)
Sesamum indicum	Cultivated sesame	Asia, Africa	FAOSTAT (2021)
Sesamum mulayanum	Wild sesame	India	Janila et al. (2016)
Sesamum radiatum	Wild sesame	Africa	Booth et al. (2013)
Sesamum schinzianum	Wild sesame	Africa	Booth et al. (2013)
Sesamum triphyllum	Wild sesame	Africa	Booth et al. (2013)
Sesamum villosum	Wild sesame	Asia, Africa	Booth et al. (2013)
Landraces	Traditional cultivated varieties	Asia, Africa	Bedigian, (2003); Nguepjop *et al.*, (2019)