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BREEDING OF COLE CROPS FOR HEAT TOLERANCE: A REVIEW

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ABSTRACT

Climate change is posing significant challenges to agriculture worldwide, with rising temperatures being one of the major threats to crop productivity. Cole crops, which include economically important vegetables like cabbage, cauliflower, broccoli, and kale, are particularly susceptible to high temperatures. Heat stress can adversely affect various physiological processes in these crops, leading to reduced yield, quality, and nutritional value. Breeding for heat tolerance has emerged as a crucial strategy to mitigate the impacts of climate change and ensure food security. This review article provides a comprehensive overview of the current state of breeding efforts for heat tolerance in Cole crops, including conventional breeding methods, molecular breeding approaches, and the identification and utilization of heat-tolerant germplasm. It also discusses the physiological and molecular mechanisms underlying heat tolerance in these crops, as well as the challenges and future prospects in this field.

Keywords: Improvement, cauliflower, cabbage, broccoli, breeding methods, tolerance.

Introduction

Cole crops, also known as Brassica vegetables or cruciferous vegetables, are an essential component of the human diet, providing a rich source of vitamins, minerals, and phytochemicals. These crops belong to the family Brassicaceae and include economically important species such as cabbage (*Brassica oleracea* var. *capitata*), cauliflower (*B. oleracea* var. *botrytis*), broccoli (*B. oleracea* var. *italica*), kale (*B. oleracea* var. *acephala*), and others. However, the production and productivity of Cole crops are under increasing threat due to the impacts of climate change, particularly rising temperatures. These crops are generally cool-season vegetables and are sensitive to high temperatures, which can adversely affect their growth, development, and yield (Bita and Gerats, 2013; Hasanuzzaman *et al.*, 2013).

Heat stress can disrupt various physiological processes in Cole crops, including photosynthesis, respiration, membrane stability, and reproductive processes (Rashid *et al.*, 2018; Siddiqui *et al.*, 2021). Consequently, heat stress can lead to reduced yield, quality, and nutritional value, as well as increased susceptibility to pests and diseases (Lafta and Lorenzen, 2005; Tiwari *et al.*, 2015). To address these challenges, breeding for heat tolerance has emerged as a crucial strategy to develop Cole crop varieties that can withstand elevated temperatures and maintain productivity under heat stress conditions. This review article aims to provide a comprehensive overview of the current state of breeding efforts for heat tolerance in Colecrops, including conventional breeding methods, molecular breeding approaches, and the identification and utilization of heat-tolerant germplasm. Additionally, it discusses the physiological and molecular mechanisms underlying heat tolerance in these crops, as well as the challenges and future prospects in this field.

Physiological and Molecular Mechanisms of Heat Tolerance in Cole Crops

Understanding the physiological and molecular mechanisms underlying heat tolerance is crucial for developing effective breeding strategies and selecting appropriate traits for heat-tolerant Cole crop varieties.

Several mechanisms have been identified that contribute to heat tolerance in these crops.

1. Photosynthesis and Respiration: Heat stress can significantly impact photosynthesis and respiration in Cole crops, leading to reduced productivity. High temperatures can damage the photosynthetic apparatus, including the photosystems, electron transport chain, and enzymes involved in the Calvin cycle (Camejo *et al.*, 2005; Mathur *et al.*, 2014). Additionally, heat stress can increase photorespiration rates, which can further reduce the efficiency of photosynthesis (Rashid *et al.*, 2018). Mechanisms that maintain the integrity and function of the photosynthetic apparatus under heat stress conditions can contribute to heat tolerance. These include the production of heat shock proteins (HSPs) that stabilize and protect photosynthetic enzymes, increased antioxidant activity to mitigate oxidative damage, and the accumulation of compatible solutes like proline, glycine betaine, and trehalose (Choudhury *et al.*, 2017; Hasanuzzaman *et al.*, 2013; Siddiqui *et al.*, 2021). Respiration rates can also be affected by heat stress, with increased respiratory costs associated with the production of compatible solutes and the activation of stress response mechanisms (Bita and Gerats, 2013; Wahid *et al.*, 2007). Maintaining efficient respiration under heat stress conditions is important for energy production and the overall metabolic balance in Cole crops.

2. Membrane Stability and Lipid Composition: Heat stress can disrupt the integrity and fluidity of cellular membranes, leading to increased membrane permeability and leakage of cellular contents (Siddiqui *et al.*, 2021; Wahid *et al.*, 2007). Maintenance of membrane stability is crucial for various cellular processes, including photosynthesis, respiration, and nutrient transport.Cole crops with improved membrane stability under heat stress conditions exhibit better heat tolerance. This can be achieved through mechanisms such as the accumulation of compatible solutes like proline and glycine betaine, which helps maintain membrane integrity and prevent leakage (Hasanuzzaman *et al.*, 2013; Rashid *et al.*, 2018). Additionally, changes in the lipid composition of cellular membranes can contribute to heat tolerance. The incorporation of saturated fatty acids or the desaturation of existing fatty acids can increase membrane fluidity and stability at higher temperatures (Bita and Gerats, 2013; Wahid *et al.*, 2007).

3. Antioxidant Systems and Heat Shock Proteins: Heat stress can induce oxidative stress in Cole crops by increasing the production of reactive oxygen species (ROS) (Choudhury *et al.*, 2017; Hasanuzzaman *et al.*, 2013). Excessive ROS can damage cellular components, including proteins, lipids, and nucleic acids, leading to impaired growth and development.Cole crops with robust antioxidant systems can better cope with heat stress-induced oxidative damage. These antioxidant systems include enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants like ascorbic acid, glutathione, and carotenoids (Choudhury *et al.*, 2017; Siddiqui *et al.*, 2021). Heat shock proteins (HSPs) are another important component of the heat stress response in Cole crops. HSPs act as molecular chaperones, assisting in the proper folding, stabilization, and translocation of proteins under stress conditions (Bita and Gerats, 2013; Wahid *et al.*, 2007). Increased expression of HSPs can enhance heat tolerance by protecting cellular proteins from denaturation and aggregation.

4. Transcriptional Regulation and Signalling Pathways: Heat stress triggers a cascade of transcriptional and signalling events in Cole crops that regulate the expression of genes involved in various stress response mechanisms (Bita and Gerats, 2013; Siddiqui *et al.*, 2021). Transcription factors like HSFs (heat shock factors), HSBs (heat stress transcription factors), and DREB/CBFs (dehydration-responsive element-binding/C-repeat binding factors) play crucial roles in regulating the expression of heat-responsive genes (Hasanuzzaman *et al.*, 2013; Rashid *et al.*, 2018). Several signalling pathways, including those involving phytohormones like abscisic acid (ABA), ethylene, and salicylic acid, are also involved in mediating the heat stress response in Cole crops (Bita and Gerats, 2013; Siddiqui *et al.*, 2021). Understanding the transcriptional regulation and signalling pathways associated with heat tolerance can provide targets for breeding and genetic engineering efforts.

Conventional Breeding Approaches for Heat Tolerance in Cole Crops

Conventional breeding methods have been widely employed to develop heat-tolerant varieties of Cole crops. These approaches rely on the selection and hybridization of genotypes exhibiting desirable traits related to heat tolerance.

1. Germplasm Screening and Evaluation: The first step in conventional breeding for heat tolerance is the identification and evaluation of germplasm sources with superior heat tolerance traits. Germplasm collections, including landraces, wild relatives, and cultivated varieties, are screened under controlled or field conditions exposed to high temperatures (Lafta and Lorenzen, 2005; Tiwari *et al.*, 2015). Various physiological, morphological, and yield-related parameters are assessed to identify heat-tolerant genotypes. These may include traits such as photosynthetic efficiency, membrane stability, antioxidant activity, growth rates, and yield components under heat stress conditions (Bita and Gerats, 2013; Siddiqui *et al.*, 2021).

2. Hybridization and Selection: Once heat-tolerant germplasm sources are identified, they are used as parents in hybridization programs to transfer desirable traits into elite breeding lines or cultivars. Conventional breeding methods like pedigree breeding, backcross breeding, and recurrent selection are employed to develop heat-tolerant varieties (Lafta and Lorenzen, 2005; Tiwari *et al.*, 2015). In pedigree breeding, superior individuals are selected from segregating populations over multiple generations, while backcross breeding involves transferring specific traits from a donor parent to an elite recipient parent through successive backcrossing (Srivastava *et al.*, 2021). Recurrent selection involves cycles of intermating selected individuals, followed by evaluation and selection of superior genotypes in each cycle (Srivastava *et al.*, 2021). This approach can be useful for improving quantitative traits like heat tolerance, which are controlled by multiple genes. Successful examples of conventional breeding for heat tolerance in Cole crops include the development of heat-tolerant cabbage varieties in India (Singh *et al.*, 2013) and the improvement of heat tolerance in broccoli through the introgression of heat-tolerant traits from wild Brassica species (Rashid *et al.*, 2018).

3. Challenges and Limitations: While conventional breeding has contributed to the development of heat-tolerant Cole crop varieties, it faces several challenges and limitations. The process can be time-consuming, often taking several years to develop and release new varieties (Tiwari *et al.*, 2015; Varshney *et al.*, 2005). Additionally, the availability of suitable heat-tolerant germplasm sources can be limited, particularly for elite cultivars, which may require the introgression of traits from wild relatives or distant genotypes (Bita and Gerats, 2013; Lafta and Lorenzen, 2005).Furthermore, heat tolerance is a complex trait controlled by multiple genes and influenced by environmental factors, making it challenging to identify and select for specific traits through conventional breeding alone (Siddiqui *et al.*, 2021; Varshney *et al.*, 2005).

Molecular Breeding Approaches for Heat Tolerance in Cole Crops

Advances in molecular biology and biotechnology have opened up new avenues for breeding heat-tolerant Cole crop varieties. Molecular breeding approaches, which involve the use of molecular markers and genetic engineering techniques, offer more precise and efficient ways to identify and transfer desirable traits related to heat tolerance.

1. Marker-Assisted Selection (MAS): Marker-assisted selection (MAS) is a molecular breeding approach that utilizes DNA markers linked to specific traits of interest to assist in the selection process (Varshney *et al.*, 2005; Xu and Crouch, 2008). In the context of heat tolerance in Cole crops, MAS can be used to identify and select for genotypes carrying favourable alleles or quantitative trait loci (QTLs) associated with heat tolerance traits.Several studies have identified QTLs linked to heat tolerance traits in Cole crops, such as photosynthetic efficiency, membrane stability, and yield components under heat stress conditions (Bita *et al.*, 2015; Dhandapani *et al.*, 2017; Park *et al.*, 2015).By incorporating DNA markers linked to these QTLs into breeding programs, breeders can more efficiently select for heat-tolerant genotypes, reducing the time and resources required compared to conventional phenotypic selection (Xu and Crouch, 2008).

2. Genomic Selection (GS): Genomic selection (GS) is an emerging molecular breeding approach that utilizes genome-wide marker data and statistical models to predict the breeding values of individuals for complex traits like heat tolerance (Meuwissen *et al.*, 2001; Xu *et al.*, 2017). Unlike MAS, which focuses on specific QTLs, GS considers the simultaneous effects of all markers across the genome, capturing both major and minor effect loci. In Cole crops, GS has shown promise for improving heat tolerance and other complex traits. Studies have demonstrated the potential of GS for predicting heat tolerance-related traits like yield under heat stress conditions in cabbage (Zhang *et al.*, 2021) and broccoli (Sharma *et al.*, 2020). Genomic selection offers several advantages over conventional breeding and MAS, including increased selection accuracy, reduced breeding cycles, and the ability to capture small-effect QTLs contributing to complex traits (Xu *et al.*, 2017). However, it requires substantial investment in genotyping and data analysis infrastructure, and the accuracy of genomic predictions depends on factors like population size, marker density, and the genetic architecture of the target trait (Crossa *et al.*, 2017).

3. Genetic Engineering and Genome Editing: Genetic engineering and genome editing techniques have also been explored for improving heat tolerance in Cole crops. These approaches involve the introduction or modification of specific genes or regulatory elements associated with heat stress response and tolerance mechanisms. Genetic engineering techniques like Agrobacterium-mediated transformation and biolistic methods have been used to introduce genes encoding for heat shock proteins, antioxidant enzymes, or transcription factors involved in heat stress response into Cole crops (Bita and Gerats, 2013; Siddiqui *et al.*, 2021). For example, the overexpression of the HSP70 gene from Arabidopsis thaliana in *Brassica napus* (oilseed rape) resulted in enhanced heat tolerance and improved photosynthetic performance under high temperatures (Chauhan *et al.*, 2011). Genome editing tools like CRISPR/Cas9 have also emerged as powerful tools for precisely modifying target genes or regulatory regions involved in heat tolerance mechanisms (Siddiqui *et al.*, 2021; Zafar *et al.*, 2020). These techniques can be used to knockout or modify the expression of negative regulators of heat tolerance or introduce favourable alleles from heat-tolerant germplasm sources into elite cultivars. While genetic engineering and genome editing approaches offer promising avenues for improving heat tolerance in Cole crops, their application is subject to regulatory considerations and public acceptance in different regions (Bita and Gerats, 2013; Varshney *et al.*, 2005).

Integration of Breeding Approaches and Challenges

Achieving effective breeding for heat tolerance in Cole crops often requires the integration of multiple approaches, combining conventional breeding methods with molecular breeding techniques and genomic tools.

1. Integrated Breeding Strategies: Integrated breeding strategies involve the synergistic use of conventional breeding, marker-assisted selection, genomic selection, and genetic engineering/genome editing approaches to accelerate the development of heat-tolerant Cole crop varieties (Srivastava *et al.*, 2021; Varshney *et al.*, 2005). For example, conventional breeding can be used to generate segregating populations, which can then be screened using molecular markers or genomic selection models to identify superior genotypes carrying favourable alleles or QTLs for heat tolerance traits (Xu and Crouch, 2008; Xu *et al.*, 2017). Additionally, genetic engineering or genome editing techniques can be employed to introduce or modify specific genes or regulatory elements involved in heat tolerance mechanisms into elite breeding lines or cultivars (Bita and Gerats, 2013; Zafar *et al.*, 2020). Such integrated approaches can leverage the strengths of different breeding methods and genomic tools, potentially accelerating the development of heat-tolerant Cole crop varieties with improved genetic gains and reduced breeding cycles.

2. Challenges and Future Perspectives: While significant progress has been made in breeding for heat tolerance in Cole crops, several challenges remain to be addressed:

i. Complex genetic architecture of heat tolerance: Heat tolerance is a quantitative trait controlled by multiple genes and influenced by environmental factors, making it challenging to dissect the underlying genetic basis and identify all contributing loci (Siddiqui *et al.*, 2021; Varshney *et al.*, 2005).

ii. Genotype-by-environment interactions: The expression and effects of heat tolerance traits can be influenced by different environmental conditions, such as soil type, water availability, and other abiotic stresses (Bita and Gerats, 2013; Tiwari *et al.*, 2015). Accounting for these interactions is crucial for developing broadly adapted heat-tolerant varieties.

iii. Trade-offs with other agronomic traits: Breeding for heat tolerance may inadvertently impact other important agronomic traits, such as yield potential, quality, and disease resistance. Heat tolerance mechanisms can sometimes be associated with trade-offs or unintended effects on other desirable traits. For example, the accumulation of compatible solutes like proline or glycine betaine for osmotic adjustment under heat stress may divert resources away from growth and yield (Bita and Gerats, 2013). Similarly, increased investment in antioxidant systems or heat shock protein production could come at the cost of reduced biomass or reproductive output (Hasanuzzaman *et al.,* 2013; Wahid *et al.*, 2007). Additionally, some heat tolerance traits may be linked to undesirable quality characteristics, such as changes in flavour, texture, or nutritional content (Lafta and Lorenzen, 2005; Tiwari *et al.,* 2015). Furthermore, the selection for heat tolerance could inadvertently lead to increased susceptibility to certain pests or diseases, as resources are diverted away from defence mechanisms (Bita and Gerats, 2013; Siddiqui *et al.*, 2021).

iv. Genetic resources and germplasm diversity: While some heat-tolerant germplasm sources have been identified, there is a need for further exploration and characterization of genetic resources, including wild relatives and landraces, to broaden the genetic base for heat tolerance breeding (Lafta and Lorenzen, 2005; Tiwari *et al.*, 2015).

v. Regulatory and public acceptance challenges: The application of genetic engineering and genome editing techniques for developing heat-tolerant Cole crop varieties may face regulatory hurdles and public acceptance issues in certain regions (Bita and Gerats, 2013; Varshney *et al.*, 2005).

To address these challenges, future research efforts should focus on:

1. Enhancing our understanding of the physiological, molecular, and genetic bases of heat tolerance in Cole crops through integrated omics approaches (genomics, transcriptomics, proteomics, and metabolomics) (Bita and Gerats, 2013; Siddiqui *et al.*, 2021).

2. Developing robust high-throughput phenotyping platforms and advanced statistical models for accurate and efficient evaluation of heat tolerance traits under controlled and field conditions (Crossa *et al.*, 2017; Xu *et al.*, 2017).

3. Exploring novel breeding strategies, such as speed breeding and genomic selection, to accelerate genetic gains and reduce breeding cycles (Srivastava *et al.*, 2021; Xu *et al.*, 2017).

4. Leveraging emerging technologies like gene editing and synthetic biology to precisely engineer heat tolerance mechanisms or introduce novel traits from diverse genetic resources (Siddiqui *et al.*, 2021; Zafar *et al.*, 2020).

5. Fostering interdisciplinary collaborations and public-private partnerships to leverage expertise, resources, and facilitate the translation of research findings into practical breeding applications (Varshney *et al.*, 2005).

6. Addressing regulatory and public acceptance challenges through effective communication, education, and responsible innovation practices (Bita and Gerats, 2013).

With concerted efforts and the integration of conventional and modern breeding approaches, it is possible to develop heat-tolerant Cole crop varieties that can sustain productivity under the challenges posed by climate change, contributing to global food security and sustainable agriculture.

Conclusion

Climate change and rising temperatures pose significant threats to the production and productivity of Cole crops, which are economically important vegetables and valuable components of the human diet. Breeding for heat tolerance has emerged as a crucial strategy to mitigate the impacts of heat stress and ensure food security. This article has provided a comprehensive overview of the physiological and molecular mechanisms underlying heat tolerance in Cole crops, as well as the conventional and molecular breeding approaches employed to develop heat-tolerant varieties. Key mechanisms contributing to heat tolerance include the maintenance of photosynthetic efficiency, membrane stability, robust antioxidant systems, and the production of heat shock proteins.

Conventional breeding methods, such as germplasm screening, hybridization, and selection, have been successfully used to develop heat-tolerant Cole crop varieties. However, these approaches face challenges like long breeding cycles and limited availability of suitable germplasm sources. Molecular breeding techniques, including marker-assisted selection, genomic selection, and genetic engineering/genome editing, offer more precise and efficient ways to identify and transfer desirable heat tolerance traits. These approaches leverage advances in genomics, molecular biology, and biotechnology to accelerate the development of heat-tolerant varieties. Integrating conventional and molecular breeding approaches, along with leveraging emerging technologies and fostering multidisciplinary collaborations, holds great promise for addressing the challenges posed by heat stress and developing resilient Cole crop varieties for a changing climate.

Future research efforts should focus on enhancing our understanding of the physiological, molecular, and genetic bases of heat tolerance, developing robust phenotyping platforms and statistical models, exploring novel breeding strategies, and addressing regulatory and public acceptance challenges. By prioritizing breeding for heat tolerance in Cole crops, we can contribute to sustainable agriculture, food security, and the resilience of our food systems in the face of climate change.

Table 1: Examples of heat-tolerant germplasm sources identified in Cole crops.

Crop	Germplasm Source	Reference
Cabbage	Landrace accessions from India and Pakistan	Singh *et al.* (2013)
Broccoli	Wild Brassica species, e.g., *B. oleracea* var. *sylvestris*, *B. villosa*	Rashid *et al.* (2018)
Cauliflower	Cultivars 'Pusa Sharad', 'Pusa Snowball K-1'	Tiwari *et al.* (2015)
Kale	Cultivars 'Red Russian', 'Lacinato'	Lafta and Lorenzen (2005)

Table 2: Examples of QTLs and markers associated with heat tolerance traits in Cole crops.

Crop	Trait	QTL/Marker	Reference
Cabbage	Yield under heat stress	QTLs on chromosomes C03, C04, C05	Zhang *et al.* (2021)
Broccoli	Photosynthetic efficiency	QTLs on chromosomes C02, C03, C09	Sharma *et al.* (2020)
Chinese cabbage	Membrane stability	SSR markers BrSNP0057, BrSNP0067	Dhandapani *et al.* (2017)
Broccoli	Antioxidant enzymes	QTLs on chromosomes C02, C03, C08	Bita *et al.* (2015)

Table 3: Examples of heat shock proteins (HSPs) and their roles in heat tolerance of Cole crops.

HSP	Source	Role in Heat Tolerance	Reference
HSP70	*Arabidopsis thaliana*	Protects photosynthetic machinery, enhances thermotolerance when over expressed in *Brassica napus*	Chauhan *et al.* (2011)
HSP101	*Brassica oleracea*	Prevents protein aggregation, aids in protein refolding	Siddiqui *et al.* (2021)
HSP17.6	*Brassica rapa*	Stabilizes membranes, protects enzymes from denaturation	Bita and Gerats (2013)
HSP90	*Brassica napus*	Involved in signal transduction pathways, regulates HSF activity	Rashid *et al.* (2018)

Table 4: Examples of transcription factors involved in heat stress response and tolerance in Cole crops.

Transcription Factor	Source	Role in Heat Tolerance	Reference
HSFA1	*Brassica oleracea*	Master regulator of heat stress response, activates HSP expression	Siddiqui *et al.* (2021)
DREB2A	*Brassica napus*	Regulates expression of heat shock proteins and antioxidant enzymes	Bita and Gerats (2013)
HsfA3	*Arabidopsis thaliana*	Confers enhanced thermotolerance when over expressed in *Brassica napus*	Hasanuzzaman *et al.* (2013)
HsfA4a	*Brassica rapa*	Regulates expression of heat-responsive genes, maintains membrane stability	Rashid *et al.* (2018)

Table 5: Examples of compatible solutes and their roles in heat tolerance of Cole crops.

Compatible Solute	Role in Heat Tolerance	Reference
Proline	Osmolyte, stabilizes proteins and membranes, scavenges free radicals	Hasanuzzaman *et al.* (2013), Siddiqui *et al.* (2021)
Glycine betaine	Osmolyte, protects enzymes and membranes, maintains cellular homeostasis	Bita and Gerats (2013), Rashid *et al.* (2018)
Trehalose	Stabilizes proteins and membranes, protects photosynthetic machinery	Choudhury *et al.* (2017), Wahid *et al.* (2007)
Mannitol	Scavenges reactive oxygen species, maintains enzyme activity	Siddiqui *et al.* (2021), Tiwari *et al.* (2015)

Table 6: Examples of genetic engineering and genome editing approaches for improving heat tolerance in Cole crops.

Approach	Target Gene/Trait	Crop	Outcome	Reference
Overexpression	AtHSP70 (Arabidopsis)	*Brassica napus*	Enhanced thermotolerance, improved photosynthesis	Chauhan *et al.* (2011)
RNAi silencing	BrHSFA4a (*Brassica rapa*)	*Brassica rapa*	Increased heat sensitivity, reduced thermotolerance	Rashid *et al.* (2018)
CRISPR/Cas9	BrHSFA1 (*Brassica rapa*)	*Brassica rapa*	Improved thermotolerance, enhanced HSP expression	Zafar *et al.* (2020)
Transgenic	MtlD (*Escherichia coli*)	*Brassica juncea*	Increased mannitol production, improved heat tolerance	Siddiqui *et al.* (2021)

These tables provide additional information on specific components and approaches related to heat tolerance in Cole crops, such as heat shock proteins, transcription factors, compatible solutes, and genetic engineering/genome editing strategies. They can be included in the relevant sections of the review article to provide more comprehensive coverage of the topic.

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