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REVIEW ARTICLE

Genetic frontiers in tomato breeding: Overcoming heat stress for sustainable yield

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Abstract

Tomatoes (*Solanum lycopersicum*) are a vital global crop, valued for their nutrition and culinary uses. However, rising heatwaves from climate change threaten tomato production, making it critical to enhance heat tolerance for food security and sustainable agriculture. This review highlights strategies to improve tomato resilience to high temperatures. Traditional breeding focuses on traits like deeper roots, smaller leaves and thicker cuticles, which enhance heat tolerance, supported by Marker-Assisted Selection (MAS) to identify and incorporate heat-tolerant genes. Genetic engineering introduces genes like those for Heat Shock Proteins (HSPs), boosting plant resilience. Understanding physiological and biochemical responses to heat stress enables targeted measures, such as applying osmoprotectants and plant hormones, to mitigate damage. Agronomic practices, including adjusted planting schedules, shading, optimized irrigation and soil enhancement, create favorable conditions under heat stress. Precision agriculture technologies provide real-time monitoring, enabling timely interventions. Beneficial microorganisms like plant growth-promoting rhizobacteria and mycorrhizal fungi enhance nutrient uptake, water retention and overall plant health, further improving heat tolerance. A multidisciplinary approach combining traditional breeding, genetic engineering, physiological insights, agronomic methods and technological innovations is essential to develop heat-resilient tomato varieties. These integrated strategies ensure sustainable agricultural practices, enhance crop resilience and safeguard global food security in the face of climate change.

Keywords

breeding; heat stress; omics; resilience; TILLING; tomato

Introduction

Climate change describes the continuous long-term alterations in weather patterns and atmospheric conditions happening over large geographic areas. It presents significant ecological, social and economic risks, affecting almost every aspect of human activity. A major area impacted by the global trend of rising temperatures is crop production. Climate change amplifies heat stress in plants, which occurs when temperatures exceed the optimal range for growth and development. These changes can reduce agricultural productivity, alter crop distributions, increase susceptibility to pests and diseases and disrupt ecosystems. By 2017, the Earth's average surface temperature had risen between 0.8 °C and 1.2 °C above pre-industrial levels, causing notable ecological disruptions and major social impacts (1). It is anticipated that global temperatures will rise by approximately 1 °C by 2025 and 3 °C by 2100 compared to current levels. This warming trend could lead to earlier planting seasons, shifting crop maturity thresholds and altering the geographical distribution of crops (2).

Heat stress poses a major challenge to plant growth, occurring when temperatures exceed a critical threshold, leading to permanent impairment of growth and physiological functions. Short-term temperature increases, typically between 10 °C and 15 °C above normal, are often referred to as heat shock or stress and involve various interacting factors. These factors include the intensity of the heat, its duration and the rate at which temperatures rise. High temperatures pose a major global threat to crop production.

In numerous areas, elevated summer temperatures restrict tomato cultivation (3). In regions where temperatures can surpass 38 °C, the insufficient heat tolerance of most tomato cultivars presents a significant limitation (4). High temperatures negatively impact physiological and biochemical processes, resulting in reduced fruit yields (5, 6). These effects include reduced flower formation and fruit setting, as well as impaired fruit growth and ripening.

This review provides a detailed analysis of how tomatoes respond to high-temperature stress, ranging from cellular processes to whole-plant impacts. It examines the mechanisms behind these responses and explores strategies for breeding heat-resistant tomato varieties, forming a strong basis for future research efforts in this field. Influence of temperature on growth stages of tomato is shown in Table 1.

Overview of HSP (Heat Shock Proteins)

Thermotolerant plants primarily rely on activating the Heat Shock Response (HSR), which reprograms gene expression to enhance resistance against heat stress. Heat stress destabilizes mRNAs coding for proteins not involved in heat response.

The HSR triggers several signalling pathways, including ABA-responsive genes, calcium ion signalling, osmolyte production, ROS detoxification and protein folding mediated by HSPs (7). When plants detect heat stress signals, they activate HSFs and other stress-responsive genes to reduce cellular damage. The HSF cycle boosts the production of HSP mRNAs. In normal conditions, HSFs exist as monomers bound to HSP70 proteins. Under heat stress, HSP70 dissociates from HSF, allowing HSF to form trimers and bind to Heat Shock Elements (HSE) on HSP gene promoters. This binding initiates the transcription and translation of HSPs, especially HSP70.

HSF trimers bound to HSE undergo phosphorylation, which facilitates the binding of HSP70. Afterward, the HSP70-HSF complex dissociates, with the HSF dephosphorylating and returning to its monomeric state to reassemble with HSP70 (8). Newly synthesized HSPs play a crucial role in the protein lifecycle by ensuring correct folding of nascent polypeptides and preventing misfolding and aggregation. Additionally, HSPs work alongside protein quality control systems, including the ubiquitin-proteasome pathway and autophagy, to manage misfolded proteins and support cellular function recovery (9).

The impact of heat stress on factors such as water and nutrient balance, photosynthetic performance, assimilate distribution, crop yield and oxidative damage. The research emphasized the molecular functions of various HSPs, including sHSPs, HSP60, HSP70, HSP90 and HSP100, in conferring heat stress tolerance. The study also explored advanced molecular techniques, such as CRISPR, genome editing and omics approaches, which offer new opportunities for understanding heat stress tolerance mechanisms and improving crop thermo tolerance (10).

Crop response to heat stress

Excessive heat is an important global threat to agricultural productivity, as plant metabolism undergoes rapid changes in response to temperature fluctuations. Molecular techniques are being increasingly employed to improve heat tolerance, with current research targeting the physiological and biochemical reaction to heat stress. In tomatoes, heat tolerance is recognized as a quantitative trait (11).

Evaluation of heat tolerance in tomatoes using several indicators. Heat stress causes membrane damage, with the rate of electrolyte leakage serving as a measure of heat tolerance (12). Physiological and biochemical indicators, like chlorophyll content, have proven useful in assessing heat stress responses (13, 14).

Cellular signalling mechanisms

Under heat stress, plants trigger a cascade of cellular responses, including the opening of calcium channels that permit calcium ions to flow into the cell. These ions interact with phospholipase D (PLD), phosphatidylinositol 4, 5-bisphosphate (PIP2), phosphatidic acid (PA) and inositol triphosphate (IP3), which are part of phospholipid signaling pathways. Additionally, calcium ions bind to CaM3 proteins,

Table 1. Influence of temperature on growth stages of tomato (37, 38)

Temperature range (°C)	Seed germination	Vegetative growth	Flowering	Fruit set	Fruit development	Fruit ripening
<10	Very slow	Stunted	No flowering	No fruit set	No fruit development	No ripening
10-15	Slow	Slow	Delayed	Poor	Slow	Very slow
16-24	Optimal	Optimal	Optimal	Optimal	Optimal	Slow
25-30	Suboptimal	Optimal	Optimal	Optimal	Optimal	Optimal
31-35	Poor	Good	Good	Suboptimal	Rapid	Rapid
36-40	Poor	Moderate	Poor	Poor	Abnormal fruit development	Rapid, poor quality
>40	No germination	Stunted	No flowering	No fruit set	No fruit development	No ripening

triggering cytoskeletal changes. Heat stress also generates the production of ROS and signaling molecules like hydrogen peroxide (H_2O_2) and nitric oxide (NO), which propagate stress signals throughout the cell. Together, calcium ions and ROS activate MAPK and CDPK cascades, which in turn activate nuclear transcription factors. These transcription factors initiate the expression of stress-response genes, antioxidants and ROS-detoxifying enzymes. This signaling cascade ultimately enhances the plant's heat stress resistance by promoting the accumulation of protective compounds and activating defense systems. Fig.1 depicts the effect of heat stress in plants.

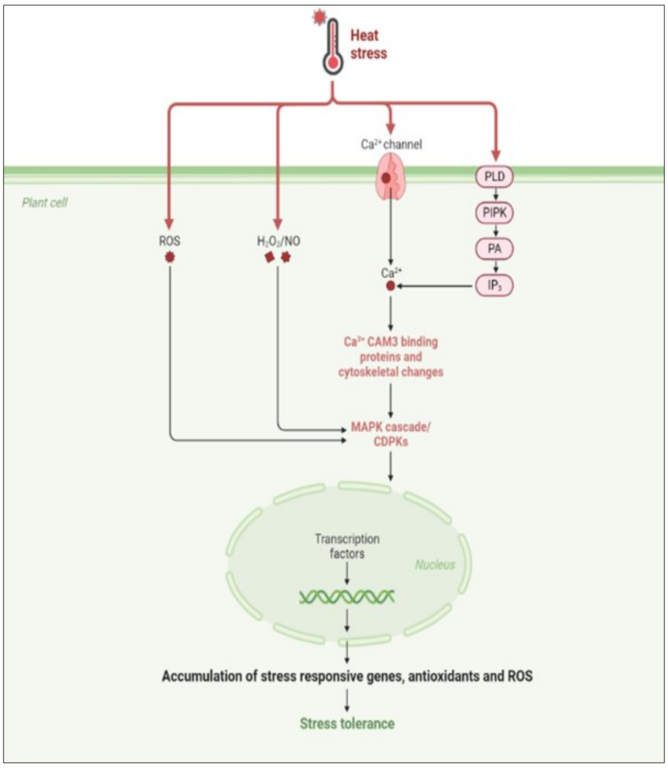

Fig. 1. Effect of heat stress in plants (Source - Biorender).

Morpho-physiological responses

Temperature influences flower organization in tomato plants, which exhibit simple, branched, or simple cyme inflorescences, with the number of flowers per inflorescence being temperature-dependent.

Two common approaches for evaluating plant heat tolerance include measuring ion leakage through electrical conductivity before and after heat exposure and estimating basal heat tolerance by heating cell suspensions or plant segments (15). Tomatoes rely on antioxidant defenses to manage abiotic stress, with heat stress causing significant damage to antioxidant enzymes. Plants improve heat tolerance by regulating salicylic acid (SA) levels and activating alternative pathways (16). To mitigate the harmful impacts of increased temperatures, tomatoes utilize superoxide dismutase (SOD) and ascorbic acid peroxidase (APX), with reactive oxygen species (ROS) serving a signalling function in promoting heat tolerance.

Reproductive traits

Thirteen tomato cultivars under Long Term Moderate Heat (LTMH) and Short Term Heat Shock (STHS), showing significant reductions in reproductive parameters like pollen viability and fruit set under LTMH has been examined (17). Some cultivars demonstrated better heat tolerance, with pollen viability emerging as a key factor for fruit set under heat stress, emphasizing the importance of understanding the genetic pathways underlying heat tolerance. The tomato roots experienced more damage from severe heat stress (40 °C–42 °C) than shoots, reducing nutrient uptake proteins and leading to slower recovery. This could result in lower total protein concentrations in roots, impacting both crop yield and nutritional quality (18). Heat-tolerant 'LA1994' and heat-sensitive 'Aromata' tomato cultivars, finding that heat stress decreased photosynthesis, chlorophyll content and glucose levels in 'Aromata' during seedling and anthesis stages, reducing pollen viability and fruit set. In contrast, 'LA1994' maintained these functions, ensuring better fruit set under heat stress (14). This suggests that early screening for heat tolerance is feasible based on seedling-stage sensitivity to heat stress.

Photosynthesis and respiration

Photosynthesis is highly temperature-sensitive and adjustments in the thermal resistance of Photosystem II (PSII) are influenced by leaf temperature and light intensity (19). Prolonged heat exposure (38 °C for four days) reduces the net photosynthetic rate due to pigment degradation. Additionally, at 40 °C, the efficiency of PSII declines significantly (20).

Elevated CO_2 levels improve tomato heat tolerance by boosting photosynthesis and maintaining photosystem function. Exposing tomato plants to high CO_2 (800 µmol mol^{-1}) at 42 °C increased photosynthetic rates, PSII efficiency and redox balance. Elevated CO_2 reduced photoinhibition and ROS buildup during heat stress and recovery, enhancing resistance by optimizing energy flux, electron transport and redox balance (21).

The effects of high CO_2 levels (800 ppm) on two tomato genotypes ('OuBei' and 'LA2093') under heat and drought stress. Elevated CO_2 enhanced the net photosynthetic rate but had varied effects on different genotypes. While elevated CO_2 reduced damage from combined stress, it increased water consumption, suggesting that it may not always improve plant growth under stress (22). These insights can inform future tomato breeding and management practices.

High humidity mitigates heat stress in tomatoes by increasing the root-to-shoot ratio, chlorophyll content and photosynthetic efficiency, while also enhancing antioxidant enzyme activity and reducing oxidative stress markers. High humidity reduced photoinhibition and oxidative damage, supporting tomato seedling growth under high-temperature conditions (23).

Flower morphology and gene expression

Heat stress also disrupts the balance of floral morphology, as seen in tomatoes, by altering the expression of B-class genes (PI, TM6 and TAP3) in anthers. Increased temperatures suppress the TM6 expression, leading to fewer pistilloid anthers, lower pollen production and decreased pollen viability. The down regulation of these genes directs to anther abnormalities and a decrease in male fertility (24).

Pollen function

Pollen germination, viability and tube development are crucial for fruit set (25). Heat stress negatively impacts pollen viability, retention within anthers and germination rates (26). The Cysteine-R-like Protein Kinase (CRK) gene family in tomatoes, focusing on its function in tolerance to high temperatures (27). CRK genes act as receptors for both external and internal stimuli, activating target genes. A genome-wide study identified 35 potential CRK genes in tomatoes, with most being downregulated during high-temperature conditions. Abscisic Acid (ABA) regulates pollen development, noting that heat stress reduces male fertility in tomatoes by disrupting pollen maturation at higher temperatures (28).

Hormonal influence on fruit set

In tomato fruit development, sugars play a crucial role and are regulated by genes such as Phospho Enol Pyruvate Carboxy Kinase (PEPCK), biochemical elements and vacuolar processing enzymes. Abiotic stressors, such as heat stress, affect sugar content and fruit quality by altering the tomato's morphology. Sugar accumulation occurs in three stages: sucrose and water influx, starch synthesis and sugar metabolism and starch breakdown during fruit softening. Total Soluble Solids (TSS), which range from 4 to 6 Brix, are influenced by environmental stresses.

The signaling pathways of auxin and GA are essential during the initial phases of fruit development. SlDELLA and the SlARF7/SlIAA9 complex facilitate the interaction between gibberellin (GA) and auxin, thereby regulating fruit initiation. The breakdown of SlDELLA, a negative regulator, activates the GA pathway and facilitates fruit set (29). Moreover, SlPIN4, an auxin efflux transporter, impacts the local distribution of auxin in flower buds, thereby influencing fruit set (30). Additionally, overexpressing the SlNCED1 gene which encodes a crucial enzyme for ABA biosynthesis, affects pistil development and subsequently impacts fruit set (31).

Genetic factors in fruit development

The cytosolic A/N-INV NI6 gene in tomatoes, which is expressed across multiple tissues such as leaves, stems, flowers and fruits. Knockdown of this gene results in delayed flowering and poor vegetative growth, ultimately reducing fruit set (32). Genetic studies identified several Quantitative Trait Loci (QTLs) linked to fruit number and set (33, 34). Pad-1 gene regulates auxin accumulation in unpollinated ovaries, contributing to fruit set, with its suppression leading to parthenocarpic fruit formation (35).

Phenological reactions

Tomato plants are vulnerable to heat stress throughout their growth, particularly during fruit set and flowering. The temperatures above 26 ˚C at night and 35 ˚C during the day significantly affect fruit set, although temperatures exceeding 20 ˚C at night and 26 ˚C during the day have minimal impact (36).

Characteristics to assess for heat tolerance in tomatoes

Female fertility: Traditionally, tomato heat tolerance screening has focused on fruit set and yield. However, it is increasingly important to evaluate other heat tolerance mechanisms, like pollen quantity per flower, pollen viability, pollen tube length, style length, cell membrane integrity and photosynthetic efficiency. While male reproductive organs are more sensitive to heat stress, research indicates that female organs are also impacted. To evaluate female fertility under heat stress, flowers pollinated with pollen from heat-sensitive plants are analyzed for seed set. The heat stress decreased female fertility, leading to fewer fruits with seeds (15). Although measuring female fertility through seed count is complex and time-consuming, identifying indirect traits associated with fertility may simplify screening.

Male reproductive organs: Under heat stress, pollen viability, quantity and release are critical factors affecting fruit set. Numerous studies reveal that heat stress reduces pollen viability and quantity in tomatoes. However, high pollen production may not always correlate with fruit set, as factors like humidity can impede pollen release. Thus, pollen release is a more reliable indicator of heat tolerance than pollen quantity. Viable pollen is strongly positively correlated with fruit set, which makes pollen viability a crucial characteristic for assessing heat tolerance in tomatoes and other crops such as soybeans, cotton, canola, wheat and rice.

Thermostability: Membrane thermostability is a reliable and effective method for evaluating heat tolerance, particularly during the vegetative stages. High temperatures disrupt the tertiary and quaternary structures of membrane proteins, affecting the functionality of biological membranes. An increase in electrolyte leakage signals impaired membrane permeability. The high day time temperatures (36 °C) and warm nighttime temperatures (25 °C) led to deformities in tomato anthers, caused by the accumulation of Reactive Oxygen Species (ROS), highlighting the importance of membrane stability in assessing heat tolerance (39).

Biochemical traits in heat stress responses of tomatoes

Under stress conditions, plants accumulate various metabolites, either directly in response to the stress or as part of their adaptive mechanisms. Profiling these metabolites provides a valuable strategy for identifying thermo-tolerant genetic resources, mapping metabolic QTL and developing biochemical markers to enhance breeding efficiency. In heat-tolerant genotypes, changes in secondary metabolites support essential plant functions such as nourishing pollen, regulating osmotic balance, promoting pollen germination and scavenging Reactive Oxygen Species (ROS). These alterations also contribute to maintaining membrane fluidity and facilitating pollen tube growth while activating signaling pathways that enhance pollen viability and fruit set. For instance, the buildup of polyamines such as spermidine and spermine is essential for successful pollen germination. Studies have shown that increased polyamine biosynthesis in genetically modified tomatoes can enhance heat tolerance under stress conditions.

Proline levels

The accumulation of proline is a typical plant response to different abiotic stresses. A rise in proline levels in tomato leaves under biotic stress. Proline levels are regulated through a balance between biosynthesis and degradation (40, 41).

Sugar levels

The heat-tolerant tomato plants have higher soluble sugar levels in their leaves during heat stress, particularly during flowering, compared to heat-sensitive varieties (14). The inability of sensitive genotypes to efficiently regulate carbohydrate synthesis under heat stress was recognized as a major factor behind this difference.

Polyamine changes

Elevated polyamine levels enhance plant resilience to various abiotic stresses. The enzyme S-Adenosyl-L-Methionine Decarboxylase (SAMDC) is crucial for polyamine biosynthesis and its overexpression has been linked to enhanced resistance against various stresses, including salinity, drought, oxidative stress and heat (42).

Polyphenol oxidase

Heat stress causes significant changes in metabolite composition and enzyme activity in tomatoes, particularly affecting phenolic compounds. There was a decrease in peroxidase and polyphenol oxidase activities under heat stress, which contributed to membrane damage, nutrient depletion and oxidative stress.

Aroma volatiles inhibit Poly Phenol Oxidase (PPO) and POD activity in tomatoes, finding that d-limonene and β-damascenone inhibited PPO activity by 50 % at 40 mM and 80 mM, respectively. Thermal inactivation experiments revealed that POD is more heat-tolerant than PPO (43).

Salicylic acid

The SA affects the heat shock response in tomato plants (44). Furthermore, SA improves heat tolerance by enhancing photosynthetic efficiency through proline accumulation and stabilizing heat shock transcription factors, allowing them to bind effectively to heat shock elements in the promoters of HSP genes (45).

Fatty acids

Changes in membrane fatty acid composition help plants adapt to heat stress by creating an environment conducive to the proper functioning of key proteins (46). The fatty acids responded significantly to heat stress (47). Oleic acid levels decreased on the first day (D1H8) and continued declining without recovery overnight (D2H0), dropping further under a second heat stress cycle (D2H8). Linoleic acid also showed a steady decline, with a significant reduction from the first day (D1H4, D1H8) and continuing through the second day (D2H0, D2H8). They suggested that heat stress rapidly depletes key fatty acids, potentially impacting plant stress responses. This depletion may hinder the plant's ability to maintain cellular integrity and function under adverse conditions. Consequently, understanding the mechanisms behind fatty acid metabolism during heat stress could provide valuable insights for developing more resilient crop varieties.

Electrolyte leakage

Electrolyte leakage is a commonly used indicator for evaluating plant resilience to heat stress and differentiating between genotypes. Heat stress compromises membrane integrity, leading to increased electrolyte leakage. The heat-tolerant genotypes exhibit less leakage and greater membrane stability under high temperatures (48). Electrical conductivity measurements to assess genetic variability in heat tolerance, finding that heat-tolerant genotypes had increased membrane thermal stability (49).

The accumulation of polyamines, soluble sugars, proline, flavonoids and other osmolytes offers a promising approach for selecting heat-tolerant plant lines. However, further research is needed to investigate the interactions between these metabolites and their impact on heat tolerance. Additionally, investigating the genetic diversity of secondary metabolites in tomato germplasm will enhance our understanding of their role in improving yield under heat stress conditions.

Breeding perspective

Wild relatives of tomato in breeding for heat tolerance

Cultivated tomatoes exhibit limited genetic variation regarding heat tolerance, leading to heightened interest in leveraging wild tomato relatives. These wild varieties possess traits linked to resistance against both abiotic and biotic stresses, along with characteristics that enhance yield. Genetic resources found in tomato gene banks remain underutilized due to insufficient screening for heat tolerance, which has hindered their integration into breeding programs. Pollen viability and pollen count per flower in 17 tomato accessions was investigated, which included six *S. pimpinellifolium* and 11 cultivated varieties, under heat stress conditions. They observed significant variation, with wild relatives such as *S. pimpinellifolium*, *S. pennellii* and *S. corneliomulleri* showing good pollen viability, while *S. peruvianum* exhibited a high pollen count. Some cultivated varieties, such as CLN1621F and NCHS-1, displayed promising heat tolerance, particularly in terms of pollen count per flower, whereas other cultivars like Nagcarlang exhibited high pollen viability under heat stress (50).

These wild relatives, along with heat-tolerant cultivated varieties, represent valuable resources for breeding tomatoes with enhanced heat tolerance. Therefore, wild tomato species are essential for expanding the genetic diversity for heat tolerance within the primary tomato gene pool.

Breeding for heat tolerance in tomatoes

One of the key challenges faced by tomato farmers is the widespread lack of heat tolerance in most tomato cultivars (51). A modest rise of 2 to 4 °C above optimal temperatures can substantially impact gamete development, hinder the conversion of pollinated flowers into seeded fruits and ultimately reduce yield. This approach combines modern breeding techniques with the genetic diversity found in wild relatives to produce more heat-tolerant tomato varieties. Fig. 2 depicts a visual representation of advanced breeding strategies incorporating various methods to create cultivars resilient to high temperatures.

Conventional breeding

Conventional breeding has been crucial in developing many tomato varieties, although the process is typically time-

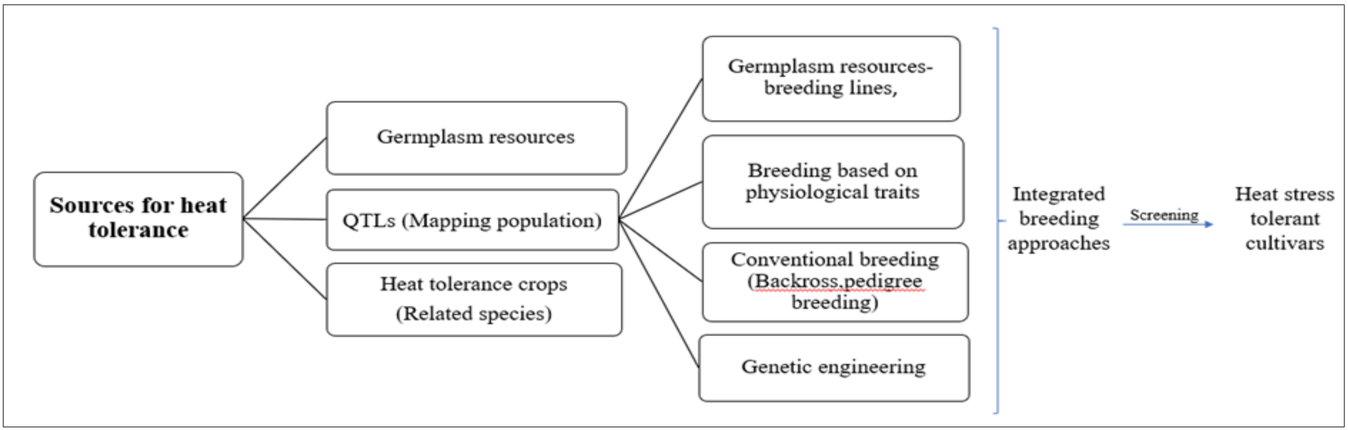

Fig. 2. A visual representation of advanced breeding strategies incorporating various methods to create cultivars resilient to high temperatures.

consuming and labor-intensive (52). To breed for heat tolerance, the focus should be on selecting physiological traits such as canopy architecture, delayed leaf senescence, photosynthetic efficiency, lower respiration rates, reproductive traits and harvest index (53). Prioritizing these traits can help develop heat-tolerant genotypes without compromising yield (54). Heat tolerance genes can be sourced from wild relatives, germplasm collections and materials adapted to harsh environments (55). Candidate genes for enhancing heat tolerance in tomato is given in Table 2.

Traditional breeding methods for heat tolerance typically rely on selection, often conducted in regions with climates similar to the target area, allowing natural selection for thermotolerance traits (56). Heat-tolerant lines can be backcrossed with desired varieties to develop locally adapted plants, though incorporating traits from wild relatives may introduce unwanted characteristics.

Pollen viability screening was used to classify tomato accessions into heat-tolerant (e.g., LA2854, LA1478, LA0417) and heat-sensitive (e.g., LA1719, LA1580, SWEET4) categories. Similarly, in previous studies various wild tomato species including *S. pimpinellifolium, S. corneliomulleri, S. pennellii* and *S. peruvianum*, exhibited strong pollen viability even under heat stress. A Line × Tester design to assess heterosis for growth, yield and quality, identifying cross-combinations like 'CLN2237 × Sweet-72' and 'CLN2237 × Punjab Chhuhara' as candidates for improved commercial lines (50). Some of the heat tolerant varieties of tomato is given in Table 3.

Molecular breeding

Both traditional and hybrid breeding methods, which rely on additive genetic effects and genetic interactions, show potential for breeding heat-tolerant tomatoes. Despite some analyses of QTL, the creation of molecular markers for Marker Assisted Selection (MAS) in breeding heat-tolerant tomatoes is still in the initial phases. Further QTL research is needed to confirm consistent genetic control and shared mechanisms of heat tolerance across various tomato varieties.

Several QTLs associated with heat tolerance have been identified in tomatoes. For example, five key QTLs (qHII-1-1, qHII-1-2, qHII-1-3, qHII-2-1 and qCC-1-5) were discovered on chromosome 1, associated with traits such as heat damage, electrical conductivity, chlorophyll content and maximum quantum yield (Fv/Fm). Four genes-*SlCathB2*, *SlGST*, *SlARG and SlUBC5* that contribute to thermotolerance and can be used to develop heat-resistant varieties was

Table 2. Candidate genes for enhancing heat tolerance in tomato

Gene	Expression	Function	Reference
codA	Overexpression	Glycine betaine (GB) synthesis - acts as an osmoprotectant, helping cells maintain water balance and stabilize proteins and membranes under stress condition	(79)
slmapk3	CRISPR/Cas9	Mitogen-activated protein kinases (MAPKs) family - plays a crucial role in various cellular processes, including signal transduction, stress response, growth and development in plants.	(80)
HSP101	Overexpression	Molecular chaperone	(81)
LeAN2	Overexpression	Anthocyanin-associated R2R3-MYB transcription factor - plays a key role in regulating anthocyanin biosynthesis	(20)
LeCDJ1	Overexpression	Chloroplast-targeted DnaJ protein - plays a crucial role in protein homeostasis, stress tolerance and photosynthesis regulation	(82)
DREB2A	Upregulated	Transcription factor - Upregulates genes involved in osmoprotection, heat shock response and ROS scavenging and activates Heat Shock Proteins (HSPs) and LEA (Late Embryogenesis Abundant) proteins, which prevent protein denaturation and protect cellular structures.	(83)
HSP90	Upregulated	Molecular chaperone - plays a crucial role in protein folding, stabilization and stress response	(84)
CaM	Upregulated	Calcium sensor protein - Helps in ROS (Reactive Oxygen Species) detoxification by regulating antioxidant enzyme activity.	(85)
DHN	Upregulated	Protein chaperone - Prevents protein aggregation and denaturation during dehydration and binds to membranes and macromolecules, stabilizing them under water-deficit conditions.	(86)
MT-sHSP	Expression	Accumulation of heat shock proteins, transcription regulatory network, prevents protein denaturation and aggregation in mitochondria, assists in refolding misfolded proteins under high temperatures and also maintains ATP synthesis by stabilizing mitochondrial proteins under heat stress.	(87)

Table 3. Heat tolerant varieties of tomato

Varieties	Institute	Description
Mukthi	It is developed the College of Horticulture, Vellanikkara, of Kerala Agricultural University.	This variety is resistant to bacterial wilt and thrives in high temperatures. It produces medium-sized, flat, circular fruits that are yellowish-green without green shoulders. However, the fruits are prone to cracking.
Vellayani Vijay	It is developed by Regional Agricultural Research Station, Vellayani, Kerala.	Resistant to bacterial wilt and thrives in warm climates. Optimal fruit color and quality are achieved in bright sunlight with temperatures between 21 °C and 24 °C.
Pusa shakti	It is an open Pollinated Variety developed by ICAR-Indian Agricultural Research Institute, New Delhi.	This tomato variety grown in the states of Chhattisgarh, Odisha andhra Pradesh and Telangana. It is well-suited for open-field cultivation from May to October. The ripe fruits feature a thick pericarp (7 mm), a moderate TSS of 4.8° Brix and a lycopene content of 6 mg per 100 g. Its thick pericarp enhances transportability. Additionally, it exhibits high-temperature tolerance and delivers an average yield of 351 q/ha.

identified (57). Phenotyping and genotyping of tomato fruits, linking SNP markers to various quality traits was identified (58). SNP analysis to assess hybridity in tomato F1 progenies and identified a gene associated with extended shelf life (59). Mapped QTLs related to heat tolerance in reproductive traits, highlighting significant phenotypic variability in pollen viability under heat stress (12).

15 genotypes were assessed for yield traits under high temperatures and identified potential resistance alleles in the parental genotypes (60). They also discovered genes associated with biotic stress resistance using SNP analysis, which led to the development of seven high-performing hybrid varieties. The phenotypic and genomic diversity of tomato landraces under heat stress, identifying genes involved in floral structure development and abiotic stress response (61). The use of genetic and molecular tools, such as Chromosome Segment Substitution Lines (CSSL) and Backcross Inbred Lines (BIL), to enhance genetic diversity and minimize linkage drag in tomatoes (62). The population structure and diversity of wild and cultivated tomato lines, grouping them based on their heat stress responses (63).

Omics approaches for heat stress tolerance

Multi-omics approaches have advanced our understanding of how plants respond to abiotic stresses. Techniques like genomics, ionomics, proteomics, transcriptomics, metabolomics and phenomics offer a comprehensive perspective on stress biology, facilitating the development of crops that are resilient to climate-related challenges (64). By leveraging these methodologies, researchers aim to expedite the creation of plants that can withstand environmental stresses. At the genomic level, DNA serves as the foundation for identifying genes linked to heat stress tolerance in plants, encompassing a variety of heat-responsive genes. These genes produce mRNA transcripts, forming the transcriptome, which translates into functional proteins that make up the proteome, crucial for stress adaptation.

Additionally, plants can modulate gene expression post-transcriptionally through non-protein-coding short RNAs, like microRNAs (miRNAs) (65). Gaining insights into the roles of these short RNAs in stabilizing the transcriptome, enhancing cellular resilience and supporting plant development under heat stress and recovery can facilitate the genetic engineering of stress-tolerant crops (65). Research indicates that the RNA binding protein ATGRP7 increases in reaction to moderate temperature stress but decreases under extreme conditions.

The combined salt and heat stress in tomatoes led to decreased plant height, dry weight and photosynthetic rate while increasing leaf Na^+ accumulation. Physiological responses, including photosynthetic adjustments and defense enzyme activities, were regulated by gene expression and metabolite accumulation. Transcriptomics and metabolomics identified five key pathways, with oxidative phosphorylation (map00190) playing a central role. Heat stress was found to be the dominant factor in combined stress conditions. Alternative oxidase (Aox1a) and other key genes require further functional analysis for improving stress tolerance (66). The transcriptome changes in tomato ovaries under heat stress (HS) was analyzed and 837 differentially expressed genes was identified. These genes varied between heat-tolerant and heat-sensitive genotypes. Expression changes in these genes were linked to traits like yield, phenology and fruit quality under HS (67).

The transcriptome-wide differences between heat-tolerant (CLN1621L) and sensitive (CA4) tomato cultivars, revealed both shared and cultivar-specific regulatory mechanisms. Functional characterization confirmed Solyc09g014280 (Acyl sugar acyltransferase) and Solyc07g056570 (Notabilis) as positive regulators, while Solyc03g020030 (Pin-II proteinase inhibitor) acted as a negative regulator of heat stress (HS) tolerance. SNP analysis of promoters highlighted cultivar-specific transcription factor regulation. Overexpression of ethylene response transcription factors (ERF.C1/F4/F5) enhanced thermotolerance (68).

The transcriptomics and metabolomics were used to investigate high-temperature (HT)-induced stigma exsertion in cultivated tomatoes, revealing that stamens shorten more severely than pistils due to differential cell wall remodeling. Pectin, sugar metabolism, expansin and cyclin genes regulate selective cell division and expansion, affecting organ length. Auxin and Jasmonate (JA) signaling were implicated in these developmental changes, with JA/COI1 signaling effectively rescuing stigma exsertion under HT. Gene expression analysis confirmed distinct transcriptional responses in stamens and pistils (69). Fig. 3 depicts application of omics in enhancing breeding.

Effective management of heat stress in plants necessitates collaboration among molecular biologists, plant

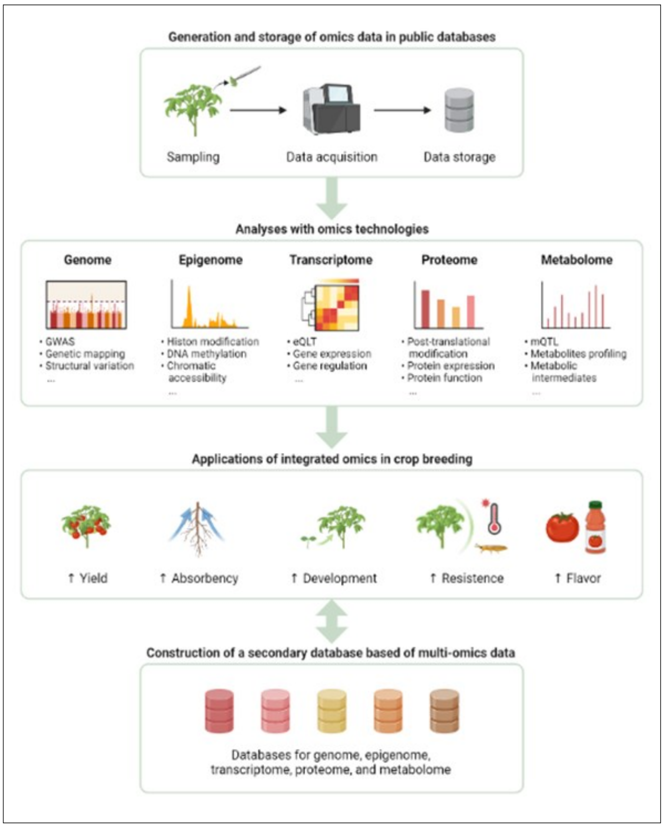

Fig. 3. Application of omics in enhancing breeding (source- Biorender.com).

physiologists and crop modelers. Significant progress has been made in developing heat-resistant varieties through insights gained from studying wheat's responses to thermal stress.

Genome editing

Gene editing has proven to be a powerful tool for enhancing crop traits across various plant species, including those in the Solanaceae family. The most prevalent genome editing techniques include transcription activator-like effector nucleases (TALENs), zinc finger nucleases (ZFN) and CRISPR/Cas9. These methods aim to make precise modifications to the genome, resulting in the creation of desirable alleles that expedite the development of new varieties and broaden the genetic pool of beneficial traits. Notably, CRISPR/Cas9 can target multiple genes simultaneously, making it particularly advantageous for enhancing heat tolerance traits governed by several genes. To implement gene editing effectively, two primary conditions must be fulfilled: the accessibility of genome sequencing and efficient transformation techniques. Fortunately, both requirements are met for tomatoes, as their genome has been completely sequenced, annotated and made publicly accessible, along with a library of over 500 resequenced accessions.

A CRISPR mutant (CRISPR-bzr1) affects tomato heat tolerance via RBOH1-dependent ROS signaling, primarily regulated by FERONIA 2&3 (70). CRISPR/Cas9 editing of the Ethylene Response Factor (ERF) family, which plays a vital role in resilience to abiotic stresses, especially heat stress (71). CRISPR-Cas9 s employed to modify the hybrid proline-rich protein 1 (SlHyPRP1) gene, resulting in multiple stress-tolerant variants suitable for stress-breeding programs (72). While research on CRISPR/Cas9's use for heat stress is still developing, its potential to enhance heat stress tolerance is significant. Fig. 4 depicts the methods of genetic engineering for development of heat tolerant variety.

A parthenocarpic (seedless fruit) tomato mutant was identified through EMS mutagenesis, capable of setting high-quality fruit under heat stress conditions. Using next-generation sequencing, marker-assisted mapping and CRISPR/Cas9, they confirmed that a mutation in SlAGAMOUS-LIKE 6 (SlAGL6) was responsible for the trait. Unlike other parthenocarpy mutants, Slagl6 does not alter flower structure, maintains pollen viability and allows sexual reproduction. The mutant overcomes fertilization failure under heat stress, making it valuable for climate-resilient breeding. SlAGL6 regulates ovary arrest release, enabling fertilization-independent fruit set (73).

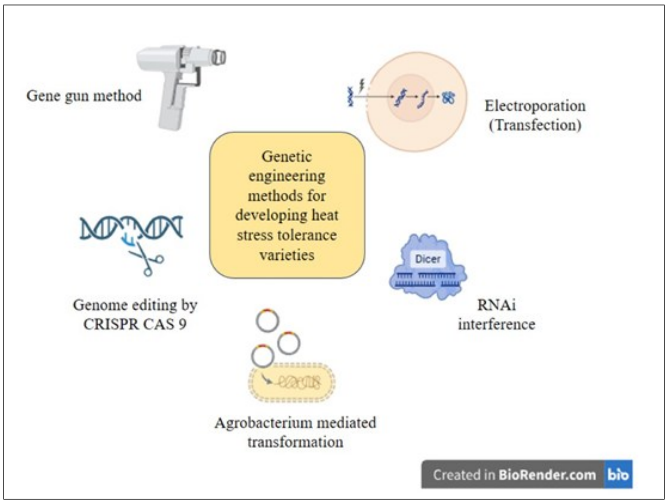

Fig. 4. Methods of genetic engineering for development of heat tolerant variety (source- Biorender.com).

SlMAPK3 was identified as a negative regulator of heat stress tolerance in tomatoes. qRT-PCR analysis showed that SlMAPK3 expression decreased under heat stress and CRISPR/Cas9-generated slmapk3 mutants (L8 and L13) exhibited higher thermotolerance than wild-type (WT) plants (74). Mutants had lower ROS levels, less membrane damage and increased antioxidant enzyme activity. Additionally, they showed higher expression of Heat Stress Transcription Factors (HSFs) and Heat Shock Proteins (HSPs). These findings suggest that SlMAPK3 suppresses heat stress tolerance by regulating antioxidant defenses and stress-responsive genes (75).

SlMPK1 was identified as a negative regulator of heat stress tolerance in tomatoes. Silencing SlMPK1 enhanced thermotolerance by increasing antioxidant-related proteins, reducing lipid peroxidation and boosting antioxidant enzyme activity. SlSPRH1, a serine-proline-rich protein, was identified as a direct phosphorylation target of SlMPK1, with Ser-44 being crucial for its function. Yeast two-hybrid and in vitro assays confirmed their interaction, linking SlMPK1 to oxidative stress regulation. SlSPRH1 overexpression in Arabidopsis decreased thermotolerance, confirming its role in heat stress sensitivity and highlighting the complex interplay between these proteins. Further investigation into the downstream signaling pathways activated by SlMPK1 could provide deeper insights into the molecular mechanisms governing heat stress responses in tomatoes and potentially lead to the development of more resilient crop varieties. These findings underscore the importance of understanding plant stress responses at a molecular level, as they may inform breeding strategies aimed at enhancing resilience. By elucidating the roles of key proteins like SlMPK1 and SlSPRH1, researchers can pave the way for innovative approaches to improve crop performance under challenging environmental conditions (74).

Speed breeding

To address evolving agricultural challenges and consumer demands, it is crucial to expedite breeding cycles. Strategies such as speed breeding and genomic selection (GS) play a significant role in enhancing thermotolerance in tomatoes (76, 77, 34). This innovative approach focuses on optimizing growth conditions by controlling factors such as light (continuous exposure) and temperature (optimal thermal settings), using high-density planting and applying the single seed descent method to select for key traits. This strategy has already proven successful in groundnut cultivation, allowing for two growth cycles per year instead of one. In wheat farming, it has facilitated the completion of six generations annually. Given that tomatoes thrive in greenhouse environments, this method supports the rapid generation of inbred lines. The integration of MAS, speed breeding, genomic selection and high-throughput phenotyping holds significant promise for greatly enhancing heat tolerance in tomatoes.

TILLING

TILLING (Targeting Induced Local Lesions in Genomes) employs chemical or physical mutagenesis to generate mutations in specific genes, which can then be rapidly identified. These TILLING mutants can facilitate gene functional studies and, because they are not transgenic, can be easily integrated into pre-breeding programs. A tomato HSBP1 gene mutant was identified using TILLING, which exhibited a substitution of methionine for isoleucine, partially impairing protein function and leading to reduced suppression of Hsf activity. The resulting mutant seedlings displayed enhanced basal thermotolerance and adult plants demonstrated improved resilience to repeated heat stress without compromising normal growth. This HSBP1 mutant allele holds potential for the development of heat-tolerant tomato varieties (78).

Transgenic breeding

While our understanding of the genetic basis of heat tolerance remains limited, progress in both traditional breeding and modern molecular biology techniques-such as molecular markers and genetic transformation-has facilitated the genetic analysis and development of plants with enhanced heat stress tolerance. The consistent production of specific proteins has been associated with improved heat resilience, along with the modulation of HSPs and HSF gene expression. Although there has been some success in creating transgenic plants with varying levels of heat tolerance, research in this area has lagged behind efforts to engineer resistance to other stressors like drought, salinity, or cold.

Changes in membrane fluidity can affect how plants perceive stress through lipid signaling, which in turn influences the activation of their defense responses. As a result, these transgenic plants had lower levels of trienoic fatty acids and higher levels of dienoic fatty acids in their chloroplasts compared to wild-type plants. This alteration helped maintain photosynthetic function during short high-temperature exposure and enhanced the tobacco plants' resilience to both chronic and acute heat stress. While wild tomato species harbor genes for stress tolerance, genetic barriers often impede the transfer of these traits to cultivated varieties. Transgenic technologies enable the transfer of genes across species, thereby bolstering tomato plants' resistance to drought, heat and salinity.

Future prospects

To effectively overcome the challenges provided by climate change and heat stress in tomato production, a multidimensional strategy must be implemented, integrating contemporary breeding techniques, genetic engineering and creative agronomic practices. Future research should focus on using modern genomic technologies, such as CRISPR/Cas9 and gene editing, to create heat-tolerant tomato cultivars with increased stress tolerance, yield stability and superior fruit quality. Furthermore, high-throughput phenotyping methods, which use drones, sensors and AI-driven analysis, can speed the identification and selection of heat-resistant characteristics in breeding programs. The combination of metabolomics and proteomics will provide more insight into biochemical pathways that aid in stress adaption, whereas microbiome engineering-the use of beneficial microbes-can improve plant health, nutrient absorption and stress tolerance. Implementing climate-resilient agricultural practices, such as precision irrigation, controlled-environment agriculture and soil health management, will boost tomato productivity during heat waves. Exploring varied genetic resources, such as wild cousins and landraces, will be critical for expanding the genetic base and introducing new heat-tolerance genes.

Predictive modeling and AI-driven climate simulations will help predict future stress patterns and guide breeding and management decisions. These approaches not only enhance the resilience of tomato crops but also contribute to sustainable agricultural practices that can mitigate the impacts of climate change. By integrating technological advancements with traditional knowledge, farmers can adapt to shifting environmental conditions and ensure food security for future generations. Collaboration between the public and private sectors will be critical for accelerating the translation of research discoveries into commercial solutions and guaranteeing widespread adoption by farmers. Furthermore, educational outreach and training programs should be enhanced to provide farmers with knowledge about adaptable tactics and developing technologies.

Finally, supportive policies and investments in agricultural research will be critical for driving innovation and guaranteeing long-term food security. By focusing on these comprehensive, long-term solutions, the agricultural sector can create resilient tomato production systems, minimizing the negative effects of climate change and ensuring sustainable food production for future generations. These efforts will not only improve the livelihoods of farmers but also contribute to the overall stability of local and global food systems. As collaboration among stakeholders increases, the agricultural community can better navigate the challenges posed by an ever-changing environment.

Conclusion

In light of the pressing challenges posed by climate change, the review on genetic frontiers in tomato breeding underscores the critical need for developing heat-tolerant cultivars to ensure sustainable agricultural practices and food security. As rising temperatures increasingly threaten tomato production, it becomes imperative to adopt a multifaceted approach that integrates traditional breeding techniques, genetic engineering and marker-assisted selection. These strategies are essential for enhancing the physiological and biochemical resilience of tomatoes to heat stress, which adversely affects key processes such as flower formation, fruit setting and overall yield. The review highlights the importance of understanding the complex interactions between various genes and environmental factors, which can be achieved through advanced genomic technologies like CRISPR/Cas9. This technology allows for the simultaneous targeting of multiple genes, thereby facilitating the enhancement of heat tolerance traits. Furthermore, the utilization of wild relatives of tomatoes, which possess inherent traits for abiotic stress resistance, presents a valuable resource for breeding programs that aim to improve heat tolerance. Agronomic practices, including optimized irrigation, adjusted planting schedules and the use of beneficial microorganisms, can further bolster the resilience of tomato crops under heat stress conditions. The review emphasizes that a collaborative effort among researchers, breeders and farmers is essential to navigate the complexities of climate change and its impact on agriculture. By fostering innovation and integrating diverse strategies, the agricultural sector can develop robust tomato varieties that not only withstand rising temperatures but also contribute to global food security. Ultimately, the synthesis of genetic advancements, agronomic practices and collaborative efforts will be pivotal in creating sustainable tomato production systems capable of thriving in a warming world.

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Authors' contributions

AP conducted critical literature reviews and drafted the manuscript. Valuable guidance, critical suggestions and overall supervision throughout the preparation of manuscript was done by VKS. BA made significant corrections and provided insights that enhanced the quality and accuracy of the manuscript. All co-authors RJ, BA and GK reviewed the final version and approved the manuscript before submission.

Compliance with ethical standards

Conflict of interest: The authors have no conflicts of interest to declare. All co-authors have seen and agree with the contents of the manuscript and there is no financial interest to report. We certify that the submission is original work and is not under review at any other publication.

Ethical issues: None

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