

Review

Understanding heat tolerance in vegetables: Physiological and molecular insights, and contemporary genomic approaches for enhancing heat stress resilience

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ABSTRACT

The increasing threat of heat stress in agriculture, fueled by the relentless rise in global temperatures, presents a formidable challenge for vegetable crops. High-temperature stress instigates intricate morphological, anatomical, and physiological changes in vegetables, resulting in a noticeable decline in yield and an overall compromise in quality. Mitigating these challenges necessitates the imperative development of heat-tolerant vegetable varieties, underscoring the need for a nuanced understanding of crop responses to the rigors of high-temperature stress. This comprehensive review systematically explores the multifaceted impacts of heat stress on vegetable crops, spanning morphological traits, physiological processes, and molecular dynamics. Beyond the identification of challenges, the review explores into the intricate adaptive mechanisms employed by vegetables to counteract the stresses imposed by elevated temperatures, besides exploring in detailed how these crops navigate and respond to the physiological disruptions caused by heat stress. Further, it also assesses the efficacy of diverse genomic approaches in the development of heat-tolerant vegetable varieties. In addition, the review explores genomic tools such as genomic selection, transgenic approaches, and genome editing technologies, which hold promise in expediting the development of vegetable varieties endowed with enhanced thermo-tolerance and heightened productivity. By synthesizing insights from diverse scientific realms, the review aspires to provide a comprehensive and integrative perspective on mitigating the adverse impacts of heat stress on vegetable crops, paving the way for sustainable agricultural practices in the face of escalating global temperatures.

Keywords: Abiotic stress, climate change, genome editing, genomics, heat tolerance

INTRODUCTION

Human-induced greenhouse gas emissions have indisputably driven a 1.1°C global surface temperature increase from pre-industrial levels (1850–1900) to 2011–2020, and despite the consistent expansion of mitigation policies since Assessment Report 5 (AR5), the projected emissions for 2030 suggest a trajectory that is likely to surpass the 1.5°C warming threshold, making it increasingly challenging to limit global warming below 2°C (IPCC, 2023). This escalating temperature trend has significantly impacted the growth and development of nearly all crops, leading to substantial losses in yield and quality on a global scale. Heat stress exerts detrimental effects on essential physiological processes such as photosynthesis,

respiration, and membrane stability. Exceeding the crop-specific threshold temperature induces morphological and physiological injuries, severely affecting seed germination, as well as reproductive and vegetative growth. Vegetables play a crucial role in addressing micronutrient deficiencies, offering income prospects for small landholding farmers, and creating more employment opportunities per hectare compared to staple crops; however, the substantial reductions in yield and quality resulting from heat stress pose a significant threat to livelihoods. The biochemical, metabolic, and physiological processes crucial for vegetable growth are temperature-dependent, and elevated temperatures negatively impact these vital processes, resulting in diminished vegetable production.



Temperatures surpassing 25°C contribute to fruit-setting failure due to factors such as bud drop, reduced pollen production, low pollen viability, abnormal flower development, ovule abortion, inadequate carbohydrate supply, and other reproductive abnormalities (Hazra et al., 2007). Addressing the adverse effects of global warming on vegetables necessitates the development of heat-tolerant varieties. In response to heat stress, various mechanisms, including the activation of heat stress-related genes, metabolite production, and signal transduction, come into play. Vegetables have evolved intricate biochemical, physiological, cellular, and molecular systems to adapt and respond to heat stress. Breeding heat-tolerant vegetable varieties requires a deep understanding of the genetic basis of heat tolerance and the response mechanisms to heat stress. Modern genomics plays a crucial role in vegetable heat stress breeding, encompassing techniques such as marker assisted selection (MAS), quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), genomic selection (GS), transgenic approaches, and genome editing tools. These advanced genomic tools enhance the efficiency of developing heat stress-tolerant genotypes with improved yield. This comprehensive review elucidates the impact of elevated temperatures on vegetables, explores the adaptation mechanisms employed by these crops, and provides an in-depth discussion on the use of both conventional breeding approaches and modern genomic tools to effectively combat heat stress in vegetables.

High temperature effects on different stages of vegetables

Over the past two decades, research has consistently demonstrated the adverse impacts of increasing temperatures on various types of vegetables across different growth phases.

Seed germination: The germination of seeds represents the initial phase of plant development, and this critical stage is significantly impacted by elevated temperatures, albeit with variations in the optimal temperature range for different vegetables. Heat stress negatively influences seed germination across various crop species, manifesting in reduced germination percentages, delayed emergence, weakened seedlings, and impaired growth of radicles and plumules (Sehgal et al., 2018). Studies by Besma & Mounir (2010) noted diminished germination of okra at 40°C.

Heat stress adversely affects the germination and development of cucumbers (Kurtar, 2010), in carrot >35°C (Nascimento et al., 2008), in cucumber and melon 42°C and 45°C, respectively, while, seeds of pumpkin, summer squash, winter squash, and watermelon fail to germinate at 42°C (Kurtar & Balkaya, 2010), and in spinach, germination unexpectedly decreases between 25 and 30°C, and it ceases completely at 35°C (Chitwood, 2016). These findings underscore the vulnerability of seed germination to elevated temperatures across diverse vegetable species.

Vegetative growth and quality: In tomato, lycopene degradation initiated above 25°C and complete destruction occurred at 50°C (Hackett et al., 2004). Heat stress also impacts the development of red color in ripening chili fruits. Heat stress in tomatoes manifests in various undesirable outcomes, including the occurrence of green shoulders, fruit cracking, sunburn, and blossom-end rot. Wien (1997) observed that temperatures above 17-28°C in lettuce led to issues such as tip burn, leaf chlorosis, loose and puffy heads, and the accumulation of bitter compounds. Dark red lettuce plants exposed to a temperature of 33°C exhibited induced bolting and bitterness, ultimately diminishing the yield and quality of dark red lettuce (Ilić et al., 2017). High temperatures contribute to issues such as tip burn, bracting, hollow stem, and loose heads in broccoli (Kałużewicz et al., 2012). Cabbage experiences decreased leaf expansion above 32°C, while, Chinese cabbage is susceptible to tip burn, and cauliflower may exhibit bracting under elevated temperatures (Nievola et al 2017). At 40°C, Tekalign et al. (2012) observed alterations in onion bulb size accompanied by an increase in sulfur content. Heat stress in pepper (Valles-Rosales et al., 2016), manifested in fruit cracking, sunburn, and blossom-end rot, ultimately diminishing the quality of the produce. For potatoes, temperatures exceeding 22°C led to a reduction in tuber development, with tuberization inhibited at 25°C and above, while, Suzuki et al. (2014) documented responses to heat stress in okra, including a reduction in plant shoot length, burning of leaf tips, necrosis, yellowing, and scorching of leaves.

Reproductive growth: Kałużewicz et al. (2012) reported a decrease in bud size in broccoli attributed to rising temperatures, specifically highlighting the adverse impact on flower and fertilization aspects. Bell

peppers experienced flower drop at temperatures surpassing 32°C, while hot peppers exhibited a reduction in both flower and fruit numbers at temperatures above 38°C (Erickson & Markhart, 2001). Watermelon and cucumber shows reduced flowering at temperatures exceeding 35°C, while, tomatoes faced a decline in the number of fruits and flowers at temperatures >25°C. Notably, heat stress induced stigma elongation in tomatoes, hindering the process of self-pollination (Pan et al., 2019). Several studies had shown that elevated day temperatures have been observed to negatively impact anthesis, dehiscence, and fruit setting in both tomato and capsicum. Screening studies conducted under heat stress conditions for tomatoes indicated a decrease in pollen viability, ovule viability, and the number of released pollens (Singh et al., 2015). Furthermore, high temperatures contribute to pollen abortion, consequently reducing seed viability (Chaudhary et al., 2022).

Effects of heat stress on physiological processes

Various physiological processes, including photosynthesis, respiration, and membrane stability, undergo disruption in the presence of heat stress.

Photosynthesis: Elevated temperatures have a significant impact on the photosynthetic process in plants. Moderate heat stress, typically ranging from 35-40°C, induces the enlargement of chloroplasts and an increase in plastid vesicles within them, indicating a substantial alteration in the structural composition of chloroplasts and thylakoids (Zeng et al., 2021). Both heat-sensitive and heat-tolerant potato cultivars show a decrease in photosynthetic activity under heat stress conditions (Aien et al., 2011). Similarly, studies on okra genotypes reveal a reduction in photosynthetic activity at 45°C, with heat-sensitive genotypes experiencing more adverse effects than heat-tolerant ones (Hayamanesh et al., 2023). The net photosynthetic rates (A) of Chinese cabbage and radish exhibit a decline at temperatures surpassing approximately 25°C, which corresponds to their optimum temperature for photosynthesis (Oh et al., 2015). This decrease is attributed, at least in part, to elevated rates of respiration observed above 25 or 30°C. The vulnerability of PS II electron transport to heat stress can be attributed to two primary factors: firstly, the elevated fluidity of thylakoid membranes at higher temperatures leads to the displacement of

PS II light harvesting complexes from the membrane; and secondly, the integrity of PS II is reliant on the dynamic behavior of electrons (Mathur et al., 2014).

Membrane stability: The normal functioning of cellular membranes is indispensable for vital processes such as photosynthesis and respiration. However, biological membranes are highly sensitive to heat stress, and their stability can be compromised. Elevated temperatures intensify the molecular movements within biological membranes, disrupting the chemical bonds between molecules. Heat stress induces alterations in the tertiary and quaternary structures of membrane proteins, leading to increased membrane permeability and subsequent electrolyte loss. Oxidative stress induced by heat stress leads to the peroxidation of membrane lipids, proteins, and nucleic acids (Mittler et al., 2004). This results in reduced membrane stability, leading to an increase in electrolyte leakage and exacerbating membrane injuries (Wahid et al., 2007). In tomatoes, subjected to heat stress, ion leakage from the cell membrane was found to be negatively associated with inflorescence number, pollen germination, and fruit setting (Xu et al., 2017). All reported findings on the relationship between thermo-membrane stability and heat stress tolerance consistently indicate that crop genotypes with higher thermo-membrane stability exhibit greater heat stress tolerance.

Oxidative stress: Plants experiencing heat stress undergo the generation of reactive oxygen species (ROS), including singlet oxygen (O_2^1), superoxide radical ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH^{\cdot}), leading to oxidative stress (Choudhury et al., 2013), results in cell injury through the oxidation of lipids, nucleic acids, and proteins. Notably, lipids, crucial components of cell membranes and organelles, are primary targets for these active oxygen species. The autocatalytic peroxidation of unsaturated fatty acids in membrane lipids, triggered by reactive oxygen species, induces membrane permeability loss, electrolyte leakage, and ultimately cell death (Wahid et al., 2007). Investigations reveal that plants when exposed to higher temperatures accumulate more of H_2O_2 due to reduced activities of ROS scavengers such as catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), and dehydroascorbate reductase (DHAR).

Impact of heat stress at molecular level

In response to heat stress, there is a dynamic modulation in the expression of genes crucial for safeguarding vegetables from the adverse effects of elevated temperatures. These genes encompass those associated with the synthesis of osmoprotectants, detoxification enzymes, heat shock proteins, and various regulatory proteins (Slama et al., 2015). Elevated temperatures induce enzyme deactivation, inhibit protein synthesis, and cause aggregation in chloroplasts and mitochondria. Specific cellular proteins or transcription factors regulate genes linked to stress.

Under high-temperature stress, various heat shock factors (HSFs), transcription factors (TFs), chaperones, and osmoprotectants become activated (Jacob et al., 2017). Studies have underscored the efficacy of specific genes in enhancing plant resilience to heat stress. For instance, the overexpression of the *StnsLTP1* gene in potatoes enhances cell membrane integrity during heat stress (Gangadhar et al., 2016). In potato plants subjected to high-temperature stress, overexpression of the *APX*, *Cu/Zn SOD*, and *NDPK2* genes improves oxidative stress tolerance (Kim, 2010). Similarly, in tomato plants, the *LeAN2* gene, when overexpressed during heat stress, boosts fresh weight production, antioxidant activity, and photosynthesis rate (Kumar et al., 2012). Overexpression of the *cAPX* gene in tomato plants enhances tolerance to heat stress (Gerszberg & Hnatuszko-Konka, 2017). Research on chilli genotypes revealed that susceptibility to heat stress is linked to low expression of *HSP70*, while, tolerant genotypes exhibit *HSP70* overexpression, contributing to increased thermo-membrane stability (Usman et al., 2015). In onions, under heat stress, overexpression of genes related to the synthesis of osmoprotectants, ROS scavengers (*TRX*, *ANX*, *GRX*, *CAT2*, and *FDX*), transcription factors (*NAC*-domain, *WRKY*, *MYB*, and *WD-40*), genes controlling hormone production (Ethylene, Auxin, and *ABF3*), genes governing the production of signal transduction molecules (*CDPK*, *CaBP*, *CBP*, *CBL*, *MAPK20*, and *RAN*), and heat shock proteins (*HSP 40*, *HSP 60*, *HSP 70*, *HSP 90*, and *HSP 101*) confers heat tolerance compared to outer scales (Galsurker et al., 2018).

Physiological and molecular mechanisms of heat stress tolerance

To counter the challenges posed by heat stress, vegetables employ a diverse array of physiological and

molecular mechanisms to enhance heat tolerance. These mechanisms include the stabilization of thermos-membranes, scavenging of ROS, accumulation of osmolytes, production of antioxidant enzymes, activation of mitogen-activated protein kinase (*MAPK*) and (*CDPK*) cascades, chaperone signaling, and transcriptional activation. When exposed to heat stress, the plasmalemma is initially affected, resulting in increased lipid fluidity, which induces Ca^{2+} influx, leading to the upregulation of *MAPK* and (*CDPK*). The signaling cascades activated by these kinases contribute to the synthesis of osmolytes and antioxidants (Wahid et al., 2007).

To counteract the damage caused by reactive oxygen species during heat stress, plants have evolved an antioxidant defense mechanism involving the production of antioxidant enzymes. Reactive oxygen species, when maintained at optimum levels, function as signaling molecules in response to stress perception by stress sensors. These signaling molecules are disseminated throughout metabolically active plant tissues and are regulated by the ROS gene network. During heat stress, signaling ROS are mediated by calcium or the activation of *NADPH* oxidases at the plasma membrane, acting as heat stress signal transducers (Devireddy et al., 2021). Reactive oxygen species, in conjunction with other signals like Ca^{2+} , are integral to long-distance systemic signaling necessary for the activation of systemic acquired acclimation in response to heat or other abiotic stresses. For instance, plant hormones such as abscisic acid (*ABA*) and jasmonic acid (*JA*) trigger ROS production, initiating a systemic signal known as the ROS wave (Devireddy et al., 2021). This hormone-triggered ROS move through cell-to-cell propagation, forming an amplification loop and triggering systemic acquired acclimation responses. Studies have indicated that the local application of heat or cold stimuli induces similar stress transcriptional responses in both local and systemic tissues, dependent on the ROS wave. Moreover, ROS activate calcium channels, which then activate two pore channel 1 (*TPC1*), a vacuolar calcium channel transporting vacuolar-stored Ca^{2+} . This activation leads to the activation of respiratory burst oxidase homolog D (*RBOHD*) proteins, creating a feedback loop that activates ROS and calcium, inducing a comprehensive acclimation response to high temperature (Devireddy et al., 2021). In sweet potatoes, the expression of heat-responsive

genes, such as abscisic acid-responsive elements binding factors (AREB) and CBF TFs, plays a pivotal role in its robust adaptation to heat stress. The involvement of Heat Shock Proteins (HSPs) in signal transduction during heat stress is crucial. The enhanced high-temperature tolerance conferred by HSPs contributes to improvements in photosynthesis, nutrient uptake, and membrane stability (Momcilovic & Ristic, 2007).

Hormones also play a significant role in plants' adaptation to heat stress. Under high-temperature conditions, there are alterations in the synthesis, stability, quantity produced, and distribution of hormones. Stress hormones, such as ethylene (C₂H₄) and ABA, function as signaling molecules in response to heat stress, contributing to the plant's adaptive mechanisms. Research indicates that ABA activates heat shock proteins (HSPs), suggesting it as a potential mechanism for imparting heat tolerance to plants (Pareek et al., 1998). When plants experience a sudden or gradual increase in temperature, specific proteins called heat shock proteins (HSPs) are synthesized and accumulated. In tomato plants, HSPs form granular structures in the cytoplasm, protecting the protein biosynthesis machinery. HSPs/chaperones not only facilitate signal transduction but also activate genes involved in heat tolerance mechanisms, including the production of osmolytes and antioxidants. Thermotolerance alters gene expression by activating HSPs and inhibiting the expression of other genes. Destabilization of mRNAs encoding non-heat-stress-induced proteins occurs during heat stress, and reactive oxygen species (ROS) activate heat shock factors (HSFs) (Hu et al., 2015).

Salicylic acid (SA) hormones play a crucial role in heat stress tolerance, participating in signaling pathways. SA facilitates the binding of heat shock elements to the promoter of heat shock proteins. Treatment with sulphosalicylic acid (SSA) has been shown to mitigate the adverse effects of reactive oxygen species by removing H₂O₂. SSA treatment effectively eliminated H₂O₂ from cucumber seedlings by inducing the production of catalase enzymes (Snyman & Cronjé., 2008). Recent findings indicate that brassinosteroids hormones confer thermotolerance in tomato and oilseed rape. Studies stress that xanthophylls contribute to heat tolerance by enhancing thermo membrane stability. Xanthophyll molecules interact with membrane lipids, reducing their fluidity

and thereby safeguarding against lipid peroxidation in response to heat stress. Endogenous synthesis of isoprene protects biological membranes and PS II by directly interacting with reactive oxygen species generated during high-temperature conditions (Velikova et al., 2008).

Heat tolerance through conventional breeding

Plants exhibit varying degrees of thermotolerance, and considerable diversity exists in the responses to heat stress both between and within plant species, which provides an opportunity to enhance heat stress tolerance in vegetables through strategic exploitation. The development of heat-tolerant varieties via conventional breeding programs emerges as an economically viable solution. Employing recurrent selection procedures enhances the frequency of desirable alleles by selecting superior genotypes from the base population (Benites & Pinto, 2011). Figueiredo et al. (2015) utilized the recurrent selection to establish high-temperature stress tolerance in potato plants. Plant breeders have successfully developed heat-tolerant potato varieties, including Kufri Surya (Minhas et al., 2006), Haruka (Kobayashi et al., 2009), and Konyu (Iwama, 2008), utilizing conventional breeding methods. Although, heat tolerance is a complex, multi-genic trait influenced by environmental factors and various other characteristics, breeders have managed to develop commercially acceptable, heat-tolerant open-pollinated varieties and hybrids.

In cowpea selection for high pod set and abundant flower production resulted in the development of high-temperature-tolerant and high yielding genotypes (Ehlers et al., 2000). CIAT breeders in 2006 utilized heat-tolerant lines to develop a heat-tolerant bean genotype (Blair et al., 2006). The high-temperature-bearing chickpea line 'ICCV-92944' was developed through selection (Gaur et al., 2019). The Asian vegetable research and development center (AVRDC) identified thirty-nine heat-resistant lines in tomatoes through selection. Some of these lines were incorporated into the tomato breeding program of AVRDC, leading to the development of heat stress-tolerant lines such as 'Equinox' and 'Sun Leaper' (Gardner, 2000).

Genomic approaches for heat tolerance

Improving vegetable crops through conventional breeding methods faces limitations, as these

approaches involve long breeding cycles and often yield a low success rate (Parent & Tardieu, 2012). Challenges arise due to the difficulty in transferring genes from only closely related species, resulting from pre- and post-fertilization failures. Traditional breeding strategies may not effectively isolate and transfer desirable single genes, leading to the inadvertent transfer of unwanted genes alongside the targeted ones. Since, heat tolerance is a quantitative trait influenced by environmental factors, traditional breeding experiments are susceptible to failure. Advancements in plant genomics and biotechnology have significantly enhanced scientists' understanding of the molecular, biochemical, and physiological responses of plants to heat stress. This knowledge has enabled the successful and efficient selection, transfer, and expression of target genes. In the contemporary genomic era, various tools, such as molecular marker technology, QTL mapping, genome-wide identification of molecular markers, genomic selection, genetic transformation, and genome editing tools, are being employed to develop vegetable cultivars with enhanced heat tolerance. These modern genomic approaches offer more precision and efficiency in breeding practices compared to traditional methods.

Marker assisted selection for heat tolerance:

Molecular marker-assisted selection (MAS) has the potential to augment traditional breeding methods, although the current application of molecular markers in developing heat-resistant vegetable varieties is limited. The advent of genome sequencing, genome resequencing, and transcriptome sequencing has led to the discovery of an extensive array of molecular markers. In the future, these markers are expected to play a pivotal role in genetic mapping, trait recognition, and the enhancement of genetic makeup through MAS to confer high-temperature tolerance in vegetable crops. Given the intricate mechanisms of high-temperature tolerance and the challenges in phenotypic trait selection, MAS emerges as a promising technology for improving the heat stress tolerance of vegetable crops (Foolad & Panthee, 2012).

The successful application of MAS relies on the identification of genetic markers linked to genes/QTLs responsible for heat stress tolerance at the whole plant level or affecting traits related to heat stress tolerance. Marker technology enables the detection and

characterization of quantitative trait loci affecting high-temperature tolerance at various plant growth stages (Foolad et al., 2008). Various MAS schemes have been developed, including selection for multigenic traits by applying markers at multiple loci across successive selection cycles, enrichment of desirable allelic frequency in early selection cycles, and the use of markers in backcrossing with foreground and background selection. MAS can be employed for introgressing desirable alleles into an elite background and incorporating innate characters into a breeding line in progress (Bassi et al., 2016). To implement MAS effectively, markers proximal to the target locus are essential, making it particularly useful for traits with a quantitative mode of inheritance, such as high-temperature stress tolerance (Tayade et al., 2018).

For enhancing heat tolerance in vegetable crops, single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSR) are now widely employed. Among vegetables, the application of MAS is predominantly confined to tomatoes. In tomatoes, 15 yield-related markers were identified, of which 13 were deemed more reliable for identifying genes that confer tolerance to high-temperature stress (Ruggieri et al., 2019). Dominant sequence characterized amplified region (SCAR) based markers were developed to distinguish high-temperature stress-tolerant genotypes from susceptible ones in tomatoes. During the evaluation of tomato genotypes, one SSR and two random amplified polymorphic DNA (RAPD) markers were found that could be applied to differentiate susceptible and tolerant genotypes.

Quantitative trait loci mapping for heat tolerance:

Utilizing molecular biology and molecular markers to identify quantitative trait loci (QTLs) associated with high-temperature tolerance is crucial for comprehending the genetic basis of heat tolerance. Various QTLs contribute to heat stress tolerance in vegetables. In tomato, multiple studies have focused on mapping QTLs linked to traits associated with high-temperature tolerance, including style length, style protrusion, pollen viability, number of pollens, number of inflorescences, and fruit setting (Panthee & Gotame, 2020). Reliable QTL information is indispensable for successful marker-assisted breeding. While few studies have mapped QTLs associated with high temperature tolerance in vegetables, the majority of QTL mapping work has been concentrated in tomato. A search across

various search engines revealed six QTL mapping experiments related to high temperature tolerance at different growth stages in tomato (Alsamir et al., 2021). QTL mapping was applied to different genotypes of tomato, revealing significant marker relationships between the number of flowers, fruit setting, number and weight of fruits, electrolyte leakage, and dry weight of the plant.

QTL mapping has been instrumental in identifying new genetic variability as a source of heat tolerance for crop breeding. Although QTLs may encompass numerous genes, the significance of various QTL mapping studies is sometimes limited due to low marker density. In cowpea, four QTLs linked to the number of pods set/peduncle under heat stress were mapped and utilized in its heat tolerance improvement program (Pottorff et al., 2014). Nine QTLs associated with internal necrosis in potato tubers, explaining 4.5% to 29.4% of the phenotypic variability, were identified (McCord et al., 2011). QTL mapping in potato led to the identification of the HSC 70 gene, whose enhanced expression under moderate heat stress resulted in increased tuber yield (Trapero Mozos et al., 2018). In tomato, six QTLs linked with fruit setting under heat stress were identified using fluorescent AFLP markers, aiding in the rapid selection of heat-tolerant plants. Additionally, 21 QTLs related to fruit traits such as fruit weight, number of fruits, percentage of fruit setting, and brix value were mapped on four chromosomes at temperatures above 35 degrees Celsius. In Chinese cabbage, three QTLs, and in broccoli, five QTLs, explaining 17.6% to 41.1% and 62.1% variability under high-temperature stress, were detected (Branham et al., 2017). In lettuce, the main QTL Htg6.1 (high temperature germination) was identified and strongly linked to thermotolerance during sprouting (Driedonks et al., 2016).

Genome-wide identification of molecular markers in vegetable crops

Cucumber marked a pioneering achievement in vegetable genomics as the first vegetable to be fully sequenced (Huang et al., 2009). The abundance of molecular markers, such as simple-sequence repeats and single nucleotide polymorphisms, has notably enhanced the efficiency of breeding programs, genetic mapping, and trait identification (Gao et al., 2012). Whole-genome analysis in vegetables has identified a substantial number of genetic markers, providing new

avenues for germplasm characterization and the development of heat-resistant genotypes. In the genomes of potatoes, over 3.67 million, and in tomatoes, approximately 5.4 million SNPs have been detected (Tomato Genome Consortium, 2012).

The application of transcriptome sequencing technology in vegetables allows for the rapid generation of many expressed sequence tags (ESTs), facilitating the identification of molecular markers such as SNPs and SSRs. Genotyping by sequencing (GBS), a contemporary approach, has increased the number of markers, especially SNPs, evenly distributed across the genome (Spindel & Iwata, 2018). This enables the creation of genetic maps with high resolution, accurate mapping of quantitative trait loci (QTLs), and the identification of candidate genes associated with quantitative traits. Genome-wide association studies (GWAS) provide a means to identify specific haplotypes in natural and wild populations by narrowing down candidate genomic regions (Verdeprado et al., 2018). In modern crops, the emphasis on yield and uniformity, a consequence of the green revolution and conventional breeding, has resulted in a narrowed genetic diversity. Despite this, considerable genetic variability still exists in various crops. GWAS proves to be a valuable tool for understanding the genetic basis of phenotypically complex traits. Compared to conventional genetic mapping techniques, GWAS offers high genetic mapping resolution, although information on its application in vegetables remains limited.

Genomic selection: Genomic selection (GS) proves highly valuable when a trait is influenced by numerous minor quantitative trait loci (QTLs). Unlike Marker assisted selection (MAS) and marker-assisted backcrossing (MAB), GS does not necessitate QTL mapping or detailed information about trait inheritance. GS leverages various molecular markers, incorporating them into prediction models to unveil variability resulting from minor QTLs (Shamshad & Sharma, 2018). This technique has been implemented in various crops, including tomato, and is particularly advantageous for traits governed by many QTLs, providing more comprehensive insights into genetic gain (Adlak et al., 2019).

Research affirms that when a trait is controlled by numerous QTLs, GS outperforms traditional breeding techniques and MAS in terms of time efficiency and

precision in plant breeding programs. In the context of enhancing high-temperature tolerance in tomatoes, genomic selection emerges as a promising strategy. In crops, such as pepper (*Capsicum* spp.), where fruit-related traits significantly influence quality and are quantitative in nature, GS utilizes genotypic and phenotypic data from a training population to predict the phenotypes of a test population with only genotypic information. GS has found successful application in staple crops like potato, maize, wheat, and barley, focusing on quality traits, yield, and disease resistance (Habyarimana et al., 2022; Stich & Van Inghelandt, 2018). The versatility of GS across various crop species is attributed to the availability of genome-wide, high-performance, cost-effective molecular markers that can be applied to large population sizes, both in model and non-model crop species, whether possessing a reference genome sequence or not (Bhat et al., 2016). GS serves as a pre-breeding tool for identifying germplasm with valuable variations, predicting the breeding value of plants within a breeding population. This application efficiently enhances genetic gain for quantitative traits, making GS an integral part of breeding programs, particularly in the private sector where it is widely utilized for developing new varieties in different crops within a short timeframe (Tayade et al., 2022). One notable advantage of GS over MAS and marker-assisted recurrent selection lies in its ability to detect alleles with minor effects, which can be crucial in the selection process.

Transgenic approaches for heat tolerance: Through recombinant DNA methods, the creation of heat-tolerant transgenic lines can be achieved swiftly, allowing for the transfer of potential genes from diverse species to target crops. One study focused on the overexpression of the AtDREB1A gene in transgenic potatoes, revealing changes in the metabolite composition of the lines under high-temperature stress conditions (Iwaki et al., 2013). The analysis of gene sequences, transcriptomes, and proteomes provides extensive information for identifying valuable genes associated with heat stress in vegetables (Zhuang et al., 2014). Increased thermo-tolerance in transgenic lines is often attributed to elevated levels of Heat Shock Protein (HSP) chaperones. For instance, the MT-sHSP of tomatoes demonstrated molecular chaperone functionality *in vitro*. The development of transgenic lines is considered an efficient and reliable method for crop

improvement, with examples including heat-tolerant transgenic potato lines that have been successfully developed (Trapero Mozos et al., 2018). Introducing stress-related genes, such as StnsLTP1, into potatoes has shown increased tolerance to abiotic stresses and enhanced expression of genes related to other stresses. Similarly, the insertion of AtCBF3 from Arabidopsis into potatoes increased tolerance to high temperatures by improving photosynthetic efficiency and antioxidant defense (Dou et al., 2015). Transgenic potatoes with the insertion of the heat-tolerant gene sHSP17.7 from carrots demonstrated elevated high-temperature tolerance.

In major vegetable like tomato, genetic modifications have been implemented. Wheat, tomatoes, and maize have seen the development of transgenic lines with heat tolerance by targeting heat shock proteins (HSPs) and heat shock factors (HSFs) (Wang et al., 2019).

Genome editing methods: Genome editing technologies, particularly CRISPR/Cas9, have demonstrated successful performance in the Solanaceae family, surpassing earlier techniques like ZFN and TALENs due to its high specificity (RNA-DNA hybrid) and cost-effectiveness (Kim et al., 2017; Yamamoto et al., 2018). In tomatoes, the SIMAPK3 gene, belonging to the mitogen-activated protein kinase family, plays a role in responding to various environmental stresses. Mutants of SIMAPK3, created through CRISPR/Cas9-mediated genome editing, exhibited increased thermo-tolerance compared to wild-type plants, suggesting its negative regulatory role in high-temperature tolerance (Yu et al., 2019). Similarly, the BRZ1 gene, which positively regulates the production of reactive oxygen species in the apoplastic region of tomatoes for heat tolerance, was edited using CRISPR/Cas9. Mutants of *bzr1* exhibited impaired H₂O₂ production in the apoplast, indicating its significance in temperature tolerance (Kumar et al., 2023). In lettuce, CRISPR/Cas9 was used to knock out the LsNCED4 gene, resulting in increased germination of lettuce seeds under heat stress (Devi et al., 2022). The successful application of genome editing relies on two essential prerequisites: the availability of the complete genome sequence and active transformation techniques. In tomato, both conditions are fulfilled, making it an ideal candidate for genome editing. The technology has unveiled insights into genes and gene networks controlling pollen viability, ovule fertility, and photosynthetic

system efficiency under high-temperature stress. CRISPR/Cas9 has proven effective in enhancing heat tolerance in tomatoes by targeting genes involved in jasmonic acid production, invertase activity, and ethylene response (Wang et al., 2019). Notably, CRISPR/Cas9 has emerged as a rapid and precise tool for studying molecular pathways related to heat stress, allowing the creation of gene knockout mutant lines to investigate specific gene functions.

CONCLUSION AND FUTURE PROSPECTIVE

As global air temperatures continue to rise, heat stress poses a significant threat to vegetable production worldwide, impacting various aspects of quality, growth, reproduction, photosynthesis, and respiration. Addressing this challenge, requires the development of heat-tolerant vegetable varieties, necessitating a comprehensive understanding of vegetable responses and adaptive mechanisms to heat stress - a quantitative trait influenced by intricate molecular, biochemical, and physiological pathways. Conventional breeding alone falls short in improving this complex trait. Identifying specific genes and understanding the pathways governing heat tolerance are crucial. Therefore, a combination of traditional breeding, marker-assisted selection (MAS), quantitative trait locus (QTL) mapping, Genome-Wide Association (GWA) studies, and genomic selection is employed to develop heat stress-tolerant vegetable varieties, with target genes spanning different vegetable species. Advancements in genome editing technologies offer a precise means of identifying and understanding gene functions. Transgenic approaches facilitate the transfer of heat-tolerant genes across species and genera. In tomatoes, genome editing tools like TALENs, ZFNs, and CRISPR are employed to develop heat-tolerant genotypes. With increasing availability of genome sequences, these modern technologies hold the promise of delivering vegetable varieties with enhanced heat tolerance and expedited production in the future.

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