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MICROCLIMATE MODIFICATION STRATEGIES FOR MITIGATING HEAT STRESS-INDUCED POLLEN DAMAGE IN TOMATO (*SOLANUM LYCOPERSICUM L.*)

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ABSTRACT

Heat stress is a primary constraint on tomato (*Solanum lycopersicum L.*) productivity worldwide, acting most critically during the reproductive stage by impairing pollen viability, germination, and tube elongation, leading to reduced fruit set and yield losses. High temperature disrupts the microsporogenesis process, causes oxidative damage to pollen membranes, impairs carbohydrate metabolism through invertase inactivation, and destabilises the actin cytoskeleton required for pollen tube navigation. Molecular mechanisms underlying these effects include downregulation of meiotic recombinases, sporopollenin biosynthesis genes, and callose synthases, along with disruption of Ca^{2+} homeostasis and premature tapetal programmed cell death. Microclimate modification strategies including shade-net cultivation (30–50% shading), polyhouse and greenhouse systems with evaporative cooling, reflective plastic mulching, anti-transpirant and foliar osmoprotectant sprays, and IoT-based wireless sensor-actuator systems have been demonstrated to reduce canopy temperatures by (2–10°C), preserving pollen viability and improving fruit set under heat stress conditions. The combination of these microclimate interventions with heat-tolerant varieties that constitutively express heat shock proteins and enhanced antioxidant systems has been shown to provide synergistic protection of reproductive function under thermal stress, with yield gains up to 35%. This review synthesises the physiological and molecular basis of heat-induced pollen damage, systematically evaluates the efficacy of six categories of microclimate management strategies, and proposes an integrated framework for maintaining tomato reproductive success under current and projected climate warming scenarios.

KEYWORDS: Climate change; Heat tolerance; IoT monitoring; Microclimate management; Pollen viability; Protected cultivation

INTRODUCTION

Globally, food security depends on our capacity to produce more food in a changing climate. The economic value of the tomato (*Solanum lycopersicum L.)* as a food crop in human diets and farm incomes has global significance. Production of 189 million tonnes in 2021 was the highest worldwide output for vegetable crops [16], contributing to both subsistence and commercial agriculture across a variety of climatic zones. Tomato is a warm-loving plant whose reproductive cycle, in contrast to vegetative development, is highly sensitive to heat, rendering it one of the most thermosensitive crops during flowering and fruiting [46]. Male reproductive function depends on day and night temperatures of approximately 32–35°C and 22°C, thresholds that are increasingly exceeded in key growing regions such as South Asia, the Mediterranean basin, and sub-Saharan Africa [69, 7, 44, 83].

Pollen grains are acutely sensitive to high temperatures, due to their small cell volume, low hydration, dependence on nutrient transport without a vascular supply, and the stringent requirements to assemble structural, biochemical, and energetic components within a limited developmental period [46]. The tapetum, the innermost anther wall layer, is among the most heat-sensitive tissues, and impaired tapetum development, premature programmed cell death (PCD), and reduced anther dehiscence are consistently observed under elevated temperatures [20]. High temperatures during microsporogenesis accelerate microgametogenesis, yielding senescent gametophytes at anthesis and dramatically reducing pollen longevity [34]. Reactive oxygen species (ROS) accumulation at temperatures as low as 4–6°C above optimum disrupts pollen tube growth, and breakdown of the polarised actin cytoskeleton impairs germination and tube elongation through the style [61, 47, 76, 80].

A two-pronged approach has been devised to address heat-induced reproductive failure in tomato: first, elucidating the mechanisms by which heat stress interferes with pollen physiology; and second, designing and implementing strategies to buffer the reproductive environment against deleterious temperatures at both the genetic and microclimatic levels. Microclimate modification techniques offer an immediately deployable means of reducing the effect of heat on pollen development, without requiring genetic manipulation or long breeding programmes. This review synthesises recent mechanistic advances (2021–2025) on the impact of heat stress on tomato pollen during microsporogenesis, viability, and germination, and systematically evaluates six categories of microclimate management systems: shade-net technology, mulching, protected cultivation, anti-transpirant and foliar sprays, IoT-based monitoring and control, and the integration of microclimate management with heat-tolerant varieties.

2. Impact of heat stress on pollen viability in tomato

2.1. Pollen development (microsporogenesis) in tomato

Microsporogenesis in tomato spans approximately (10–14) days between archesporial cell division and anther dehiscence, encompassing meiosis, free microspore formation, and pollen maturation within a thermally sensitive anther space. Since anthers are largely non-vascular, the developing microspores rely solely on the secretory tapetum as a source of nutrition, making the anther particularly sensitive to thermal perturbation [45, 56].

2.1.1. Heat shock during meiosis

Even brief exposure (4–6 hours) to 38°C at the meiotic stage is sufficient to generate aberrant products such as dyads, triads, polyads, and polynucleate microspores, reflecting failure in spindle assembly and cytokinesis [71, 37].

2.1.2. Structural malformations and non-functional pollen

Scanning and transmission electron microscopy reveal that heat-stressed tomato pollen assumes a shrunken or collapsed morphology, loses the typical tricolporate aperture arrangement, exhibits uneven exine reticulation, and shows incomplete intine deposition defects that directly affect stigma adhesion, desiccation resistance, and rehydration capacity required for germination [11, 23]. Assessment of 15 tomato genotypes under heat stress (38/28°C, 10 days) demonstrated that structural pollen collapse and starch depletion were the strongest predictors of diminished germination and fruit set [11].

2.2 Pollen viability in tomato

Pollen viability decreases rapidly beyond 32°C and approaches zero at 40°C in most commercial tomato cultivars [71, 23]. Three biochemically linked pathways membrane damage, dehydration-related injury, and enzyme inactivation underlie heat-induced viability loss and act together in a feed forward manner to progressively reduce pollen functional capacity.

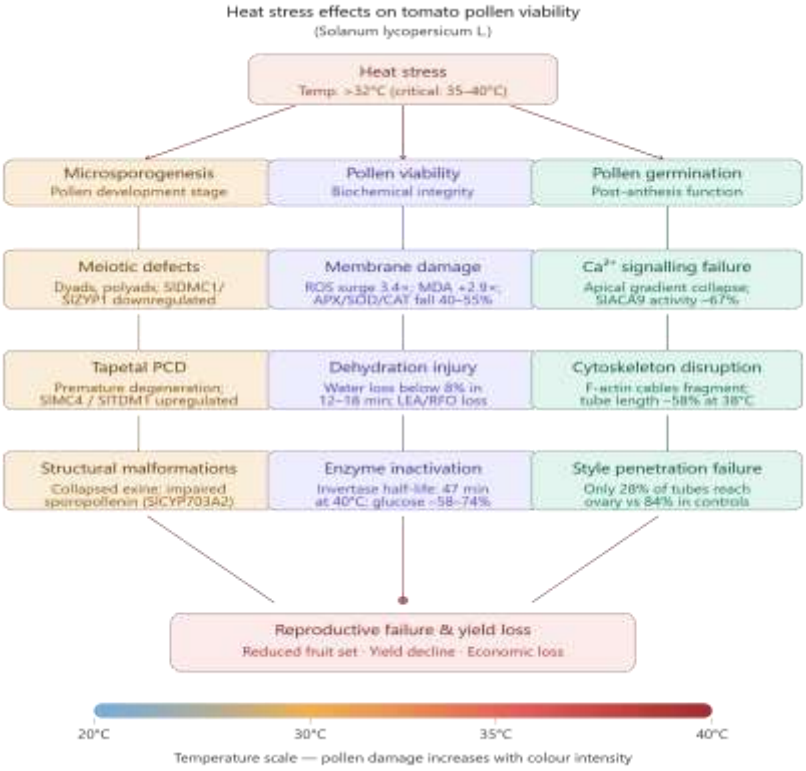

Fig. 1. Heat stress effects on tomato pollen viability

2.2.1. Membrane damage

Heat treatment at 40°C for 2 hours decreased membrane-intact pollen by 68% in heat-sensitive cultivars [19], and membrane integrity was the strongest predictor of in vitro germination under heat stress across genotypes (Pearson r = 0.91) [23]. At 38°C, intracellular ROS increased 3.4-fold above controls within 30 min, with malondialdehyde content

increasing 2.9-fold and antioxidant enzyme activity (SOD, CAT, APX) declining 40–55% [10]. Lipidomic profiling revealed dramatic phospholipid remodelling with a partial homeoviscous response and accumulation of oxidised phospholipid species acting as damage-associated molecular patterns [28, 53, 82].

2.2.2. Dehydration

Mature tomato pollen is discharged at approximately (15–20%) water content in a partially dehydrated, metabolically dormant state permitting dispersal stability. Heat stress also reduces expression of Group 3 LEA protein genes (SlLEA3-1, SlLEA3-2) and raffinose family oligosaccharide (RFO) accumulation in developing pollen, further degrading viability under dehydration conditions and establishing RFO metabolism as a genetic enhancement target for thermotolerance [48, 49, 35].

2.2.3. Enzyme inactivation

Heat stress inactivates enzymes by disrupting hydrophobic interactions and disulfide bonds supporting protein tertiary structure, impairing catalytic activity and causing irreversible aggregation when the HSP chaperone system is saturated [81]. Soluble and cell wall-bound invertase activity in tomato anthers is significantly decreased at 38/28°C day/night temperatures, inhibiting sucrose conversion to hexoses needed for microspore growth and pollen germination [63]. Antioxidant enzyme retention (APX, SOD, CAT) was strongly positively correlated with pollen germination percentage ($r = 0.87$) across 20 accessions, with the wild accession S. pennellii exhibiting 2.1-fold greater APX activity than the commercial cultivar and Moneymaker [73, 62].

Table 1. Key genes and molecular players involved in heat stress responses of tomato pollen and pollen tubes.

Gene/Protein	Category	Function in Pollen	Effect of Disruption/OE	Citation
Soluble/CW-invertase	Glycoside hydrolase	Sucrose → hexose for germination	Reduced sucrose-to-hexose conversion; germination failure	[63]
SlSAMDC1	SAM decarboxylase	Polyamine biosynthesis	Stabilises membranes; +18–24% germination	[66, 27]
Pollen Tube Growth & Ca^{2+} Signalling				
SlACA9	Ca^{2+}-ATPase	Maintains apical Ca^{2+} gradient	Ca^{2+} gradient collapse; loss of tube polarity	[84]
APX/SOD/CAT	Antioxidant enzymes	ROS scavenging; limits lipid peroxidation	3.4× ROS surge; MDA +2.9×; membrane damage	[10]
SlLEA3-1/SlLEA3-2	Group 3 LEA proteins	Cytoplasmic glass stabilization	Reduced RFO; viability loss under dehydration	[48]

2.3. Tomato pollen germination

In vitro germination percentage in tomato declines above 30°C, drops below 50% at 35°C, and is practically eliminated at 40°C in sensitive cultivars [71, 11]. High temperatures disrupt Ca^{2+} signalling, cause cytoskeleton disorganisation, inhibit vesicle trafficking, and impair cell wall synthesis during pollen tube elongation, all contributing independently to heat-induced fruit set failure.

2.3.1. Reduction in germination percentage

Germination of 15 commercial tomato cultivars declined from 71.3% at 25°C to 38.6% at 35°C and 9.2% at 40°C, with thermotolerant genotypes including 'Heatmaster' and 'Solar Fire' retaining 22–31% germination at 40°C versus less than 5% in sensitive cultivars [11]. Heat-impaired germination is mediated by disruption of Ca^{2+} homeostasis; heat stress at 38°C eliminated the typical apical Ca^{2+} gradient after 8 min, with a 67% decrease in Ca^{2+}-ATPase activity (SlACA9) compromising gradient restoration [84]. Exogenous nitric oxide donor sodium nitroprusside (50 μM) protected tomato pollen germination under 38°C stress by stimulating antioxidant enzymes and inhibiting lipid peroxidation [70]. Elevated polyamine levels driven by upregulation of SlSAMDC1 mitigated germination decline through membrane stabilisation and ROS chelation, with exogenous spermidine application increasing germination (18–24%) under 38°C stress [66, 27].

2.3.2. Pollen tube elongation

Heat-stressed tomato pollen tubes frequently exhibit reduced elongation rates, abnormal developmental patterns (helical growth, branching, burst ends), and fail to reach the ovule. Pollen tube growth in tomato, which must penetrate a 35-cm style within 24–36 hr, requires coordinated tip exocytosis, cell wall polymer cross-linking, and cytoskeleton dynamics that are all thermosensitive [84, 56]. At 38°C, tube length was 58% shorter than controls at 25°C, with disorganisation of F-actin filaments from longitudinal cable arrays to diffuse punctate patterns disrupting myosin XI-mediated cytoplasmic streaming and vesicle delivery of pectin and cellulose to the growing tip [84]. Under 38°C conditions, only 28% of pollen tubes penetrating the upper style reached the ovary versus 84% in controls, identifying the upper style as the principal bottleneck [65].

Table 2. Effect of heat stress on pollen viability in different tomato varieties and genotypes.

Variety/Genotype	Temperature Condition	Pollen Viability/Germination Response	Key Observation	References
Heatmaster	40°C	22–31% germination retained	Thermotolerant; maintains function under stress	[11]
Solar Fire	40°C	22–31% germination retained	High heat tolerance similar to Heatmaster	[11]
Moneymaker	38–40°C	<5–10% germination	Highly heat-sensitive cultivar	[11]
Solanum pennellii (wild type)	38°C	High viability retention	Strong antioxidant activity (2.1× APX)	[62]
Solanum pimpinellifolium (wild type)	38°C	Higher viability than cultivated types	Better membrane stability	[23]
Commercial cultivars (general)	35°C	~50% reduction in germination	Moderate sensitivity	[71]
Heat-sensitive genotypes (panel)	40°C (2 hrs)	68% reduction in viable pollen	Severe membrane damage	[19]
15-genotype panel (mixed)	38/28°C (10 days)	Wide variation (5–30%)	Structural integrity linked to viability	[11]

3. Microclimate modification strategies for improving pollen viability in tomato

The evidence presented above confirms compounding damage to tomato pollen at high temperatures across all three phases of microsporogenesis, viability, and germination, ultimately leading to fruit-set failure and significant yield losses during severe heat events. Since the genetic enhancement of pollen thermotolerance is constrained by trait complexity and breeding timescales, microclimate modification strategies including shade-net technology, protected cultivation, mulching, anti-transpirant foliar sprays, osmoprotectant foliar sprays, and IoT-based sensor-actuator systems can be immediately deployed to reduce canopy temperature and vapour pressure deficit during the critical anthesis window [72]. As pollen viability in tomato decreases measurably above 32°C, even a modest temperature reduction (2–5°C) in the floral microclimate can shift reproductive conditions back into the functional range, preventing the biochemical and physiological perturbations of heat-induced pollen sterility [71, 57, 74].

3.1. Shade-net technology

Shade nets, typically deployed at 30–50% shading levels, reduce canopy air temperature by (2–5°C) by capturing a fraction of incoming solar radiation, a reduction sufficient to maintain pollen germination percentage and tube extension rates within the viable range [71, 5]. Shade-net cover at 40% improved fruit set by 22% compared to uncovered controls in open-field tomatoes during summer, and also regulated vapour pressure deficit, alleviating transpirational stress and reducing pollen desiccation during anthesis [12, 26]. Plants cultivated under shade nets exhibited increased proline and decreased malondialdehyde biomarkers of thermotolerance, indicating that microclimate buffering activates protective biochemical pathways [68]. The shade percentage requires careful optimisation, since shading above 60% impairs photosynthesis and reduces carbohydrate supply to pollen-producing structures [79]. Among shade-net colours, pearl-coloured nets provided superior photosynthetically active radiation transmittance and temperature reduction in comparative trials [77, 55, 67].

3.2. Polyhouse and greenhouse systems

Controlled environment greenhouse structures allow near-real-time adjustment of temperature and humidity to maintain the optimal pollen viability range of 20–28°C and 60–70% relative humidity [72, 9]. Fan-and-pad evaporative cooling systems reduce internal temperatures by 5–10°C during peak heat events through adiabatic cooling, and have been shown to significantly improve pollen germination and fruit set in tropical and semi-arid conditions [60, 75]. Tomatoes cultivated in automated greenhouse systems maintained pollen viability above 85% even in summer months when ambient temperatures exceeded 38°C, compared to less than 40% viability in parallel open-field experiments [1]. Naturally ventilated polyhouses outperformed conventional and shaded greenhouses for controlling the microclimate and reproductive stage of tomato in hot-arid environments [58]. Diffuse polyethylene films additionally optimised light distribution, minimising local heat retention on floral tissues and enhancing photosynthate availability to pollen-producing structures [32].

3.3. Root-zone microclimate stabilisation through mulching

Mulching exerts an indirect yet physiologically consistent effect on pollen viability by stabilising root-zone temperature and moisture. On sunny days, soil surface temperatures may exceed air temperatures by 10–15°C under uncovered conditions, producing root-zone thermal stress that inhibits nutrient uptake and assimilate supply required to support microsporogenesis [33]. Reflective plastic mulches (silver and white-on-black types) reduce soil temperature variation by up to 6°C and prevent moisture loss by inhibiting surface evaporation [30, 13]. Organic mulches such as straw, paddy husk, and dried leaves act as insulators, retain moisture, and improve soil water-holding capacity through organic matter addition after decomposition [51]. Drip-irrigated tomatoes under reflective plastic mulch in north Indian plains exhibited significantly higher leaf and floral tissue relative water content, translating into enhanced pollen viability and fruit set during hot dry periods [78]. The combination of mulching with drip irrigation forms a synergistic root-zone microclimate system well adapted to the compound heat-and-drought stress that often occurs concurrently during summer production [3, 36].

3.4. Anti-transpirants and foliar sprays

Film-forming anti-transpirants such as kaolin particles (3–5%) enhance leaf reflectance, reducing canopy temperature by (1–3°C) and suppressing photo-oxidative stress during high solar radiation periods [24]. Tomato plants sprayed with kaolin during Mediterranean summer showed significantly greater pollen viability, tube germination, and fruit set than unsprayed controls, with the greatest effect occurring during peak irradiance and temperature [8]. Glycine betaine, a water-soluble compatible solute, improves pollen germination and tube growth under heat stress by stabilising membrane integrity and protecting carbohydrate-metabolising enzymes in pollen grains. Salicylic acid (0.5–1.0 mM) induces thermotolerance by activating heat shock proteins and antioxidant enzyme systems, with SA-pretreated plants retaining significantly higher pollen viability at supraoptimal temperatures than untreated controls [40, 54]. Ascorbic acid and putrescine sprays inhibit ROS formation in heat-stressed pollen grains, maintaining viability by preventing oxidative injury to pollen lipids and proteins [42, 66, 39].

3.5. IoT-based microclimate monitoring and automatic control systems

IoT-based systems deploy wireless sensor networks across the crop canopy to continuously measure temperature, relative humidity, light intensity, CO_2 concentration, and soil moisture, transmitting data to cloud-based platforms that trigger automated control of fans, evaporative cooling pads, shade curtains, or misting systems [17, 25]. The critical advantage of these systems is their capacity to detect and respond to temperature excursions within the physiologically harmful window; exposure to temperatures above 38°C for as little as 30–60 min during anthesis has been shown to reduce pollen viability by more than 50% [18]. An IoT-based smart greenhouse management system that maintained internal temperature within ±1°C of a 28°C setpoint achieved pollen viability above 80% during seasons when outdoor temperatures reached 40°C [72]. Machine learning algorithms applied to historical microclimate and crop performance data enable proactive cooling before temperatures exceed pollen viability thresholds, outperforming reactive systems [59]. Integration with weather forecasting APIs further enables anticipatory management actions deploying shade screens and pre-emptive irrigation before forecast heatwaves to provide the most comprehensive protection of pollen viability throughout the reproductive cycle [64, 41, 22, 4].

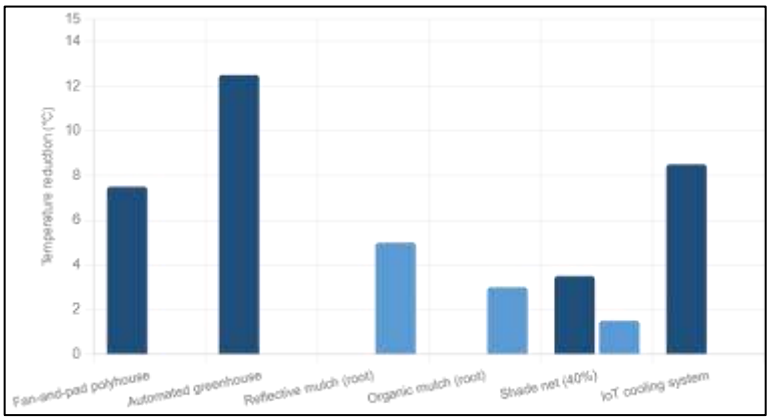

Fig 2: Mean Temperature Reduction (°C) by Microclimate Modification Strategy in Tomato Production (2005–2025)

3.6. Integration of microclimate modification with heat-tolerant varieties

The combination of microclimate modification strategies with heat-tolerant tomato varieties provides synergistic protection of pollen viability under thermal stress. Heat-tolerant varieties carry higher constitutive expression of heat shock proteins, enhanced antioxidant systems, and greater membrane thermal stability in tapetal and pollen cells, enabling viable pollen production at temperatures that eliminate fertility in sensitive genotypes [21, 52]. Microclimate modification strategies are specifically engineered to prevent ambient temperatures from exceeding the thermal tolerance limits of even improved germplasm [19]. When heat-tolerant varieties and susceptible checks were planted under shade-net conditions, the yield difference between them increased by approximately 35% relative to open-field conditions, indicating that microclimate buffering reveals the full genetic potential of improved germplasm [43]. The physiological basis for this

synergy is that genetic tolerance raises the temperature threshold above which pollen damage occurs, while microclimate modification reduces the frequency and severity of thermal events approaching or exceeding that threshold, yielding a collective protective effect achievable by neither strategy alone [6]. The combination of shade-net cultivation with heat-tolerant varieties is now recommended as an integrated package of practices for summer tomato production in hot-humid zones [31, 50, 2].

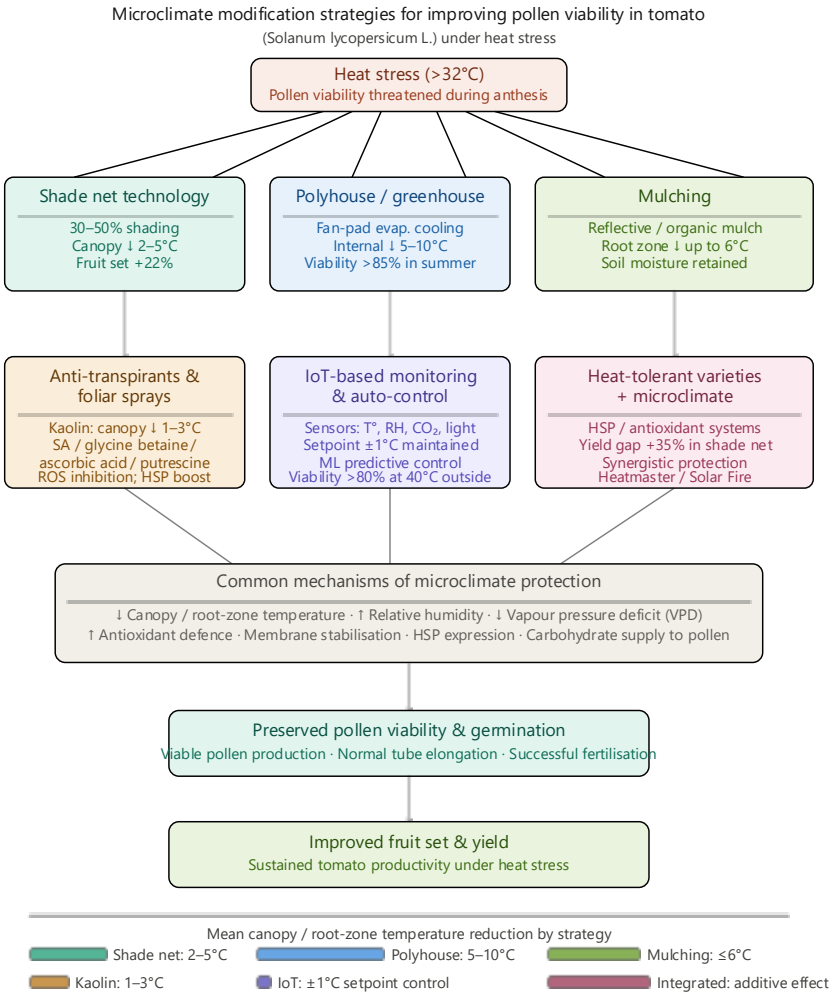

Fig 3. Microclimate modification strategies for improving pollen viability in tomato

4. CONCLUSION

Heat stress substantially limits tomato production by impairing pollen viability, fertilisation, fruit set, and yield through a cascade of physiological, biochemical, and molecular mechanisms including oxidative membrane damage, dehydration-induced cytoplasmic glass destabilisation, invertase inactivation, disrupted Ca^{2+} signalling, and actin cytoskeleton disorganisation that operate synergistically to eliminate reproductive success under supraoptimal temperatures. Shade-net technology, protected cultivation, mulching, anti-transpirant and foliar osmoprotectant sprays, and IoT-based microclimate monitoring systems represent a portfolio of effective and scalable interventions that reduce thermal stress by maintaining optimal temperature and humidity conditions around flowering tomato plants, thereby preserving pollen viability and improving reproductive success across diverse production environments.

The synergistic deployment of these microclimate management strategies with heat-tolerant varieties is a particularly promising approach for maintaining tomato productivity under growing climatic variability, as demonstrated by yield improvements of up to 35% compared to either approach alone. Future research should focus on the coupling of advanced IoT and machine learning systems with physiological and genetic methods, including manipulation of ROS homeostasis, flavonol accumulation, and thermostable pollen energetics, to further enhance thermotolerance. The implementation of these integrated interventions will be essential for ensuring stable and sustainable tomato productivity in a warming climate.

Data Availability Statement

All data supporting this review are obtained from previously published studies cited in the reference section. No new experimental data were generated or analyzed.

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Writing: Sourav Lokesh B; visualization & supervision: Kokilavani S; critical review: Ga.Dheebakaran, A. Sankari, K.Vanitha, K. Chandrakumar.

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The authors declare no conflicts of interest.

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Abbreviations
APX — Ascorbate peroxidase
ATPase — Adenosine triphosphatase
Ca^{2+} — Calcium ion
CAT — Catalase
CBL–CIPK — Calcineurin B-like protein–CBL-interacting protein kinase (calcium-signalling module)
CO_2 — Carbon dioxide
CW-invertase — Cell-wall invertase
DOI — Digital object identifier
FAOSTAT — Food and Agriculture Organization Corporate Statistical Database
HS — Heat stress
HSP — Heat shock protein
ICAR-IIVR — Indian Council of Agricultural Research – Indian Institute of Vegetable Research
IoT — Internet of Things
LEA — Late embryogenesis abundant (protein)
MDA — Malondialdehyde
OE — Overexpression
PCD — Programmed cell death
RFO — Raffinose family oligosaccharides
RH — Relative humidity
RNA — Ribonucleic acid
ROS — Reactive oxygen species
SA — Salicylic acid
SAM — S-adenosylmethionine
SC — Synaptonemal complex
sHSP — Small heat shock protein
SOD — Superoxide dismutase
TF — Transcription factor
VPD — Vapour pressure deficit

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