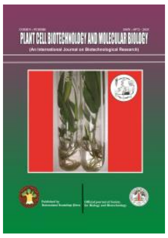

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Heat Stress in Indian Mustard (*Brassica juncea* L.): A Critical Review of Impacts and Adaptation Strategies

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Indian mustard, a member of the Brassicaceae family, is a cool-season crop cultivated extensively in various agro-ecological conditions, contributing significantly to vegetable oilseed production. However, being a thermosensitive and C3 plant [1], Indian mustard is highly susceptible to high-temperature stress, particularly during critical developmental stages [2]. High temperatures disrupt physiological, morphological, and biochemical mechanisms essential for plant growth and development. From altered chlorophyll content and osmotic water potential to impaired photosynthesis and reduced seed oil accumulation, heat stress detrimentally affects various aspects of Indian mustard physiology. This comprehensive review examines the impacts of heat stress on Indian mustard, a significant oilseed crop, and explores adaptation strategies to mitigate its adverse effects. Additionally, heat stress during reproductive stages leads to flower abortion, reduced fertility, and poor seed development, significantly impacting yield potential. To cope with

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heat stress, plant response mechanisms involve intricate signaling pathways, leading to cellular readjustments at transcriptome, epigenome, proteome, and metabolome levels. Breeding approaches, including conventional techniques and advanced molecular tools like CRISPR/Cas-based genome editing, offer promising avenues for developing heat-tolerant cultivars. Integration of multi-omics approaches aids in identifying stress-responsive genes and metabolic pathways crucial for adaptation. Agronomic strategies, such as nutrient management and microbial inoculation, play vital roles in mitigating heat stress effects and enhancing plant resilience. Collaborative efforts and interdisciplinary research are essential to deepen our understanding of heat stress responses and develop sustainable solutions to ensure oilseed crop productivity and food security in the face of climate change. This review underscores the urgency of addressing heat stress challenges in Indian mustard cultivation and highlights the need for concerted efforts to develop effective adaptation strategies for sustainable agriculture.

Keywords: Biochemical; heat-tolerant; morphological; physiological; resilience; thermosensitive.

1. INTRODUCTION

Indian mustard (*Brassica juncea* L.) is an amphidiploid plant (2n=36) belongs to mustard family called *Brassicaceae. Brassicas* are second largest most important vegetable oil seed crop followed by soyabean in area and production [2]. Indian mustard occupies 90% of area under brassica oil seeds in India. It ranks as the second most important vegetable oilseed crop in India and holds the fifth position globally, contributing to 7.4% of the world's oilseed output [3]. India is responsible for approximately 7.4% of the global oilseed production but consumes 9.3% of the world's edible oil. In 2019, the country imported around 15 million tonnes of edible oils each year, representing nearly half of its total expenditure on agricultural imports. As the second-largest consumer and the top importer of vegetable oil worldwide, India's per capita consumption is expected to continue growing at an annual rate of 2.6%, with projections indicating that it could reach 14 kilograms per capita by 2030. However, its sensitivity to high temperature stress poses a significant challenge, affecting various physiological, morphological, and biochemical mechanisms critical for normal plant growth and development [4]. High temperature stress, exacerbated by climate change, adversely impacts Indian mustard during its early developmental stages, leading to disruptions in chlorophyll content, osmotic water potential, plant height, leaf area index, dry matter accumulation, and antioxidant enzyme activity [5,6]. The reproductive period, particularly flowering, is highly susceptible to temperature fluctuations, with even minor increases in maximum daily temperatures resulting in significant reductions in seed yield [7]. High temperatures induce declines in chlorophyll content and impair pigment synthesis in plants, slowing down various physiological processes and ultimately leading to substantial yield reductions [8].

Conventional breeding techniques play a vital role in developing heat-tolerant cultivars by harnessing the genetic diversity found in wild accessions. Although incorporating traits from wild species presents challenges, a systematic approach can unlock the vast genetic variability they offer. Exotic libraries, which integrate marker-defined genomic segments from wild species into elite crop backgrounds, present a promising avenue for enhancing agricultural performance [9]. Molecular genetic markers, such as amplified fragment length polymorphism (AFLP), are instrumental in unraveling plant genomes and identifying heritable traits associated with genetic diversity [10]. The advent of molecular marker technology has transformed plant breeding, facilitating the rapid identification of heat-tolerance quantitative trait loci (QTLs) and stress-responsive genes through techniques like QTL mapping, QTL-seq analysis, and RNA sequencing [11].

Advancements in 'omics' technologies, particularly next-generation sequencing and comprehensive proteome profiling, offer invaluable insights into how plants respond to heat stress. By integrating molecular analyses with physiological understanding, breeders can strategically enhance adaptability and productivity in crops confronted with rising global temperatures [11,12]. The integration of traditional breeding methods with cutting-edge molecular techniques provides a promising pathway for developing heat-tolerant crops [9-10]. By capitalizing on genetic diversity and leveraging advanced genomic tools, breeders can expedite the breeding process and meet the urgent need for climate-resilient agricultural systems. Research comparing three species of oilseed Brassica highlighted Indian mustard's greater tolerance to heat and water stress compared to Canola quality Indian mustard [13]. Further studies are needed to understand the direct effects of high temperature stress on *Brassica juncea* at the seedling stage.

2. IMPACT OF STRESS ON VARIOUS TRAITS OF MUSTARD

Understanding the impact of high temperature stress at different developmental stages is critical for cultivating heat-tolerant cultivars. Various species and genotypes exhibit considerable variation in optimal temperature ranges, emphasizing the need for targeted research efforts. During early vegetative growth, elevated temperatures stimulate photosynthesis and above-ground growth in well-watered *Brassica napus* plants. However, under combined heat and drought stress, photosynthesis is severely impaired, accompanied by decreased stomatal conductance [14]. Plants respond to heat stress by increasing transpiration to prevent leaf damage, while drought induces stomatal closure to conserve water, exacerbating the effects of heat stress (see Fig. 1).

At the molecular level, heat stress disrupts membrane proteins, enzymatic activities, and metabolic processes, leading to oxidative damage, protein degradation, and DNA disruption [15]. In *Brassica napus* seedlings, heat stress results in reduced chlorophyll content, inefficient antioxidant defense systems, and morphological abnormalities in floral organs [12]. During reproductive stages, plants are highly susceptible to heat stress, particularly during pollen development, fertilization, and embryo development [11]. Heat stress leads to reduced flower fertility, poor pod and seed development, and structural abnormalities in reproductive organs. In wheat and *Arabidopsis thaliana*, heat stress causes impaired gametogenesis, reduced floret fertility, and abnormal pollen development, ultimately affecting seed number and weight [16]. Physiological impact of heat stress varies across developmental stages, highlighting the need for targeted research to develop heat-tolerant cultivars capable of withstanding temperature fluctuations during different growth phases [17,18].

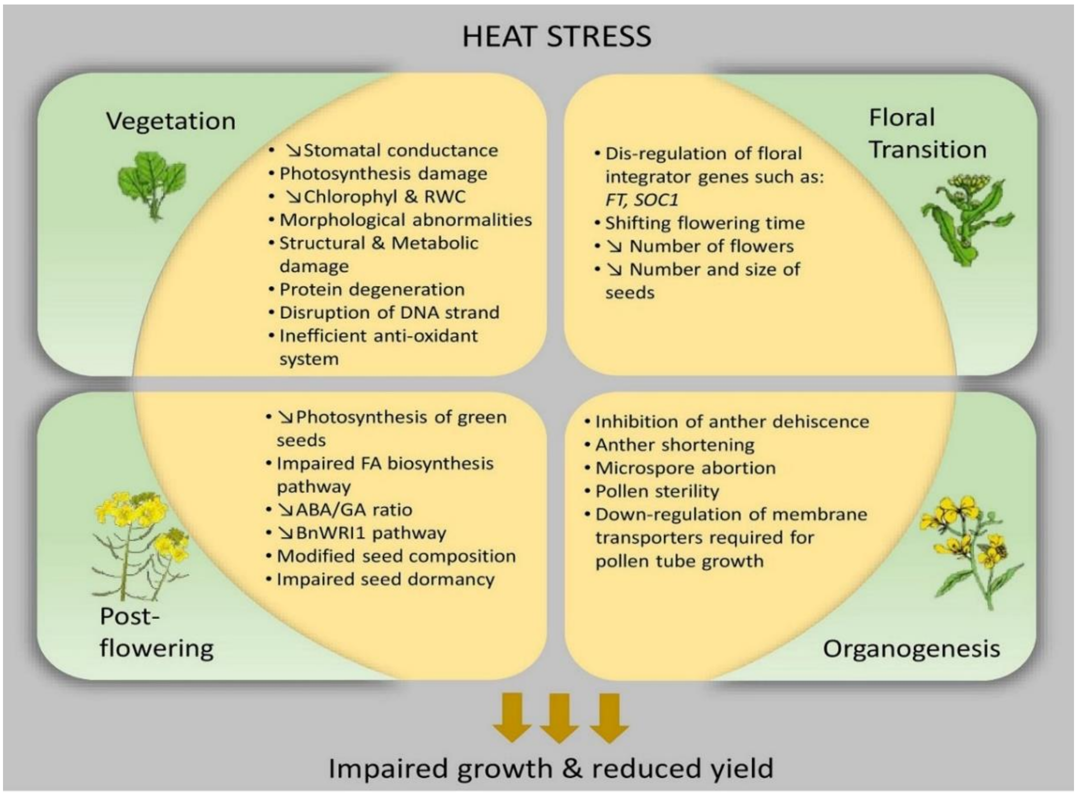

Fig. 1. Physiological impact of heat stress at different developmental stages of *mustard* [19]

2.1 Impact of High Temperature on Morphological Traits

High temperatures can have significant impacts on the morphological characteristics of crops, particularly in cool season crops like Indian mustard. Even a slight increase in temperature beyond the optimal range of around 28^{o} C can lead to drastic changes in growth and development. Studies have shown that a temperature increase of 3-4^{o} C from the mean high temperature after 30-45 days after sowing can result in reduced growth of Indian mustard. One of the key morphological changes observed under high temperature conditions is a significant reduction in plant height, which can decrease by up to 22.8% when sown late. This decline in height is attributed to decreased soil moisture, limiting the plant's ability to reach its genetic potential. Additionally, high temperatures can negatively affect parameters such as crop growth rate, leaf area index (LAI), and plant height. These reductions in growth parameters are often used to identify stress-tolerant genotypes for future breeding efforts (Fig 2).

The reduction in LAI due to warmer temperatures ultimately leads to lower radiation use efficiency and decreased net photosynthesis, resulting in reduced dry matter accumulation in crops like Indian mustard. This has been observed in various studies using models like the Info crop Model. High temperatures also impact meristematic cell division and elongation, further contributing to reduced plant height. Moreover, high temperatures can affect other morphological characteristics such as the number of branches per plant, with studies indicating a reduction in branch number under heat stress conditions. Moderate periods of high temperature have also been shown to decrease dry matter accumulation in mustard species.

2.2 Impact of High Temperature on Physiological Traits

High temperatures have profound effects on the physiological characteristics of plants, impacting various metabolic activities and processes crucial for their growth and development. One significant consequence of rising air temperatures is the acceleration of plant growth, leading to a shorter crop duration. This reduction in the overall duration of the plant's life cycle results in decreased cumulative light perception and absorption rates. At the vegetative stage, high temperatures can cause malformed organs in plants, disrupting fundamental processes such as respiration and carbon assimilation [20]. Additionally, heat stress often increases

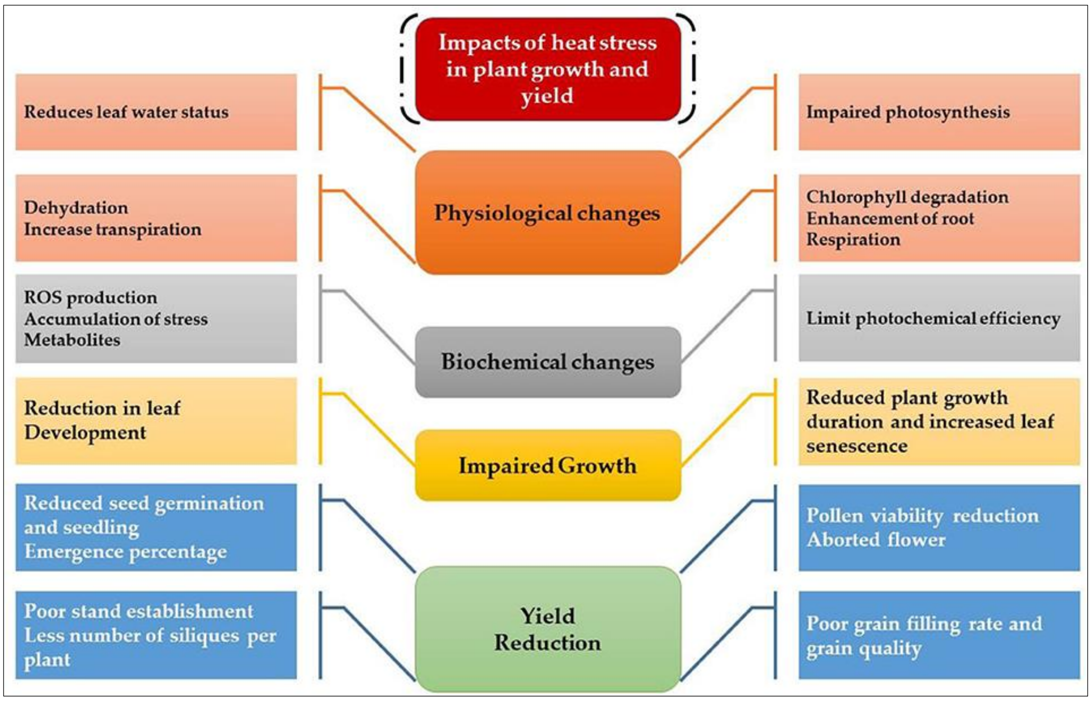

Fig. 2. Impact of heat stress on physiological, biochemical, growth & yield responses in plants [26]

transpiration rates and stomatal conductance while decreasing water usage efficiency and chlorophyll 'a' levels in plants like Chinese cabbage, further exacerbating physiological stress [21]. One of the key physiological impacts of high temperature stress is the inhibition of photosynthesis. Heat stress alters the structure of thylakoids and depletes photosystem II antennae, leading to diminished photosynthetic and respiratory activities. Moreover, the generation of free radicals, known as reactive oxygen species (ROS), under high temperature conditions damages the oxidative system of plants, resulting in lipid peroxidation and membrane damage (Fig 2).

The inactivation of crucial enzymes like Rubisco due to temperature stress further impairs photosynthetic efficiency. This enzyme breakdown leads to the formation of inhibitory molecules, disrupting metabolic activities within the plant. Temperature stress also affects other physiological parameters such as relative water content (RWC), membrane stability index (MSI), and chlorophyll content [22]. These parameters serve as selection indices for identifying heat-tolerant plant genotypes. For example, MSI decline under high temperature stress has been observed in Indian mustard genotypes like Pusa Agrani, indicating susceptibility to heat stress [23]. Overall, understanding the physiological responses of plants to high temperatures is essential for developing strategies to mitigate the impacts of climate change on agricultural productivity and ensure food security. Overall, understanding the impact of high temperatures on morphological characters is crucial for developing strategies to mitigate the effects of climate change on crop productivity and ensure food security.

2.3 Impact of High Temperature on Yield and Yield Attributing Traits

Yield in crops like mustard is influenced by a multitude of factors, including genotype, environment, and their interaction. Changes in sowing time expose the crop to various environmental conditions, affecting its phenological phases and ultimately impacting crop yield. High temperature stress during the terminal stages of growth can significantly reduce plant growth and production [20]. Abiotic stress factors, such as high temperatures, are primary limitations for plant development and productivity in agriculture. Phenological shifts induced by changes in photoperiod and temperature affect crucial plant structures and processes, including floral development, pollination, and seed formation, leading to yield reduction [24].

High temperatures during flowering and grain filling stages cause substantial agricultural production losses due to their impact on pollen and grain development, anthesis, and fertilization [25]. Temperature stress can result in reduced seed size, poor growth, and increased abortion frequency of reproductive organs, further reducing grain yield. Studies have shown that even a short period of high temperature exposure can lead to significant yield losses in mustard crops. Increases in seasonal temperature have been associated with decreases in seed yield, with a reduction in yield reported when temperatures exceed certain thresholds during different growth stages of the crop. Overall, temperature stress poses a significant threat to mustard crop productivity, highlighting the importance of understanding its impact and developing strategies to mitigate its effects on yield [26].

2.4 Impact of High Temperature on Biochemical Traits

The growth and development of plants are intricately linked to various biochemical reactions, many of which are sensitive to temperature fluctuations. Key biochemical parameters include both enzymatic and non-enzymatic components. Non-enzymatic parameters like proline, ascorbic acid, and carotenoids play crucial roles in plant stress responses [27]. Proline, for instance, acts as a secondary amino acid that accumulates under adverse conditions like high temperatures, aiding in maintaining relative water content and osmotic potential [28]. Studies on Indian mustard have shown that thermotolerant genotypes accumulate more proline compared to thermosensitive genotypes, indicating their ability to cope with heat stress [27]. Similarly, carotenoid synthesis helps reduce oxidative damage caused by reactive oxygen species (ROS), with temperature-tolerant genotypes exhibiting higher concentrations of ascorbic acid during terminal heat stress (Fig 2).

Enzymatic activators like hydrogen peroxide (H_2O_2) serve as stress indicators, with higher accumulation observed under heat stress conditions in mustard. Conversely, malondialdehyde (MDA), a byproduct of lipid peroxidation due to ROS, increases under high temperatures, leading to greater oxidative damage [29]. Selection of stress-tolerant genotypes involves minimizing MDA accumulation. To counteract ROS damage, plants synthesize antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione peroxidase (GPX), and ascorbate peroxidase (APX) [30]. Studies in Indian mustard have demonstrated increased activity of these enzymes under heat stress conditions, particularly in genotypes capable of withstanding terminal heat stress. For example, SOD activity was found to increase significantly in tolerant cultivars, along with elevated peroxidase activity observed in both tolerant and sensitive cultivars. Biochemical responses of plants to temperature stress is essential for identifying and developing stress-tolerant crop varieties, crucial for ensuring agricultural resilience in the face of climate change [27, 29].

2.5 Impact of High Temperature on Oil Attributing Traits

Heat stress significantly impacted the oil attributing traits in mustard, as evidenced by alterations in various biochemical parameters [27]. An increase in sugar content was observed, while there was a decrease in seed oil accumulation, indicating impaired incorporation of carbohydrates into triglycerides [31]. This shift in metabolic processes suggests a disruption in the normal pathways of oil biosynthesis under high temperature conditions. Furthermore, the seed oil percentage was notably reduced due to heat stress, highlighting the sensitivity of mustard oil accumulation to environmental fluctuations. The maximum seed oil content can be achieved under suitable conditions of temperature and relative humidity, emphasizing the importance of environmental factors in oil productivity. Zebarjadi *et al.* [32] have shown significant variations in oil content between stress and non-stress conditions, with differences of up to 40.01% to 38.1% observed in *Brassica juncea*, particularly under terminal heat.

These findings underscore the complex interplay between temperature stress and oil biosynthesis in mustard, with implications for both oil yield and quality. Understanding the mechanisms underlying these effects is crucial for the development of strategies to mitigate the adverse impacts of high temperatures on mustard oil production, ensuring the sustainability of oilseed cultivation in the face of climate change.

3. BREEDING MECHANISMS FOR HIGH TEMPERATURE STRESS

Conventional breeding techniques remain a cornerstone in the development of heat-tolerant cultivars, leveraging the inherent genetic diversity present in wild accessions. While incorporating traits from wild species can be challenging, a systematic approach can overcome these barriers and tap into the rich reservoir of genetic variability. Exotic libraries, comprised of marker-defined genomic segments from wild species introgressed into elite crop backgrounds, offer a promising avenue for enhancing agricultural performance. Molecular genetic markers, such as amplified fragment length polymorphism (AFLP), play a pivotal role in elucidating plant genomes and identifying heritable traits linked to genetic diversity [33]. The advent of molecular marker technology has revolutionized plant breeding, enabling rapid identification of heat-tolerance quantitative trait loci (QTLs) and stress-responsive genes through techniques like QTL mapping, QTL-seq analysis, and RNA sequencing [34].

Advancements in 'omics' technologies, particularly next-generation sequencing and comprehensive proteome profiling, provide invaluable insights into plant responses to heat stress. By integrating molecular analyses with physiological understanding, breeders can strategically enhance adaptability and productivity in crops facing rising global temperatures [20,21]. The synergy between traditional breeding methods and cutting-edge molecular techniques offers a promising pathway for the development of heat-tolerant crops. By harnessing the power of genetic diversity and leveraging advanced genomic tools, breeders can accelerate the breeding process and address the urgent need for climate-resilient agricultural systems [35].

4. PLANT RESPONSE MECHANISMS TO HEAT STRESS

Plants exhibit a sophisticated array of response mechanisms to cope with environmental stressors, including fluctuations in temperature. These responses involve intricate signaling pathways and molecular adjustments at various cellular levels, ensuring the plant's survival under adverse conditions. Upon perception of stress, multiple sensors come into play, including plasma membrane-mediated calcium flux,

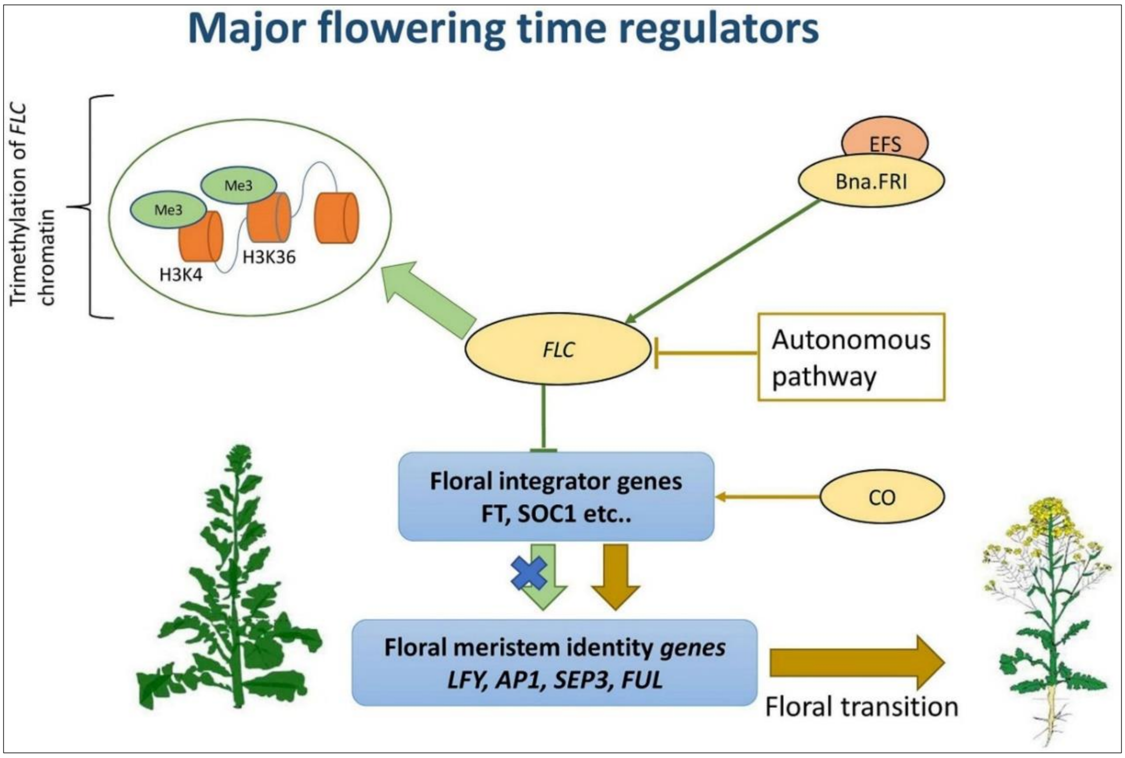

Fig. 3. Regulatory and signalling events involved in plant heat-stress response [26]

endoplasmic reticulum (ER) and cytosolic unfolded protein response (UPR) sensors, and changes in histone occupancy within the nuclei [19]. These sensors initiate a cascade of signaling events involving calcium fluxes, calmodulin, phosphatases, transcriptional regulators, hormones, and protein kinases such as CDPKs and MAPKs [36] (see Fig 3). The complexity of the heat stress response lies in the interconnected network of pathways involved, which exhibit tissue and developmental stage-specific responses [37-38]. This intricate machinery ensures that plants can adapt and mount appropriate responses to withstand heat stress and maintain optimal growth and development.

5. BREEDING APPROACHES TO COPE WITH HEAT STRESS IN MUSTARD

Breeding for heat stress tolerance in mustard (*Brassica juncea*) involves a multifaceted approach that integrates traditional breeding methods with cutting-edge molecular techniques. Given the complex genetic makeup and physiological responses of mustard to heat stress, a combination of strategies is essential to develop resilient cultivars capable of thriving under adverse conditions.

5.1 Conventional Breeding

Conventional breeding remains a fundamental approach to developing heat-tolerant mustard cultivars. This method involves selecting and crossing heat-tolerant parental lines to create progeny with improved tolerance to high temperatures. Phenotypic selection for traits such as early flowering, reduced flower abortion, and increased seed yield under heat stress conditions is crucial in this process [39]. Additionally, screening large populations under controlled heat stress environments helps identify promising genotypes with enhanced heat tolerance.

5.2 Marker-Assisted Selection (MAS)

Marker-assisted selection has revolutionized mustard breeding by enabling the identification and introgression of heat tolerance-related genes into elite cultivars. Molecular markers linked to heat tolerance QTLs (Quantitative Trait Loci) are identified through techniques like QTL mapping and QTL-seq analysis [40,1]. These markers facilitate the precise selection of heat-tolerant genotypes in breeding programs, expediting the development of resilient cultivars with improved adaptation to high-temperature environments.

5.3 Genomic Selection and Omics Technologies

Genomic selection, coupled with omics technologies such as next-generation sequencing and proteome profiling, offers promising avenues for enhancing heat stress tolerance in mustard [41]. By analysing the entire genome and proteome of mustard plants exposed to heat stress, breeders can identify candidate genes and proteins associated with heat tolerance. This information guides the selection of parental lines and facilitates the development of molecular breeding strategies aimed at enhancing heat stress resilience in mustard cultivars [42,43].

6. FUTURE PERSPECTIVES

The looming threat of climate change presents a significant challenge for oilseed crops, which serve as vital sources of food, fuel, and industrial products. The reproductive stage, critical for determining the economic value of oilseeds, is particularly vulnerable to high heat stress, impacting male and female reproductive organs. Physiological responses to heat stress, including lipid peroxidation, antioxidant changes, and metabolite reconfiguration, underscore the complex interplay of factors influencing plant resilience. Despite the adaptation mechanisms plants employ, further research is needed to deepen our understanding, particularly regarding the source-to-sink partitioning of assimilates.

Advancements in molecular breeding tools, such as CRISPR/Cas-based genome editing, offer promising avenues for developing heat-tolerant genotypes in oilseed crops. The integration of multi-omics approaches, encompassing genomics, transcriptomics, proteomics, and phenomics, will be instrumental in identifying stress-responsive genes and unraveling metabolic pathways crucial for heat stress adaptation. By expanding the gene pool and leveraging biotechnological tools, such as CRISPR/Cas9 and omics technologies, breeders can enhance the resilience of oilseed crops to climate-induced stresses. Furthermore, agronomic strategies, including nutrient management, microbial inoculation, and innovative agricultural technologies, play pivotal roles in mitigating the adverse effects of heat stress on oilseed crops. Future studies should focus on elucidating the mechanisms underlying the efficacy of microbial treatments in reducing heat stress, thus enhancing plant productivity and food security in the face of climate change. Through collaborative efforts and interdisciplinary research, we can strive towards sustainable improvements in oilseed crop productivity, ensuring resilience in the face of a changing climate and securing global food supplies.

7. CONCLUSION

The urgent need to address heat stress in Indian mustard cultivation, with a focus on developing adaptive strategies that can mitigate these adverse effects. To combat heat stress, plant response mechanisms involve complex cellular readjustments, requiring advanced knowledge at the transcriptome, epigenomic, proteome, and metabolome levels. Breeding approaches, incorporating both traditional methods and cutting-edge technologies like CRISPR/Cas-based genome editing, are paving the way toward creating heat-tolerant cultivars. Additionally, multi-omics studies are proving invaluable in identifying stress-responsive genes and pathways crucial for plant adaptation. Agronomic practices, including nutrient management and the use of beneficial microbes, play a critical role in boosting plant resilience to heat stress. However, addressing these challenges requires collaborative and interdisciplinary efforts. By integrating expertise across various scientific disciplines, researchers can further explore heat stress responses and develop comprehensive solutions to ensure the sustainability and productivity of oilseed crops, contributing to food security in the context of climate change. The way forward demands sustained attention, innovation, and cooperation to develop and implement effective adaptation strategies for Indian mustard cultivation. This review serves as a call to action, underlining the importance of addressing heat stress in this essential crop to promote sustainable agriculture and food security.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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