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Heat stress in chilli (*Capsicum annuum* L.): Reproductive vulnerability, fruit quality and mitigation strategies

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ABSTRACT

Rise in atmospheric temperature, exposing chilli crops to heat episodes that coincide with flowering and early fruit development, stages that are especially sensitive to temperature stress. High yield depends on a sequence of tightly coordinated events, including anther and pollen development, pollen release, pollen germination, pollen-tube growth, stigma and ovule function, fertilization and retention of young fruits. This review illustrates recent evidence, with emphasis on studies published in this decade, on how heat stress disrupts reproductive development in *Capsicum annuum* and how these effects translate into reduced fruit set, unstable yield and changes in fruit quality. Particular attention is given to pollen traits and reproductive anatomy because physiological, histological, QTL and GWAS studies indicate that reproductive thermotolerance is genetically variable and cannot be explained by a single trait. Heat also affects photosynthesis, source-sink relations, membrane stability, reactive oxygen metabolism and hormone signalling, thereby increasing the risk of flower abscission and fruit abortion. Evidence on capsaicinoids is more limited, but recent multi-omics studies suggest that high temperature can alter capsaicin accumulation through coordinated changes in biosynthetic genes, proteins and metabolites. The review also examines practical adaptation options, including thermotolerant rootstocks, moderate shading, irrigation management, signalling compounds, osmoprotectants and genetic improvement through phenotyping, QTL mapping, GWAS, marker-assisted selection and genome editing. Future research should place greater emphasis on reproductive success under realistic heat regimes while measuring yield and market-relevant quality traits. This integrated approach can support future chilli cultivars and production systems better adapted to increasingly hot growing seasons.

Keywords: Chilli, *Capsicum annuum*, Heat stress, Pollen viability, Fruit set, Capsaicin, Thermotolerance, Climate-smart production

1. Introduction

Chilli (*Capsicum annuum* L.) is grown both as a vegetable and as a spice and its commercial value depends on more than total biomass. Growers require consistent flowering, fruit set, marketable pod yield and, for pungent types, a desirable level of capsaicinoids. A plant may remain visibly alive during a hot spell while experiencing substantial injury in anthers, pollen, stigmatic tissues or young ovaries; the economic damage becomes obvious only later as flower drop, poor fruit set, malformed fruits or reduced yield. Recent reviews have established high temperature as a major constraint to chilli productivity and have summarized vegetative, physiological and molecular heat responses (Khattak *et al.*, 2026; Prasad *et al.*, 2026; Sajjad *et al.*, 2025; Upadhyay *et al.*, 2025) [1, 2, 3, 4]. Presently, the more specific challenge is to understand how those responses connect to the reproductive sequence that ultimately determines harvestable yield.

Temperature sensitivity in chilli depends on genotype, developmental stage, exposure duration and the balance between day- and night-time temperatures. For that reason, a single numerical value should not be treated as a universal heat-stress threshold. Controlled experiments have used a wide range of heat regimes. In the studies considered here, treatment temperatures ranged from 36 °C to 42 °C, including day/night regimes of 38/22 °C and 40/32 °C (Gisbert-Mullor *et al.*, 2023; Liu *et al.*, 2022; Poudyal *et al.*, 2023; Rajametov *et al.*, 2021) [5, 6, 7, 8]. Foundational work also showed that particular floral stages are especially vulnerable and that pollen performance can be a useful indicator of reproductive thermotolerance (Erickson *et al.*, 2002; Gajanayake *et al.*, 2011; Reddy *et al.*, 2007) [9, 10, 11]. More recent studies reinforce this view while also showing that heat-stable fruit set cannot be explained by pollen alone (Manoharan *et al.*, 2026; Yamazaki *et al.*, 2025) [12, 13].

The urgency of this issue has increased because heat events are becoming more frequent, longer and more likely to overlap with flowering in open-field and protected systems. Process-based simulations indicate that warming can substantially reduce chilli yield while climate-focused reviews of horticultural crops emphasize that temperature effects interact with radiation, water availability and other stresses rather than acting in isolation (Park *et al.*, 2025; Raza *et al.*, 2025; Saeed *et al.*, 2023; Shah *et al.*, 2024) [14, 15, 16, 17]. This interaction matters in practical production. A high-temperature episode accompanied by strong radiation and soil-

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water limitation imposes a different physiological load from the same air temperature under adequate root-zone water and moderated radiation.

A further reason to focus on reproductive heat stress is that the quality consequences have received less attention than yield. Chilli fruits are valued for colour, vitamin C, phenolics and pungency and the biochemical pathways responsible for these traits remain active during fruit development. Multi-omics evidence now shows that heat can alter capsaicin and ascorbic acid accumulation in developing pepper fruit (Liu *et al.*, 2022) [6]. However, this evidence base is still much smaller than the literature on vegetative heat responses. A review that links flowering, reproductive organ function, fruit set, yield and capsaicinoid accumulation can therefore identify where the evidence is strong where it is contradictory and where further experimentation is needed.

Heat sensitive stages

Reproduction compresses several highly coordinated processes into a short period. Before anthesis, microsporogenesis and microgametogenesis must produce viable pollen; the anther must mature and dehisce; pollen must be released and reach a receptive stigma; pollen grains must hydrate, germinate and extend a tube through the style; ovules must remain functional; and fertilization must be followed by sufficient hormonal and assimilate support to retain the young fruit. Heat

can disturb any of these steps. Because failure at one stage cannot always be compensated later, reproductive heat damage often causes a disproportionate yield penalty compared with a similar episode during vegetative growth (Driedonks *et al.*, 2016; Kaur *et al.*, 2016; Reddy *et al.*, 2007) [18, 19, 11].

Recent anatomical work strengthens this interpretation. In heat-tolerant and heat-susceptible *C. annuum* material, high temperature caused contrasting changes in anther organization, pollen abundance and viability, vascular integrity and ovary tissues. Tolerant plants retained a more intact reproductive structure whereas susceptible material showed greater tissue degeneration (Manoharan *et al.*, 2026) [12]. These observations move the discussion beyond the simple statement that pollen viability declines and suggest that maintaining reproductive tissue organization and carbohydrate status is also part of heat tolerance.

Genotype changes the extent of reproductive damage considerably. Reproductive-stage screening has repeatedly separated tolerant and susceptible material on the basis of pollen performance, flower retention and fruit set (Kaur *et al.*, 2016; Singathiya *et al.*, 2026; Srivastava *et al.*, 2020) [19, 20, 21]. Whole-plant comparisons also show useful variation in photosynthesis, cooling, recovery and oxidative injury under heat (Kim *et al.*, 2023; Poudyal *et al.*, 2023; Srivastava *et al.*, 2022) [22, 7, 23]. Earlier screening and breeding studies likewise reported exploitable variation within chilli germplasm (Chowdhury *et al.*, 2020; Kumar *et al.*, 2020) [24, 25].

Table 1. Examining heat responses in *Capsicum annuum* at different stages

Study	Material & heat context	Key response	Main implication
Rajametov <i>et al.</i> , 2021	Hot pepper seedlings; 42 °C for 10 d, then recovery	Tolerant plants maintained photosynthesis, transpiration and proline; recovered faster	Whole-plant resilience can support later fruit set and yield.
Gisbert-Mullor <i>et al.</i> , 2021	Sweet pepper grafts; prolonged heat plus greenhouse validation	Tolerant rootstocks reduced injury and improved marketable yield	Rootstock choice can buffer heat damage.
Padilla <i>et al.</i> , 2026	Sweet pepper ovaries during flowering/early fruit set	Heat altered ovary hormones; A57 rootstock reduced fruit-set and seed losses	Female reproductive tissues and hormonal balance are part of thermotolerance.
Gisbert-Mullor <i>et al.</i> , 2023	Sweet pepper grafts; 28/22 vs 38/22 °C	Tolerant rootstock improved leaf physiology, pollen germination and fruit set	Vegetative buffering and pollen performance are linked.
Kim <i>et al.</i> , 2023	Three hot-pepper genotypes under prolonged warm conditions	Recovery, photosynthesis and yield loss differed among genotypes	Genotype strongly modifies heat response.
Poudyal <i>et al.</i> , 2023	Akabare chilli landraces; 40/32 °C for 7 d	Tolerant landraces retained better gas exchange, cooling and biomass	Heat avoidance and recovery traits vary within chilli germplasm.
Singathiya <i>et al.</i> , 2026	Contrasting <i>C. annuum</i> genotypes at reproductive stage	Pollen viability, germination and tube growth tracked fruit and seed set	Pollen traits are useful reproductive screening indicators.
Yamazaki <i>et al.</i> , 2025	Chilli mapping populations under hot greenhouse conditions	<i>qFS6</i> improved fruit set without clear effects on pollen germination/dispersal	Heat-stable fruit set can arise through non-pollen mechanisms.
Yogananda <i>et al.</i> , 2026	146 pepper accessions across two hot seasons	Fourteen marker-trait associations were stable across seasons	Natural diversity offers markers for heat-resilient breeding.
Manoharan <i>et al.</i> , 2026	Heat-tolerant vs susceptible <i>C. annuum</i> at reproduction	Tolerant genotypes preserved anther, pollen, ovary and vascular integrity	Reproductive tissue stability is a useful tolerance trait.
Gisbert-Mullor <i>et al.</i> , 2026	Sweet pepper grafts; 28/22 vs 38/22 °C	Thermotolerant rootstock raised marketable yield and reduced blossom-end rot	Yield protection can occur without an obvious quality penalty.

Note: The examples are representative rather than exhaustive. Heat regimes differ among studies, so temperatures should be interpreted in relation to genotype, developmental stage and exposure duration.

Flower initiation, anthesis and flower retention

Heat can alter flowering through both direct developmental injury and broader resource limitation. Under sustained high temperature, pepper plants often retain fewer flowers and show greater abscission. Part of this response reflects restricted carbon supply: heat can depress pho-

tosynthetic gain, raise maintenance respiration and increase the metabolic cost of protection (Moore *et al.*, 2021; Rajametov *et al.*, 2021) [26, 8]. Genotype comparisons and yield modelling further indicate that the size of this penalty varies with genetic background and the heat regime imposed (Kim *et al.*, 2023; Park *et al.*, 2025; Srivastava *et al.*, 2022) [22, 14, 23]. Stress-related hormonal signalling also

changes, although the direction and magnitude depend on genotype, treatment and interacting stresses (Otalora *et al.*, 2020; Otalora *et al.*, 2022) [27, 28]. Direct ovary profiling in pepper shows that heat can disrupt auxins, cytokinins, gibberellins, abscisic acid, jasmonic acid, salicylic acid and the ethylene precursor ACC during early fruit set; a thermotolerant rootstock also reduced losses in fruit set and seed number (Padilla *et al.*, 2026) [29].

Field and controlled-environment studies support the practical importance of flower retention. Heat-tolerant chilli genotypes selected over successive summer generations have shown superior fruiting ability under hot conditions (Srivastava *et al.*, 2020) [21]. More recent physiological comparisons similarly reveal differences among genotypes in recovery, photosynthesis, proline accumulation and oxidative injury (Kim *et al.*, 2023; Poudyal *et al.*, 2023; Rajametov *et al.*, 2021; Srivastava *et al.*, 2022) [22, 7, 8, 23]. These whole-plant traits do not substitute for reproductive measurements but they help explain why one genotype can continue to support flowers while another experiences rapid abscission.

Pollen development, viability and germination

Pollen is one of the most consistently heat-sensitive components of chilli. High temperature can disrupt tapetal function, carbohydrate supply to developing microspores, pollen wall formation, dehydration status and membrane integrity. The resulting pollen may appear morphologically present but have low viability or weak germination. In vitro studies across *Capsicum* species established strong genetic variation in temperature responses of pollen germination and pollen-tube growth (Reddy *et al.*, 2007) [11]. Recent reproductive-stage screening further showed that pollen viability, pollen germination, pollen-tube growth, fruit set and healthy seed set are strongly interrelated under heat stress (Singathiya *et al.*, 2026) [20]. Screening of ornamental pepper and hot-pepper germplasm likewise demonstrated that pollen-based traits can discriminate more tolerant from susceptible material (Gajanayake *et al.*, 2011; Kaur *et al.*, 2016) [10, 19]. The value of pollen traits is confirmed by recent grafting work. Under heat, a susceptible sweet-pepper scion grafted onto a tolerant rootstock maintained better leaf physiology, higher anther proline, improved pollen germination and higher fruit set than less tolerant plant combinations (Gisbert-Mullor *et al.*, 2023) [5].

Pollen-tube growth, stigma, ovary and fertilization

After pollination, heat can alter the probability that a pollen grain completes fertilization. Pollen-tube growth is temperature sensitive and both very high temperatures and heat-damaged pollen can shorten the effective fertilization window (Erickson *et al.*, 2002; Reddy *et al.*, 2007) [9, 11]. At the same time, the pistil is not passive. Stigma receptivity, style physiology, ovule longevity and ovary vascular function can all be affected. The 2026 histological study in *C. annuum* pro-

vides direct evidence that tolerant and susceptible genotypes differ in the structural integrity of both male and female organs under temperature stress (Manoharan *et al.*, 2026) [12].

Fruit yield and quality

At fruit set stage, multiple heat responses become agronomically visible. Flower can be produced normally yet fail to set because of pollen injury, poor pollen-pistil interaction, ovule damage or inadequate assimilate and hormonal support after fertilization. Aruna *et al.*, 2023 [30], Kaur *et al.*, 2016 [19], Srivastava *et al.*, 2020 [21], Yamazaki *et al.*, 2025 [13] reported that fruit set remain a primary selection trait in reproductive heat-tolerance breeding rather than being inferred from vegetative measurements alone. Yield losses also accumulate through effects on fruit number, individual fruit mass and the duration of productive flowering. Process-based modelling across locations in Korea predicts progressively larger pepper-yield penalties as temperature increases, emphasizing that chronic warming affects more than a single flowering event (Park *et al.*, 2025) [14].

Beside the yield parameters, fruit colour, dry matter, soluble solids, vitamin C, phenolics and pungency influence market value. Temperature can alter these traits directly through fruit metabolism and indirectly through changes in source-sink relations and fruit-development rate. Older temperature-regime studies already demonstrated that pepper fruit development and quality are temperature responsive (Oh *et al.*, 2019) [31].

Temperature also interacts with cultural practices that modify light and plant water status. Moderate shading has improved plant water relations and marketable yield in bell pepper under warm conditions (Kabir *et al.*, 2020; Kabir *et al.*, 2022; Kabir *et al.*, 2023) [32, 33, 34] and a hot-pepper study found that intermediate shade levels improved several physiological, yield and quality attributes compared with excessive shade (Ahmed *et al.*, 2023) [35]. Colored shade nets can also affect fruit colour and chemical composition (Diaz-Perez *et al.*, 2020) [36]. These responses illustrate an important management trade-off: reducing canopy heat and radiation can protect reproduction and fruit from sun injury but excessive shade may constrain photosynthesis and carbon supply. The appropriate shade intensity therefore depends on climate, cultivar, season and production objective.

Rootstock studies provide another useful example of a possible yield-quality and benefit-cost ratio. Under heat, thermotolerant rootstocks improved marketable yield and, in recent work, maintained major biochemical quality attributes while improving marketable performance (Gisbert-Mullor *et al.*, 2021; Gisbert-Mullor *et al.*, 2023; Gisbert-Mullor *et al.*, 2026) [37, 5, 38]. This suggests that heat mitigation need not inevitably trade quality for yield. However, pungent chilli types should be tested directly because sweet-pepper fruit-quality responses cannot automatically be extrapolated to capsaicinoid-rich cultivars. The available quality evidence is summarized in Table 2.

Table 2. Effects of temperature and heat-mitigating practices fruit quality and capsaicinoid-related traits

Study / condition	Main quality response	Practical meaning	Caution
Liu <i>et al.</i> , 2022; fruit heat at 36 °C	Capsaicin and ascorbic acid declined; related pathways were reprogrammed	Heat can directly alter pungency and nutritional quality	Short controlled exposure does not define all field responses.
Oh and Koh, 2019; 15-30 °C regimes	Fruit development declined at the warmest regime while capsaicinoids increased across the tested range	Temperature effects on yield and pungency can move in different directions	Not equivalent to acute extreme heat.
Gisbert-Mullor <i>et al.</i> , 2026; thermotolerant rootstock	Higher marketable yield, less blossom-end rot and no clear loss of major biochemical quality traits	Rootstocks may protect both yield and quality	Evidence is from sweet pepper.
Gisbert-Mullor <i>et al.</i> , 2021, 2023; grafting	Improved stress physiology, pollen performance and fruit set	Better plant status can indirectly protect fruit development	Quality traits were secondary endpoints.
Ahmed <i>et al.</i> , 2023; graded shade	Intermediate shade improved productivity and selected quality traits	Moderate shading can reduce heat load	Optimum shade is climate- and cultivar-specific.
Diaz-Perez <i>et al.</i> , 2020; Kabir <i>et al.</i> , 2020, 2022, 2023; shade nets	Moderate shade improved water status/yield and altered fruit composition	Radiation management can protect marketable quality	Most evidence is from bell pepper.
Kabir <i>et al.</i> , 2021; irrigation levels	Moderate deficit maintained yield/quality in the cited trial while improving water-use efficiency	Good water status can support heat avoidance	The study was not a direct heat-stress experiment.

Mitigation strategies

For recurrent heat, genetic improvement offers the most durable long-term option. Chilli contains substantial usable variation for heat response. Reproductive-stage studies have separated tolerant and susceptible genotypes on the basis of pollen function and fruiting ability (Kaur *et al.*, 2016; Singathiya *et al.*, 2026; Srivastava *et al.*, 2020) [19, 20, 21] while physiological comparisons reveal differences in recovery, cooling and carbon balance (Kim *et al.*, 2023; Poudyal *et al.*, 2023; Srivastava *et al.*, 2022) [22, 7, 23]. QTL work extends this variation to mapped genomic regions (Aruna *et al.*, 2023) [30]. Earlier screening and breeding reports, together with experience from heat-tolerance breeding in related crops, also support the value of broad genetic diversity (Ayanan *et al.*, 2019; Chowdhury *et al.*, 2020; Kumar *et al.*, 2020) [39, 24, 25].

Genome editing could eventually speed up both validation and breeding. In chilli, CRISPR/Cas systems have already been demonstrated through PDS editing and newer virus-mediated or heritable editing platforms (Bulle *et al.*, 2024; Kang *et al.*, 2025; Zhao *et al.*, 2024) [40, 41, 42]. Broader crop-editing literature outlines how negative regulators or stress-responsive transcription factors might be targeted for temperature resilience (Chakraborty *et al.*, 2024; Ikram *et al.*, 2024; Zafar *et al.*, 2020) [43, 44, 45]. A recent chilli-focused review makes a similar case for transcription-factor optimization (Bulle *et al.*, 2025) [46]. Even so, direct editing for reproductive heat tolerance in commercial chilli is still a research opportunity rather than a routine breeding tool. Transformation efficiency, genotype dependence, off-target assessment and regulatory acceptance remain practical constraints.

Grafting is one of the management options supported by several pepper-specific heat studies. Appropriate rootstocks can improve growth, membrane stability, chlorophyll fluorescence and marketable yield during prolonged heat (Gisbert-Mullor *et al.*, 2021) [38]. A heat-tolerant rootstock can also improve anther proline, pollen germination and fruit set (Gisbert-Mullor *et al.*, 2023) [5], directly connecting rootstock choice with reproductive performance. The most recent hybrid-rootstock study further demonstrates improved marketable yield and lower blossom-end rot under hot greenhouse conditions (Gisbert-Mullor *et al.*, 2026) [37]. For protected cultivation where high root-zone and air temperatures recur predictably, thermotolerant rootstocks therefore offer a practical bridge while new heat-tolerant cultivars are being bred.

Heat load in the field is shaped by solar radiation and plant water status as well as air temperature. Shade nets can lower radiation and

modify canopy and root-zone conditions. In bell pepper, moderate shading has improved plant water status, photosynthetic performance and marketable yield under warm environments while very strong shade can restrict carbon gain (Kabir *et al.*, 2020; Kabir *et al.*, 2022; Kabir *et al.*, 2023) [32, 33, 34]. Hot-pepper experiments similarly indicate that intermediate shade levels can improve physiology, yield and selected quality traits (Ahmed *et al.*, 2023) [35]. Coloured nets may also alter fruit colour and composition (Diaz-Perez *et al.*, 2020) [36]. These studies support site-specific shading rather than a single universal shade percentage.

Adequate irrigation is equally important because transpirational cooling depends on water supply. Bell-pepper work shows that irrigation level affects plant growth, physiology, yield and quality (Kabir *et al.*, 2021) [47]. Under heat, maintaining root-zone water can help sustain stomatal conductance and leaf cooling but excessive irrigation may create nutrient or root-health problems. Practical climate-smart management therefore involves matching irrigation frequency and volume to evaporative demand, soil or substrate water-holding capacity and shading level. Where water is limited, breeding for reproductive tolerance and water-use efficiency must be pursued together rather than treating heat and drought as separate problems (Dos Santos *et al.*, 2022; Poudyal *et al.*, 2023; Raja *et al.*, 2020) [48, 7, 49].

Foliar application of bio-stimulants can provide short-term protection, although their reliability varies. Salicylic acid, epibrassinolide, methyl jasmonate and proline have all shown stress-mitigating physiological benefits in pepper experiments but not all studies isolated heat as the only stress factor (Masoumi *et al.*, 2024; Otalora *et al.*, 2020; Otalora *et al.*, 2022; Preet *et al.*, 2020) [50, 27, 28, 51]. Their proposed mechanisms include improved antioxidant capacity, membrane protection, osmotic adjustment and altered stress signalling.

Basic crop scheduling remains important. Adjusting sowing and transplanting dates can reduce overlap between peak flowering and the hottest part of the season where local climate permits. Protected structures can use ventilation, evaporative cooling, reflective materials or shading while mulches can influence root-zone temperature (Saeed *et al.*, 2023; Shah *et al.*, 2024) [16, 17]. These measures should be treated as components of an integrated heat-management system. No single intervention is likely to fully compensate for a highly susceptible cultivar exposed to repeated heat waves.

In practice, resilience is most likely to come from combining genetics with crop management. A cultivar that maintains reproductive function under heat reduces dependence on expensive climate control; a tolerant rootstock can add physiological buffering; moderate shade can reduce radiation load; and well-managed irrigation can sustain

evaporative cooling. In high-value protected cultivation, these layers may be economically justified. In lower-input open-field systems, heat-tolerant cultivars, planting-time adjustment and efficient water management are generally more practical and scalable. Climate-smart recommendations should therefore be differentiated by production environment rather than presented as a single package (Raza *et al.*, 2025; Saeed *et al.*, 2023; Shah *et al.*, 2024) [15, 16, 17].

Conclusion

Heat stress poses a major threat to chilli production, particularly during flowering and early fruit development, by disrupting pollen development, germination, fertilization and fruit retention. Genetic, physiological, anatomical and genomic studies indicate that heat tolerance involves multiple mechanisms beyond pollen viability, including maintenance of photosynthesis, membrane stability, redox balance, osmotic adjustment and hormonal regulation. Heat stress can also reduce fruit quality by affecting capsaicin and ascorbic acid accumulation, although genotype $\times$ environment interactions require further study. Short-term adaptation can be achieved through thermo-tolerant rootstocks, moderate shading, irrigation management and validated bio-regulators, while long-term resilience requires breeding for reproductive success and marketable fruit quality under realistic heat conditions. Integrating reproductive phenotypic, genomics and climate-smart management can help to achieve stable chilli production under rising temperature.

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