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Developing resilience to heat stress in fruit orchards: A comprehensive review

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ABSTRACT

Heat stress is emerging as a major constraint in fruit production across the globe, driven by rising temperatures and increasing climate variability. Fruit crops are particularly vulnerable to high temperatures, which adversely affect physiological processes, flowering, fruit set, quality and yield. Developing resilience is hindered by factors such as the complex genetic basis of heat tolerance, limited availability of heat-resilient cultivars and economic or infrastructural limitations faced by growers, particularly in resource-constrained regions. Developing resilience to heat stress has become critical for sustaining orchard productivity, especially in tropical and subtropical regions. This review synthesizes current knowledge on the physiological, biochemical and molecular responses of fruit crops to heat stress, while also examining practical orchard management strategies-including shading nets, mulching, regulated deficit irrigation and anti-transpirants as well as the role of exogenous applications of plant growth regulators and nutrients in mitigating heat-induced damage, with emerging biological solutions such as microbial inoculants and biostimulants providing eco-friendly alternatives for enhancing plant tolerance. Furthermore, advancements in breeding-through marker-assisted selection, genomics and gene editing technologies are accelerating the development of heat-resilient cultivars. An integrated approach combining technological, agronomic and genetic tools is essential to build long-term heat resilience in fruit orchards. The paper concludes by emphasizing the need for region-specific interventions, farmer-centric research and policy support to promote climate-smart horticulture.

Keywords: *Heat stress, fruit crops, climate change, physiological responses, orchard management, resilience, plant growth regulators, microbial inoculants, sustainable agriculture, breeding technologies, gene editing.*

Introduction

Climate change is resulting in an increase in the frequency and severity of heatwaves, an elevation in global average temperatures and a rise in extreme meteorological phenomena. These ecological transformations are particularly adverse to agricultural practices, particularly impacting perennial fruit crops. In contrast to annual crops, fruit orchards exhibit extended life cycles and possess fixed geographical locations, rendering their adaptation to environmental alterations more intricate. In nations such as India, along with various other regions characterized by subtropical and tropical climates, heat stress has emerged as one of the most significant abiotic factors adversely influencing horticultural productivity [24].

Fruit crops exhibit heightened susceptibility to elevated temperatures during their pivotal growth phases, which include flowering, fruit set and fruit maturation. Sudden increases in temperature, protracted heat waves and elevated nighttime temperatures can all lead to a decline in yield and quality. These conditions frequently result in phenomena such as floral abscission, diminished pollen viability, suboptimal fruit set, heightened fruit drop and sunburn affecting fruits and foliage. For instance, in mango cultivation, temperatures exceeding 35°C during the flowering phase are correlated with pollen sterility and unfavorable fertilization results [24]. In apple-producing regions, a reduction in chilling hours and premature flowering are increasingly becoming significant challenges attributable to climate change.

Forecasts pertaining to climate change suggest that average temperatures in India may rise by 2-4°C by the conclusion of the 21st century, contingent upon various greenhouse gas emission trajectories. This scenario will have substantial ramifications for the production zones of fruit crops. Conventional cultivation areas may cease to be appropriate for specific crops, necessitating a realignment of geographical cultivation zones or the introduction of novel cultivars exhibiting heat-resistant characteristics. In light of the considerable economic significance of fruit crops and their vital role in maintaining nutritional security, there exists an urgent necessity to establish heat-resilient orchard systems. This can be accomplished through a synergistic approach involving physiological insights, sophisticated breeding methodologies, agronomic management practices and the application of biotechnological advancements. Moreover, farmers and orchard managers must be empowered with adaptive methodologies and technologies to alleviate heat stress, bolstered by governmental initiatives and supportive institutional frameworks.

The objective of this review is to investigate the effects of thermal stress on fruit-bearing crops and to delineate approaches for enhancing resilience via physiological, agronomic and molecular strategies.

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It synthesizes contemporary research, with a particular emphasis on studies conducted in India and context-specific results.

Why Heat Resilience Matters?

In fruit orchards, thermal stress exerts a complex influence, impacting plant physiology, fruit quality and overall market value. Elevated temperatures can trigger a spectrum of plant responses that, if not properly managed, result in substantial reductions in productivity. These responses encompass modifications in membrane fluidity, enzymatic activity, hormonal signaling pathways and the accumulation of reactive oxygen species (ROS) [10].

Fruit-bearing crops exhibit heightened sensitivity during their reproductive phases. The viability and germination of pollen are markedly diminished under elevated thermal conditions. For example, in mango and citrus species, heat stress occurring during the flowering period adversely affects pollination and fruit set, primarily due to the inactivation of pollen grains and stigmatic receptivity. Consequently, there is an increased incidence of flower and fruit abscission, which directly correlates with a decline in yield.

The commercial viability of fruits is similarly compromised. Excessive heat can precipitate sunburn in fruits, wherein the exposed surfaces develop necrotic lesions as a result of extended exposure to solar radiation. This phenomenon not only detracts from the aesthetic appeal but also inflicts physiological harm, adversely influencing internal quality metrics such as sugar concentration, acidity and vitamin C content. For instance, in grape cultivation, sunburn results in diminished flavor and a decrease in sugar accumulation [27].

From a physiological standpoint, heat stress induces stomatal closure to mitigate water loss. While this mechanism conserves water, it concurrently restricts CO_2 absorption, consequently diminishing photosynthetic efficiency and biomass production. Moreover, sustained heat stress escalates respiration rates, further exhausting the plant's carbohydrate reserves. These physiological compromises have implications for both growth and reproductive success over extended periods [2].

Economically, the aggregate ramifications of heat stress culminate in diminished agricultural revenues, heightened input expenses for remedial measures (such as irrigation, shading and mulching) and potential long-term alterations in cropping strategies. This situation is particularly pressing for smallholder and marginal farmers, who may lack the necessary resources to implement adaptive strategies.

The resilience of crops to heat stress transcends mere agronomic issues, implicating socioeconomic dimensions as well. The development of orchards capable of withst anding elevated temperatures is vital for ensuring food security, stabilizing livelihoods and maintaining the sustainability of agricultural practices. This endeavor entails the selection of tolerant cultivars, the implementation of climate-smart agricultural techniques and the application of technological innovations suited to local climatic contexts.

Physiological and Biochemical Effects of Heat Stress

Exposure to elevated temperatures significantly disrupts key physiological and biochemical processes in fruit-bearing plants. One of the earliest and most sensitive targets is photosynthesis, primarily due to the deactivation of photosystem II (PSII) reaction centers, reduced Rubisco activity and impaired chlorophyll biosynthesis.

High temperatures destabilize chloroplast membranes, accelerating chlorophyll degradation and reducing photosynthetic efficiency [27].

Stomatal behavior under heat stress plays a critical role in regulating water balance and gas exchange. As temperatures rise, stomatal closure helps conserve water but also restricts CO_2 uptake, limiting carbon fixation and reducing biomass accumulation. Studies in mango and guava have shown significant declines in stomatal conductance and net photosynthetic rates under thermal stress [10].

Heat stress also accelerates respiration and increases the production of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), superoxide anions (O_2^-) and hydroxyl radicals (OH), which damage lipids, proteins and nucleic acids. Lipid peroxidation compromises membrane integrity and disrupts ionic balance [9].

To counteract oxidative damage, fruit crops activate antioxidant defense systems. Enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) neutralize ROS, while non-enzymatic antioxidants such as ascorbic acid, glutathione and carotenoids further mitigate oxidative stress. Elevated antioxidant activity has been observed in citrus and grape under heat stress [1].

Osmotic adjustment is another key adaptation. Compatible solutes like proline, glycine betaine and soluble sugars stabilize proteins and membranes, maintain osmotic balance and protect cellular structures. Proline also acts as a ROS scavenger, while glycine betaine preserves protein structure and membrane fluidity [14].

Heat stress induces the expression of heat shock proteins (HSPs), including HSP70, HSP90 and small HSPs, which function as molecular chaperones to refold denatured proteins and prevent aggregation. Transcriptomic studies have shown upregulation of HSPs in banana, apple and grape under heat stress [2].

Hormonal imbalances also play a role. Elevated ABA promotes stomatal closure and stress gene activation, while excess ethylene can accelerate senescence and fruit drop. Exogenous salicylic acid (SA) and jasmonic acid (JA) enhance antioxidant defenses and improve heat resilience [24].

Agronomic and Cultural Interventions

Agronomic and cultural approaches remain among the most practical and affordable tools for managing heat stress in fruit production systems. These interventions aim to buffer the orchard microenvironment, improve water retention in the soil and strengthen plant physiological status under heat extremes. Unlike genetic modifications, these methods can be rapidly adopted by growers using local materials and techniques, often yielding immediate outcomes. A widely adopted technique is mulching, which entails spreading materials-either organic like straw, dry foliage, or manure, or inorganic such as plastic films-over the soil surface. This helps reduce surface evaporation, moderate soil temperatures and preserve moisture in the root zone. Organic mulches also decompose over time, enriching soil health and supporting microbial populations. In commercial orchards, plastic mulches are especially beneficial for water conservation. Research indicates that mulching can lower soil temperature by 2 to 5°C and enhance moisture availability at the root level, thereby boosting plant resilience to heat [10].

Canopy management is another essential strategy, involving practices like pruning, thinning and training of branches to enhance light distribution and airflow within the tree canopy. A well-structured canopy not only prevents localized heat buildup but also reduces water loss through transpiration by minimizing foliage density. In crops like mango and citrus, pruning carried out before peak summer has been shown to lower leaf temperatures and mitigate sunburn injuries.

Lastly, efficient irrigation management is crucial when plants are under thermal stress. High temperatures drive up evapotranspiration, necessitating timely and precise water delivery to prevent drought stress. Technologies such as drip irrigation and micro-sprinklers provide focused watering, maintaining consistent soil moisture and minimizing wastage. Studies have demonstrated that applying frequent, light irrigation during heat waves can significantly reduce canopy temperature and enhance fruit set and retention. Tools like tensiometers and evapotranspiration-based models enable accurate irrigation scheduling, optimizing water use and supporting plant health under extreme weather conditions.

Modern horticulture is increasingly embracing protective cultivation techniques such as shade nets, reflective mulches and windbreaks, particularly in high-value fruit systems. Shade nets help to moderate the microclimate by lowering light intensity and ambient temperatures by approximately 20-40%, shielding sensitive crops like strawberries and grapes from intense solar radiation. In parallel, reflective mulches-especially white or silver variants-repel sunlight, thereby keeping canopy and root zone temperatures cooler. Windbreaks, constructed from tall trees or engineered barriers, act as shields against hot, drying winds, effectively minimizing water loss through evapotranspiration.

Incorporating intercropping and agroforestry systems offers a sustainable means of mitigating temperature extremes. Interplanting fruit trees with legumes or aromatic herbs promotes biodiversity and reduces surface soil temperatures by providing ground shade. These systems also improve soil health through better nutrient cycling, increased microbial activity and enhanced moisture retention. Agroforestry designs that include shade-giving trees can be particularly advantageous for heat-sensitive crops like guava and citrus, offering a natural buffer against temperature spikes.

The application of antitranspirants and kaolin-based sprays represents another promising agronomic tool. Antitranspirants form a semi-permeable film over leaf surfaces, reducing transpiration-driven water loss. Meanwhile, kaolin-an inert, white clay mineral-acts as a reflective coating on plant leaves, lowering foliage temperature and reducing sunburn and fruit damage. Empirical studies on crops like mango, pomegranate and guava have shown that kaolin treatments can substantially decrease incidents of fruit cracking and thermal injury under hot conditions [24].

Soil and nutrient management is equally vital in enhancing plant resilience to heat. A soil profile enriched with organic matter improves water-holding capacity and moderates temperature fluctuations. Inputs such as compost, green manures and biochar contribute to better soil structure, aeration and microbial vitality. Nutritional balance-especially with potassium and calcium, is key to strengthening plant cell walls and maintaining osmotic balance. Potassium also plays a pivotal role in regulating stomatal function and activating stress-related enzymes, critical during episodes of thermal stress.

Scheduling of field activities must be adjusted to minimize heat-related impacts.

Transplanting and grafting operations should be avoided during peak heat periods, while harvesting is better conducted in the early morning or late evening to minimize post-harvest losses and reduce stress on both crops and workers.

A key driver of successful implementation lies in farmer education and outreach. Empowering farmers through training workshops, demonstration farms and extension services can facilitate adoption of climate-resilient techniques. Collaboration among research institutions, government agencies and local communities is essential to foster awareness and build capacity. Integrating indigenous knowledge with modern scientific practices can create robust and localized solutions to climatic challenges.

Agronomic and cultural strategies provide a first line of defense against heat stress in fruit orchards. When properly integrated with other approaches such as genetic improvement and biotechnology, they contribute to a holistic and sustainable heat stress management framework in horticulture.

Molecular and Genetic Approaches

In addition to agronomic interventions, it is imperative that molecular and genetic strategies are employed in the development of fruit crops exhibiting inherent heat tolerance. Such methodologies are predicated on a comprehensive understanding of the genetic underpinnings of thermotolerance and the strategic application of this knowledge through conventional breeding, marker-assisted selection, transgenic technologies and genome editing methodologies. In perennial crops, such as fruits, characterized by extended generation cycles, molecular techniques can significantly expedite the development of resilient cultivars while simultaneously providing enhanced precision and specificity.

Among the most extensively investigated mechanisms of plant thermotolerance at the molecular level is the function of heat shock proteins (HSPs). These proteins operate as molecular chaperones, facilitating proper protein folding and inhibiting the aggregation of denatured proteins under stress conditions. HSPs are categorized into families, including HSP100, HSP90, HSP70, HSP60 and small HSPs (sHSPs), each fulfilling unique roles in the mitigation of heat stress. In fruit crops such as grapevine, citrus and apple, transcriptome analysis has shown upregulation of HSP genes in response to elevated temperatures, indicating their importance in cellular protection under thermal stress [2].

Another key group of molecules involved in thermotolerance is transcription factors (TFs). These proteins regulate the expression of downstream stress-responsive genes. Important heat-responsive TF families include heat shock factors (HSFs), DREB (Dehydration Responsive Element Binding), bZIP, MYB and NAC. HSFs in particular are central to the regulation of HSP genes. Overexpression of HsfA1 in tomato and citrus has been reported to enhance thermotolerance by improving ROS-scavenging and photosynthetic activity under stress conditions [17].

Plants enhance their thermotolerance through a combination of metabolic and genetic mechanisms. During heat stress, genes responsible for synthesizing osmoprotectants such as proline, trehalose and glycine betaine, along with those involved in antioxidant defense, are commonly upregulated responses linked to improved heat resilience in crops like banana and pomegranate. Traditional breeding methods rely on phenotypic selection for traits such as leaf scorching resistance, chlorophyll retention and fruit set stability under high temperatures;

however, these traits are often polygenic and environmentally influenced, making the process time-consuming and less predictable. To address these limitations, marker-assisted selection (MAS) has emerged as a powerful approach, enabling the identification of quantitative trait loci (QTLs) associated with heat-tolerant traits like canopy temperature regulation, membrane stability index and fruit retention in crops such as apple and citrus. MAS also facilitates the introgression of beneficial alleles from wild relatives into elite cultivars without negatively affecting other agronomic traits [5]. Furthermore, transgenic technologies have shown promise in enhancing thermotolerance by introducing specific genes, although their application in fruit crops remains limited due to regulatory and public concerns. Experimental studies have demonstrated that overexpression of heat shock proteins (HSPs), antioxidant enzymes such as superoxide dismutase (SOD) and ascorbate peroxidase (APX) and osmolyte biosynthesis genes like P5CS can significantly improve heat tolerance. For instance, transgenic tomato plants expressing the AtHSP101 gene from Arabidopsis exhibited superior growth and yield under heat stress compared to non-transgenic controls [22].

Recent breakthroughs in genome editing, particularly the CRISPR/Cas9 system, have revolutionized precision breeding by enabling targeted gene modifications without incorporating foreign DNA-an advantage that enhances regulatory acceptance. Genes associated with heat tolerance, such as HSFA2, DREB2A and HSP70, have been successfully edited in several crop models to bolster stress resilience. Although the application of CRISPR in fruit crops is still emerging, it holds significant promise for refining traits like flowering time, fruit development and leaf function under elevated temperatures. Complementary to genome editing, genome-wide association studies (GWAS) and RNA sequencing (RNA-seq) have proven instrumental in dissecting the complex genetic architecture of heat stress responses. These high-throughput tools facilitate the discovery of novel genes and regulatory pathways involved in thermotolerance. For instance, RNA-seq analysis in mango has revealed the upregulation of genes linked to heat shock proteins (HSPs), calcium signaling and abscisic acid (ABA) pathways during thermal stress [13]. Additionally, epigenetic mechanisms such as DNA methylation and histone acetylation are gaining recognition for their role in stress memory, potentially enabling heritable thermotolerance without altering the DNA sequence. Preliminary studies in fruit crops suggest that manipulating epigenetic marks could be a viable strategy for enhancing heat resilience. However, the effectiveness of molecular and genetic innovations depends on their integration with conventional breeding and agronomic practices. Field validation of heat-tolerant genotypes is essential to ensure consistent performance and yield. Moreover, scalable propagation methods like tissue culture and grafting are critical for widespread adoption. Advancing these technologies requires sustained investment in genomics, infrastructure and regulatory support, alongside collaborative efforts among research institutions, universities and private sector stakeholders to develop climate-resilient fruit cultivars for future agricultural demands.

Role of Plant Growth Regulators

Plant growth regulators (PGRs), whether naturally occurring or synthetically formulated, are essential modulators of plant physiological and developmental responses. Under heat stress conditions, PGRs play a pivotal role in enhancing plant resilience by regulating hormonal balance, improving water-use efficiency, activating antioxidant defense systems and modulating the expression of heat-responsive genes. Their targeted application in fruit crops has been shown to mitigate the adverse effects of elevated temperatures, thereby supporting sustained growth, yield and stress adaptation.

Abscisic acid (ABA) is one of the most critical PGRs in heat stress management. Its biosynthesis is rapidly triggered under abiotic stress conditions such as high temperatures and drought. ABA primarily promotes stomatal closure to reduce transpiration and conserve water. Although this limits CO_2 uptake and may affect photosynthetic efficiency, ABA also activates stress-responsive genes, enhances antioxidant enzyme activity and supports osmotic adjustment [28]. Exogenous application of ABA has been reported to improve thermotolerance in fruit crops like grapes and citrus by preserving membrane integrity and reducing oxidative damage.

Salicylic acid (SA) is another key PGR involved in abiotic stress tolerance. It enhances systemic acquired resistance and strengthens the antioxidant defense system. Under heat stress, SA increases the activity of enzymes such as catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX), which help neutralize reactive oxygen species (ROS). In crops like tomato, guava and papaya, foliar application of SA has been associated with improved membrane stability, chlorophyll retention and fruit set under high-temperature conditions [11].

Jasmonic acid (JA) and its volatile derivative methyl jasmonate (MeJA) are lipid-derived PGRs that play vital roles in stress signaling and defense. JA regulates the expression of stress-responsive genes and promotes the synthesis of secondary metabolites and antioxidants. MeJA has been shown to enhance heat tolerance in crops such as strawberry and banana by protecting photosynthetic structures and increasing proline accumulation. Additionally, MeJA application improves fruit firmness and shelf life, which are critical under high-temperature storage conditions.

Ethylene, a gaseous PGR, regulates processes like fruit ripening, leaf senescence and abscission. Under heat stress, ethylene production often increases, which can lead to premature leaf drop, fruit softening and reduced shelf life. Although ethylene can activate protective mechanisms, excessive levels may cause physiological damage. To mitigate these effects, ethylene inhibitors such as silver thiosulfate (STS) and 1-methylcyclopropene (1-MCP) have been used to extend postharvest life and reduce fruit drop in crops like mango and citrus [24].

Cytokinins (CKs), which promote cell division and chloroplast development, are typically reduced under heat stress, leading to accelerated senescence and chlorophyll degradation. External application of CKs like kinetin or benzylaminopurine (BAP) has been shown to delay senescence and maintain photosynthetic activity. In apple and pear orchards, CK sprays during heat episodes have supported fruit development and plant vitality.

Gibberellins (GAs), particularly GA_3, contribute to stem elongation, flowering and fruit development. Under heat stress, GA_3 helps reduce flower drop and supports reproductive success in crops like mango and grapes. However, excessive application can disrupt the balance between vegetative and reproductive growth, requiring precise timing and dosage.

Brassinosteroids (BRs), a class of steroidal hormones, have emerged as potent enhancers of thermotolerance. They stimulate stress-related gene expression, improve water retention and stabilize cellular membranes.

BR treatments have been effective in protecting photosynthetic pigments and enhancing nutrient uptake under heat stress [25].
Proline and glycine betaine, though primarily osmolytes, also function similarly to PGRs when applied externally. These compounds aid in osmotic regulation, ROS detoxification and membrane stabilization. In guava and banana, foliar proline application has improved heat resilience by maintaining relative water content and chlorophyll levels.
Combining different PGRs can yield synergistic effects. For instance, the joint application of SA and JA has enhanced thermotolerance in strawberry, while ABA and CKs have improved heat resilience in pomegranate. The effectiveness of PGRs depends on crop type, growth stage and environmental conditions. Application methods such as foliar spraying, soil drenching and seed treatment should be aligned with phenological stages like pre-flowering, flowering and fruit development to maximize impact.
While PGRs offer significant potential in mitigating heat stress, their use must be carefully managed to avoid phytotoxicity. Overapplication or improper combinations can disrupt hormonal balance and impair fruit quality. Therefore, site-specific guidelines and validated protocols are essential. Integrating PGRs with complementary practices-such as mulching, shading, optimized irrigation and genetic improvement provide a holistic strategy for managing thermal stress. As climate change intensifies, the responsible use of PGRs will be central to building resilient and sustainable fruit production systems.

Role of Microbial Inoculants and Biostimulants

Microbial inoculants and biostimulants are emerging as vital, eco-friendly tools for enhancing heat stress tolerance in fruit crops. These biological inputs improve plant resilience by modulating physiological processes, enhancing nutrient uptake and activating systemic defense responses. As climate change intensifies, such nature-based solutions are gaining traction for their broad-spectrum efficacy and compatibility with organic and sustainable farming systems [23].
Among microbial inoculants, plant growth-promoting rhizobacteria (PGPR) are extensively studied for their role in mitigating abiotic stresses, including high temperatures. PGPRs such as *Bacillus subtilis*, *Pseudomonas fluorescens* and *Azospirillum spp*. Enhance plant tolerance by producing phytohormones like indole-3-acetic acid and gibberellins, fixing nitrogen, solubilizing phosphorus and producing siderophores. Under heat stress, these microbes simulate root growth, increase antioxidant enzyme activity and help maintain higher relative water content in crops like tomato, banana and grapevine [26].
Arbuscular mycorrhizal fungi (AMF) also play a crucial role in thermotolerance by improving water and nutrient uptake-especially phosphorus and modulating hormonal signaling. Their colonization enhances root architecture and osmotic regulation. In fruit crops, AMF associations have been linked to improved chlorophyll content, sustained photosynthesis and reduced electrolyte leakage under heat stress. For instance, Glomus species have been shown to alleviate heat-induced damage in citrus and papaya orchards [20]. Similarly, endophytic microbes such as *Enterobacter*, *Streptomyces* and *Trichoderma spp*. Enhance heat tolerance by producing bioactive compounds that regulate hormonal activity, strengthen antioxidant systems and promote osmolyte accumulation like proline and soluble sugars [6].
Biostimulants derived from seaweed extracts, humic substances, protein hydrolysates and amino acids have also demonstrated significant potential in mitigating heat stress. Seaweed extracts from species like *Ascophyllum nodosum* and *Sargassum spp*. are rich in natural hormones such as cytokinins, auxins and betaines. These compounds regulate stress-responsive pathways and, when applied as foliar sprays, improve yield, fruit size and thermal resilience in crops like grapes, citrus and strawberries [15]. Humic and fulvic acids enhance root development, stimulate beneficial soil microbes and improve nutrient uptake. In mango and pomegranate, humic acid application has been associated with better fruit retention and growth under heat stress [3].
Protein hydrolysates and amino acid-based products support stress adaptation by supplying precursors for protein synthesis and osmotic balance. Amino acids like proline, glutamic acid and tryptophan improve nitrogen metabolism, photosynthesis and fruit quality while reducing sunburn and accelerating recovery from heat episodes [7]. Additionally, silicon, though not traditionally classified as a biostimulant, is increasingly recognized for its role in abiotic stress mitigation. Silicon strengthens cell walls, enhances water-use efficiency and activates antioxidant defenses. In mango and guava, silicon application has been linked to lower leaf temperatures, firmer fruits and improved retention during heat stress [18].
These biological agents enhance thermotolerance through multiple mechanisms: boosting antioxidant enzymes like SOD, CAT and APX; modulating hormonal pathways involving ABA, SA and JA; promoting osmoprotectant accumulation; and preserving membrane stability. They also enrich soil health by increasing microbial biomass and nutrient cycling [23]. However, their effectiveness depends on microbial compatibility, soil type, climate and application method. Advances in metagenomics and next-generation sequencing are enabling the development of customized microbial consortia tailored to specific crops and environments [6]. Improved formulations with better carriers and shelf life are making these products more commercially viable. To maximize their impact, supportive policies, farmer training and integration into climate-resilient horticulture programs are essential. As sustainable and scalable tools, microbial inoculants and biostimulants offer immense promise for safeguarding fruit orchards against rising temperatures.

Breeding and Selection of Heat-Resilient Cultivars

The breeding and selection of heat-resilient cultivars form the cornerstone of long-term strategies for managing heat stress in fruit orchards. With the increasing frequency and severity of heatwaves, there is a pressing need to develop cultivars that can maintain physiological function, fruit quality and yield stability under elevated temperatures. Traditional breeding methods, assisted selection and advanced molecular techniques are being employed to identify and incorporate heat-tolerant traits into commercial varieties [27].
The foundation of any breeding program lies in identifying genetic variability within germplasm. Wild relatives of cultivated fruit crops often possess traits such as deeper root systems, thicker cuticles, efficient antioxidant mechanisms and superior osmotic adjustment. These attributes make them valuable donors for breeding programs [16]. For example, indigenous mango (*Mangifera indica*) landraces have demonstrated superior leaf temperature regulation and reduced fruit drop under heat stress, making them promising

candidates for future cultivar development.

Phenotyping plays a critical role in identifying heat-tolerant genotypes. Traits such as canopy temperature depression (CTD), membrane stability index (MSI), chlorophyll fluorescence (Fv/Fm), relative water content (RWC) and stomatal conductance are commonly assessed. Technological advancements in high-throughput phenotyping-such as infrared thermography, remote sensing and chlorophyll fluorescence imaging-enable rapid, non-invasive screening of large germplasm collections [8]. In fruit crops, tolerance during reproductive stages is particularly vital, as high temperatures during flowering and fruit set can impair pollen viability and increase fruit drop. Evaluating reproductive traits like pollen germination and ovule viability under heat stress provides insights into thermotolerance [29].

Traditional breeding approaches like mass selection and pedigree breeding have been used to improve stress tolerance, but the polygenic and environmentally sensitive nature of heat tolerance makes these methods time-consuming. Marker-assisted selection (MAS) has emerged as a more targeted approach, with quantitative trait loci (QTLs) linked to traits such as membrane stability and delayed senescence identified in crops like tomato and grape [5]. Genomic selection (GS), which uses genome-wide markers to predict breeding values, offers a more comprehensive strategy for complex traits. Though still emerging in perennial fruit crops, GS holds promise for accelerating breeding cycles [19]. Speed breeding, involving controlled environments and rapid growth cycles, is also being adapted for fruit crops through in vitro propagation and early flowering techniques.

Integrating transcriptomic, proteomic and metabolomic analyses provides a systems-level understanding of heat tolerance. RNA sequencing (RNA-seq) identifies stress-responsive genes, while proteomics reveals protein-level changes and metabolomics highlights key compounds like proline and flavonoids [21]. These tools help identify biomarkers for selection. Biotechnological interventions, including transgenics and CRISPR/Cas9 genome editing, offer precise gene-level modifications. Genes encoding heat shock proteins, antioxidant enzymes and transcription factors like DREB and HSF have been successfully manipulated to enhance tolerance. CRISPR/Cas9, in particular, allows targeted edits without foreign DNA, making it a more publicly acceptable tool [12].

Participatory breeding and farmer-led trials ensure that new cultivars meet both stress resilience and farmer-preferred traits like flavor and shelf life. Field validation under real-world conditions enhances adoption [4]. Collaborative networks, policy support and robust extension services are essential to scale these innovations. Ultimately, integrating breeding with physiological, agronomic and molecular tools will be key to building climate-resilient fruit production systems.

Conclusion

With rising global temperatures and increasing climate variability, enhancing heat stress resilience in fruit orchards has become a critical priority. Heat stress adversely affects plant physiology, reproductive success, fruit quality and overall yield, posing a serious threat to horticultural sustainability across diverse agro-climatic regions. Addressing this challenge requires a multifaceted approach that integrates physiological, biochemical, agronomic and genetic strategies.

Field-level interventions such as anti-transpirant sprays, mulching, reflective materials, optimized irrigation and shade nets have proven effective in mitigating heat impacts. The application of plant growth regulators like salicylic acid, abscisic acid and cytokinins helps stabilize cellular structures and activate antioxidant defenses. Biological inputs-including arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria and biostimulants from seaweed or humic substances-offer eco-friendly alternatives that enhance both plant resilience and soil health.

On the genetic front, tools like marker-assisted selection, genome-wide association studies and CRISPR/Cas9 gene editing are accelerating the development of heat-tolerant cultivars. Coupled with precision agriculture, remote sensing and data-driven decision-making, these innovations enable site-specific resilience planning.

Ultimately, building heat-resilient orchards demands coordinated efforts across research, policy and extension systems. A holistic, farmer-centric approach that blends scientific advances with traditional knowledge will be key to sustaining fruit production and livelihoods in a warming world.

Future scope

With the ongoing challenges posed by climate change, future research should focus on developing multi-stress tolerant cultivars that not only withstand heat but also cope with drought and salinity. Integrating advanced phenotyping tools with high-throughput genomics, transcriptomics and metabolomics will further unravel the molecular mechanisms behind heat tolerance. There is a need for region-specific breeding programs that address local climatic conditions and farmer preferences. The potential of genome editing tools like CRISPR/Cas9 for precise trait improvement should be explored more extensively in fruit crops. Additionally, scalable propagation techniques and cost-effective management practices need to be developed to ensure wider adoption among smallholder farmers. Finally, interdisciplinary collaborations between plant scientists, agronomists, climate experts and policymakers will be critical in designing holistic strategies to secure fruit production systems for future generations.

Conflict of Interest

The authors declare that there is no conflict of interest regarding the publication of this manuscript.

Aknowledment

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