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REVIEW ARTICLE

Responses of tomato to concurrent abiotic stresses, high temperature and drought: A review

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Abstract

Tomato production is increasingly threatened by the growing occurrence and severity of combined drought and high-temperature stress. Although the individual effects of high temperature and drought stress on tomato growth, physiology, and productivity have been widely investigated, their combined occurrence exerts more severe and complex adverse effects on plant performance and yield. Therefore, a comprehensive understanding of their interactive impacts is essential for developing effective management strategies and breeding climate-resilient tomato cultivars. Here, we review the current understanding of the physiological, biochemical and molecular adaptive responses of tomato to combined drought and heat stresses. Co-occurring stresses during critical growth stages significantly impair photosynthesis through stomatal closure, reduced mesophyll conductance, chlorophyll degradation and disruption of photosystem II efficiency. Combined stress elevates reactive oxygen species (ROS), resulting in oxidative damage to cellular macromolecules despite the activation of antioxidant defences. Reproductive processes, such as pollen viability, fertilisation and fruit set, are highly vulnerable to combined stress. At the molecular level, stress-responsive genes and antioxidant enzymes are differentially regulated, indicating complex interactions among drought and heat signalling pathways. In addition to crop management strategies that alleviate the adverse effects of stresses to some extent, crop improvement strategies such as breeding for stress-tolerant cultivars, integrating omics insights and applying gene-editing tools offer promising avenues for enhancing tolerance to combined stresses. Deciphering integrative mechanisms governing combined drought-heat responses is pivotal for designing climate-adaptive tomato cultivars and sustaining production under global climate change.

Keywords: combined stress; drought; high temperature; tomato

Introduction

Climate change poses a major challenge to agriculture by altering weather patterns and intensifying extreme events such as heat waves and droughts, thereby reducing crop productivity (1). Nearly three-quarters of the world's poor live in rural regions, while almost half of the population in developing countries depends on agriculture as their primary source of livelihood. As a result, these communities are among the most severely affected by climate change (2). According to the IPCC AR6 (2023), the global mean temperature is projected to increase by 1.0–5.7 °C by 2100 and the average global surface temperature has already risen by approximately 0.9 °C since the late 19th century (3). Plants maintain dynamic interactions with their environment and when external conditions exceed their optimal functional range, stress arises, restricting growth and development (4). Water availability and temperature are two key limiting factors for crop growth (5); therefore, drought and heat stress substantially reduce crop productivity (6). In natural environments, drought and heat stresses often occur simultaneously and their frequency and severity are expected to increase under climate change (7). Failure of sexual reproduction under climate stress is a major contributor to yield loss (8, 9).

Tomato (*Solanum lycopersicum* L.) is a predominantly self-pollinated major vegetable crop of the Solanaceae (5). It ranks second only to potato in global vegetable production, accounting for about 16 % of the world's vegetable output. Tomato is also a key model plant for fruit development research and diverse physiological, biochemical, molecular and genetic studies, supported by its well-characterised genome and the availability of genomic data for over 150 cultivars and accessions (10). It also has a relatively short seed-to-seed cycle of approximately 100 days, wide morphological diversity and ease of cultivation and genetic transformation (11). Nutritionally, tomatoes are an important dietary source of vitamins A, C and K, as well as lycopene, potassium and folate (12, 13). Tomatoes also exhibit anticancer potential, protective effects against cardiovascular, neurodegenerative and metabolic diseases while supporting gut microbiome balance, skin health, reproductive and immune function and recovery after exercise. Despite its global importance, tomato is highly susceptible to both biotic and abiotic stresses (5, 14) and

multiple stresses can cause yield losses ranging from 50 to 70 % (15). As an essential food crop and major global commodity, tomato is particularly vulnerable to climate-induced shifts in temperature and water availability (1).

Although several studies have examined individual heat or drought stress responses in tomato, very few have addressed their combined effects, which often trigger unique, non-additive physiological and molecular responses. Therefore, a comprehensive synthesis of combined stress responses is needed. This review synthesises current knowledge on the physiological, biochemical and molecular responses of tomato to simultaneous high-temperature and drought stresses at critical growth stages. Particular emphasis is placed on photosynthesis, plant water relations, oxidative stress regulation, reproductive development and stress-responsive gene networks, with special attention to how responses under combined stress differ from those elicited by individual heat or drought stress. This review covers studies conducted under both controlled and field conditions that examine tomato responses to simultaneous high-temperature and drought stress. The scope encompasses biochemical traits (e.g., antioxidant activity, osmolyte accumulation and lipid peroxidation), physiological traits (e.g., photosynthesis, stomatal behaviour, plant water status and reproductive performance) and molecular mechanisms (e.g., stress-responsive genes, transcription factors and hormonal signalling pathways). This review primarily focuses on the combined effects of high temperature and drought stress, while briefly discussing individual stress responses for comparison. Interactions with biotic stresses and postharvest effects are beyond the scope of this review.

Temperature and heat stress in tomato

Temperature is a fundamental climatic factor that determines plant growth, development and productivity (16). The optimum temperatures for tomato cultivation are 30 ± 2 °C during the daytime and 20 ± 2 °C at night (17). Estimates indicate that global temperatures are expected to increase by 1.8–4.0 °C by the end of the century (18). Plant sensitivity to heat stress varies among species and across developmental stages (16). High-temperature stress is a major constraint on tomato production, severely hindering growth and yield (9, 19). To counteract these effects, tomato plants employ a suite of adaptive strategies, including immune, physiological and molecular responses (20).

Morpho-physiological responses to heat stress

The tomato crop is highly susceptible to high temperatures, particularly during developmental and reproductive stages (21). High temperature stress causes various morpho- physiological changes, including wilting, reduced growth, impaired development, disrupted photosynthesis and decreased yield and quality in tomatoes (16, 22). To cope with high temperature stress, plants develop adaptive responses such as reduction in photosynthetic pigments (chlorophyll and carotenoids) (23), alterations in membrane stability (24), increases in unsaturated fatty acids (25) and activation of heat shock transcription factors. Photosynthesis is one of the most heat-sensitive physiological processes. Genotypes that maintain photosynthetic activity under stress better sustain growth and yield (26). High temperature induced declines in chlorophyll and carotenoids promoted ROS formation and reflected higher stress levels (16, 26). Reduced photosynthetic rates lead to chlorophyll breakdown and inhibition of photosystem II (PSII), ultimately slowing growth (26-28) as depicted from Table 1. Under the same air temperature, genotypes can differ in leaf temperature; thus, canopy and leaf temperature are useful traits for screening heat tolerance (29). Heat also caused protein denaturation, which is counteracted by the induction of heat shock proteins (HSPs) (30).

Heat shock factors and molecular gene networks

Heat shock factors (HSFs) are conserved transcription factors that fine -tune heat stress responses by activating HSP and other stress-responsive genes. In tomato, the expression of HSFs rises rapidly upon exposure to high temperature, leading to accumulation of small HSPs (10). Heat stress activates HSF-regulated gene networks, including *HSFA2* and *HSFA3*, in tomato reproductive tissues. It also induces the expression of *HSP70*, *HSP90* and small heat shock proteins (sHSPs), which are closely associated with enhanced pollen thermotolerance (31). Similarly, in flower buds, HSFs regulated key target genes such as *SlGrpE*, *SlERDJ3A*, *SlTIL* and *SlPOM1,* collectively forming integrated thermotolerance gene networks that support reproductive development under high temperature stress (32). One study analysed 67 heat-responsive genes in tomato and showed that HSFs are early “first responders”, with rapid induction immediately after heat stress exposure, whereas HSPs and other stress-related genes increase more gradually during prolonged stress (22). Among the identified genes in tolerant lines, the rapidly induced key genes were *HSP17.4* (a 17.4 kDa class III sHSP), transcription factor *A-4a, HSF B -2a, HSF24, HSF30* and *HSF19* (*HSF B-3*). Functional annotation of *HSF30* and *HSF24* indicated their role in responses to water deprivation, suggesting that these genes may confer combined tolerance to heat and drought. The multifunctional NAC transcription factor *SlJA2L* has been shown to simultaneously promote thermotolerance and coordinate fruit ripening. It achieves this through the integrated regulation of ethylene biosynthesis and carotenoid metabolic pathways. This reveals the tight molecular coupling between heat stress responses and ripening control in tomato (33).

Table 1. High temperature stress-induced physiological and biochemical changes in tomato

High temperature response	Effect	References
Increased electrolyte leakage	Membrane damage	(23)
Accumulation of H_2O_2 damages proteins and nucleic acids; activation of oxidative defence	ROS production	(23,37)
Proline accumulation leading to osmotic balance	Osmotic adjustment	(89)
Induction and accumulation of heat shock proteins (HSPs)	Protein protection	(10)
Reduced transpiration and ineffective evaporative cooling; increased leaf temperature	Inhibition in stomatal regulation	(83, 29)
PS II inhibition	Reduction in photosynthetic efficiency	(28)
Chlorophyll and carotenoid degradation; reduced Pigment stability	Pigment degradation	(2)
Increased respiration rate leading to carbon loss	Reduced growth and wilting	(22)

Cellular signalling, ROS and antioxidant mechanisms

Tomato plants perceive heat stress, transduce signals, activate gene expression and adjust metabolism through complex networks involving ROS, calcium ions (Ca^{2+}), lipids and phytohormones, thereby promoting thermotolerance (34, 35). Heat stress at the cellular level damages membranes and macromolecules, leading to electrolyte leakage and ion imbalance; lesser leakage indicates greater membrane stability and stress tolerance (23). Heat stress also enhanced ROS, including the relatively stable hydrogen peroxide (H_2O_2), which played key regulatory roles under stress (36). To prevent oxidative damage, plants upregulated non-enzymatic antioxidants and antioxidant enzymes, whose activities generally increased under prolonged heat in both tolerant and susceptible genotypes (16, 23). Elevated temperatures also affected biomass accumulation by impairing cell division and growth, resulting in significant reductions in shoot and root length as well as their fresh and dry weights (10, 16, 24).

Effects on fruit quality and reproductive susceptibility

In field conditions, high temperature decreased lycopene and β-carotene content in many genotypes of tomato while often increasing the vitamin C and total phenolics (21, 37). Plants are generally more susceptible to high temperature stress at the reproductive stage than at the vegetative stage, particularly due to the vulnerability of pollen and fertilisation processes (8, 9, 25). Postharvest ripening at elevated temperatures in the 35-42 °C range profoundly disrupts the regulatory equilibrium among the principal ripening-associated phytohormones: abscisic acid (ABA), ethylene and auxin. It concurrently impairs carotenoid metabolic flux. Exposure to 35 °C selectively suppresses lycopene accumulation, manifesting as persistent orange colouration. Temperatures reaching 42 °C can abolish the ripening program entirely. Collectively, these observations delineate a narrow yet physiologically critical thermal window within which normal fruit ripening competence is maintained (38).

Pollen thermotolerance and hormonal regulation

Prolonged exposure of tomato to high temperatures (32/26 °C day/night) significantly reduced pollen production per flower and lowered pollen viability (8). Heat-tolerant tomato genotypes exhibit higher expression of genes linked with biosynthesis of compatible solutes in pollen such as *P5CS* (proline), *SPS/SuSy* (sucrose) and *GoLS1* (galactinol/raffinose family oligosaccharides), which are associated with improved pollen viability under high temperature stress (39). High temperature stress increased the ABA levels while reducing salicylic acid content (40). High temperatures contributed to enzyme denaturation, impaired PSII activity, reduced electron transport efficiency, inhibited pigment biosynthesis and disruption of Rubisco activase function (27).

Response of tomato to drought stress

Drought is the most damaging abiotic constraint to crop productivity and cultivated tomato is particularly sensitive to water deficit (41, 42). Climate change is increasing the intensity, duration and frequency of drought events, making their impact on global agricultural production increasingly evident (43). In India, overall irrigation efficiency is low and a large proportion of the net sown area is drought -prone, with many regions experiencing recurrent severe droughts.

Physiological and reproductive impacts of water deficit

In tomato, water deficit reduces vegetative growth and biomass accumulation (44, 45), impairing reproductive development, with male organs often being more sensitive than female ones, leading to pollen abortion, anther indehiscence, poor fruit set and yield loss (46, 47). At the physiological level, plants accumulated compatible osmolytes and activated antioxidant defences to limit dehydration and oxidative damage (46, 48). Drought results in reductions in chlorophyll content, the maximum and effective quantum efficiencies of Photosystem II and increased non-photochemical quenching under severe stress (49, 50). Stomatal closure is a primary avoidance response that conserves water but restricts carbon dioxide (CO_2) diffusion, leading to stomatal and, later, metabolic limitations on photosynthesis (42, 46). These responses are largely driven by increased ABA, which modulates guard cell behaviour, hydraulic conductance and stress-responsive gene expression (51, 52) as depicted from Table 2. Moderate water deficit before anthesis significantly impairs ovary cell division and expansion. Mesophyll layers account for approximately 96 % of the observed reduction in final fruit mass. This underscores the exceptional sensitivity of the peri - anthesis and early fruit set window to soil water availability (53).

Water status, genotypic variation and fruit quality under drought

Relative water content (RWC) is a key indicator of plant water status and it correlates with reduced turgor, stomatal closure, photosynthetic decline and increased ROS formation under drought (48, 54). A reduction in RWC and leaf water potential is a key physiological response to drought (46, 55). Together with morphological adjustment, osmotic regulation, stomatal control and ROS scavenging underpin the adaptive behaviour of tomato to drought, but with strong genotype-dependent variation (41, 47). Italian local cultivars under field drought exhibited higher lycopene, vitamin C, phenolics, flavonoids and rutin in several genotypes, indicating that drought stress enhanced the accumulation of bioactive compounds in certain cultivars (41). Tomato

Table 2. Physiological responses of tomato to drought stress

Trait	Drought responses	Reference
Plant water status	Decrease in relative water content and leaf water potential	(46,55)
Vegetative biomass	Reduced shoot/root length, leaf area, plant height and biomass	(44,45)
Stomatal conductance	Stomatal closure leading to reduced stomatal conductance, transpiration and net photosynthesis	(46,54)
Photosynthetic pigments & PSII	Decreased chlorophyll, F_v/F_m, ΦPSII and increased non- photochemical quenching under severe stress	(49,50)
Osmotic adjustment	Accumulation of soluble sugars, organic acids, proline	(54)
Oxidative status (ROS, membranes)	Increase in H_2O_2, MDA, electrolyte leakage indicating membrane damage	(48,67)
Antioxidant defences	Increased SOD, CAT, APX, POX, GR activities and antioxidant and metabolites (ascorbate, phenolics)	(54)
Roots & hydraulics	Decreased root hydraulic conductivity; reduced xylem area and vessel diameter	(55)
Reproductive development & fruits	Reduced fruit set, fruit size and yield; early effects on ovary cell expansion	(49,53)
Fruit quality	Often increased soluble solids, carotenoids, vitamin C under moderate deficit	(59,60)

landraces cultivated under drought showed lycopene concentrations exceeding 100 µg fresh weight (FW) (56). Furthermore, β-carotene was also maintained or increased under stress compared with full irrigation (57). An allele of lycopene ε-cyclase (SlLCY-E) increased fruit lycopene and total carotenoids and simultaneously improved drought tolerance via higher ABA and altered xanthophylls (58). Water stress imposed during the fruit expansion stage generally enhances key quality attributes. These include soluble solids content, sugar accumulation, carotenoids, vitamin C concentration, flesh firmness and lycopene content (59, 60). However, these improvements are accompanied by a measurable reduction in marketable yield. Notably, mild deficit irrigation at this stage is the most favourable strategy for achieving an optimal balance between fruit quality and yield (44).

ABA signalling and stomatal regulation under drought

Tomato plants accumulate ABA significantly in their leaves during periods of water deficit (Fig. 1). Abscisic acid transporters, such as the DELLA–regulated importer AIT1.1, carry ABA into guard cells, increasing ABA sensitivity and triggering stomatal closure to reduce transpirational water loss (61, 62). The primary ABA signalling module controlling stomatal movements consists of SnRK/OST1-type kinases, which are activated when clade A PP2C phosphatases are suppressed by *PYR/PYL/RCAR* receptors in guard cells (63, 64). Activated *OST1/SnRK2.6* phosphorylates downstream targets such as the S-type anion channel *SLAC1* (and its tomato homolog *SlSLAC-6*) and associated components including anion efflux, membrane depolarisation and subsequent potassium ion (K^+) efflux via outward-rectifying K^+ channels, leading to loss of guard cell turgor and stomatal closure (63–66).

Reactive oxygen species generation, calcium signalling and transcriptional regulation in drought response

Studies have reported that drought stress induces a marked elevation in H_2O_2 and malondialdehyde (MDA) content, along with increased electrolyte leakage, collectively reflecting enhanced oxidative stress and consequent damage to cellular membranes (48, 67). ABA-activated *SnRK2s* also stimulate apoplastic ROS production via NADPH oxidases, with H_2O_2 sensed by membrane receptors and entering guard cells through aquaporins such as PIP2;1, thereby triggering Ca^{2+} influx that further amplifies ABA signalling and activates Ca^{2+}-dependent protein kinases that regulate ion channels (61, 68, 69). In tomato, transcriptional regulators, including *SlWRKY6* and *MYC2*, modulate this pathway by altering ABA biosynthesis/signalling genes (e.g., *NCEDs*, *PYL4*, *SnRK2.6/OST1*, *SlPP2C1*) and ROS-generating enzymes such as SlRBOH1, thereby fine-tuning ROS accumulation, stomatal aperture and drought tolerance (70, 71). Moreover, tomato *SlCIPK7*, the functional homolog of *Arabidopsis CIPK8*, acts as a negative regulator of ABA-mediated stomatal closure; its loss of function confers ABA-hypersensitive stomatal closure and enhanced drought tolerance, emphasising the species-specific tuning of the conserved ABA-ROS-CA^{2+} ion channel module in tomato guard cells (72). Comprehensive transcriptomic profiling across the continuum of fruit ontogeny from early cell division and expansion through final ripening reveals extensive, stage and tissue-specific transcriptional reprogramming. Genes governing cell growth, starch metabolism, carotenoid biosynthesis and jasmonate and ethylene signalling are reprogrammed under water-deficit conditions. The placenta and seed tissues emerge as the primary sites of stress-

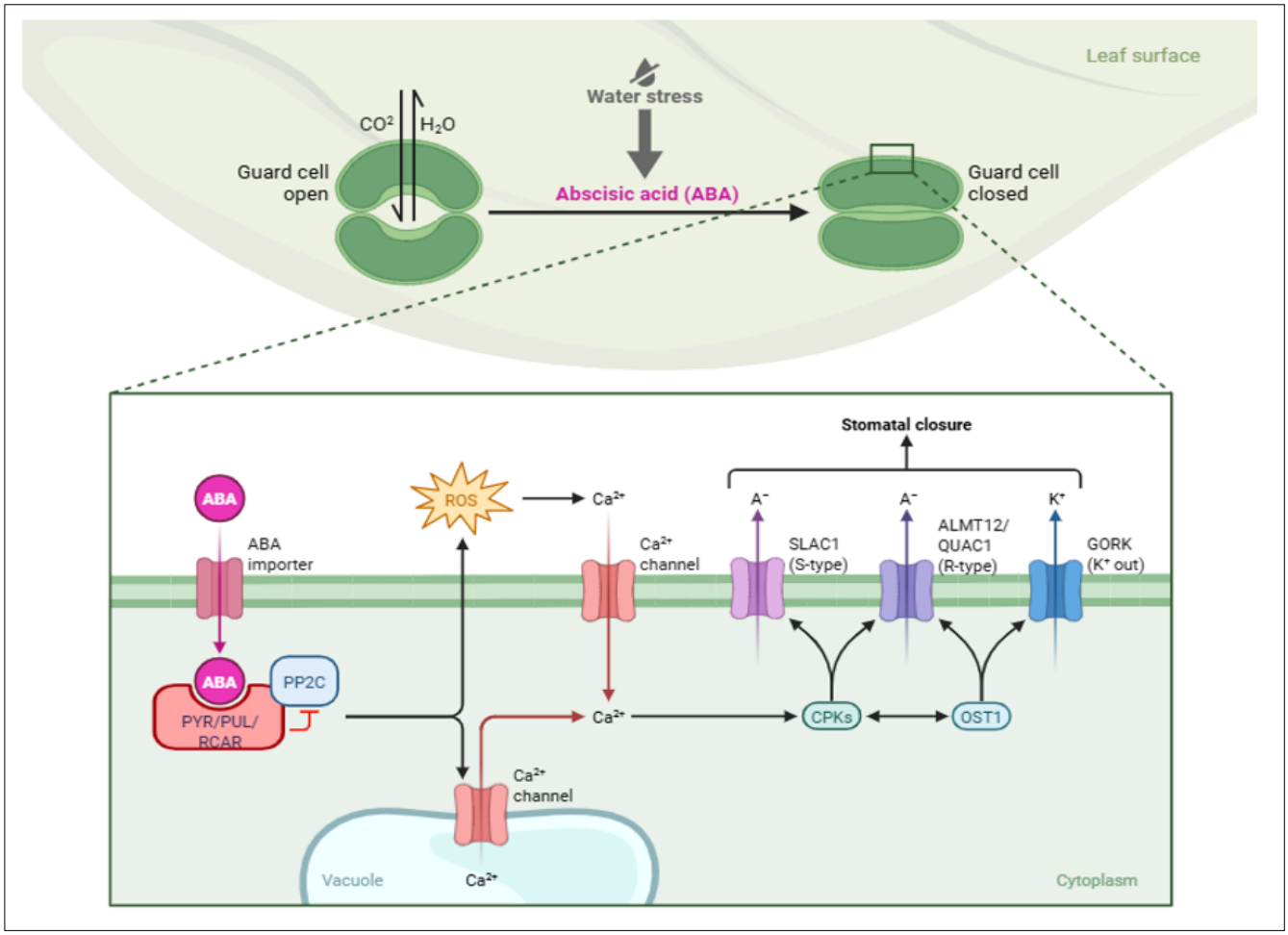

Fig. 1. Schematic representation of stomatal regulation in response to water stress, illustrating the ABA-mediated opening and closing of stomata in guard cells.

responsive gene expression during active fruit growth and ripening, respectively. Collectively, these findings implicate multiple temporally and spatially distinct critical windows in the molecular response of fruit tissues to water stress (52).

Hormonal crosstalk: abscisic acid, auxin and root development under drought

Auxin and ABA coordinate to control root development under drought stress (Fig. 2). Abscisic acid modulates the abundance and activity of PIN auxin efflux carriers and other auxin transporters, thereby limiting auxin transport and distribution. Consequently, root auxin concentration lowers under osmotic stress, leading to modifications in root development and meristem size (73, 74). The R2R3-MYB transcription factor MYB96 integrates ABA and auxin by activating GH3 auxin–conjugating genes, which decreases free auxin, suppresses lateral root meristem activation and elongation and promotes drought resistance (75, 76). Network modelling shows that ABA-dependent and ABA-independent stress responses interact with cytokinin and ethylene signalling; ABA reduces PIN1 in a CK/ethylene context-dependent manner and CK–responsive type–A ARR5 is directly linked to SnRK2 activity in ABA-mediated drought tolerance (71).

Responses of tomato to combined high temperature and drought stresses

The simultaneous occurrence of multiple abiotic stresses rather than a single specific stress poses the greatest threat to crop survival (4). The concomitant increase in daily temperatures and the reduction in water availability are the two major issues faced by present-day agriculture (77). As a result of global climate change, the frequency of co-occurrence of heat and drought stress is increasing (78). This hot, dry extreme weather condition adversely affects global crop productivity (79). When plants face one or more types of stress, they exhibit changes in their morphological traits, physiological functions and molecular mechanisms (20). High temperature accelerated evapotranspiration, leading to greater exposure of plant biomass to drought conditions (80).

Impacts on tomato growth, yield and stomatal behaviour under combined stress

The simultaneous occurrence of heat and drought stresses intensifies plant injury, leading to impaired growth and decreased yield. Plant reactions to abiotic stresses vary among species and lead to either reversible or permanent alterations in their physiological and metabolic processes (4, 81). Drought and elevated temperatures severely affected carbon assimilation in plants. These stresses affected plants at both the subcellular and whole plant level and their effects were reversible, irreversible or partially reversible (81) as depicted from Table 3. In tomato, for proper fruit set, climatic conditions should be favourable for pollen germination and pollen tube growth (8). Hence, breeding varieties tolerant to both stresses is essential to sustain tomato productivity under such adverse conditions (82). Plants exhibit distinct physiological responses when subjected to combined drought and high temperature stress compared with individual stress conditions (83). Under drought, stomatal closure minimises water loss, whereas under high temperature stress, stomata typically remain open to enhance transpiration and regulate leaf temperature (84). These stressors are closely interconnected, as prolonged heat frequently culminates in drought. The ability to retain water under high temperature stress is considered a key trait associated with tolerance in plants (22).

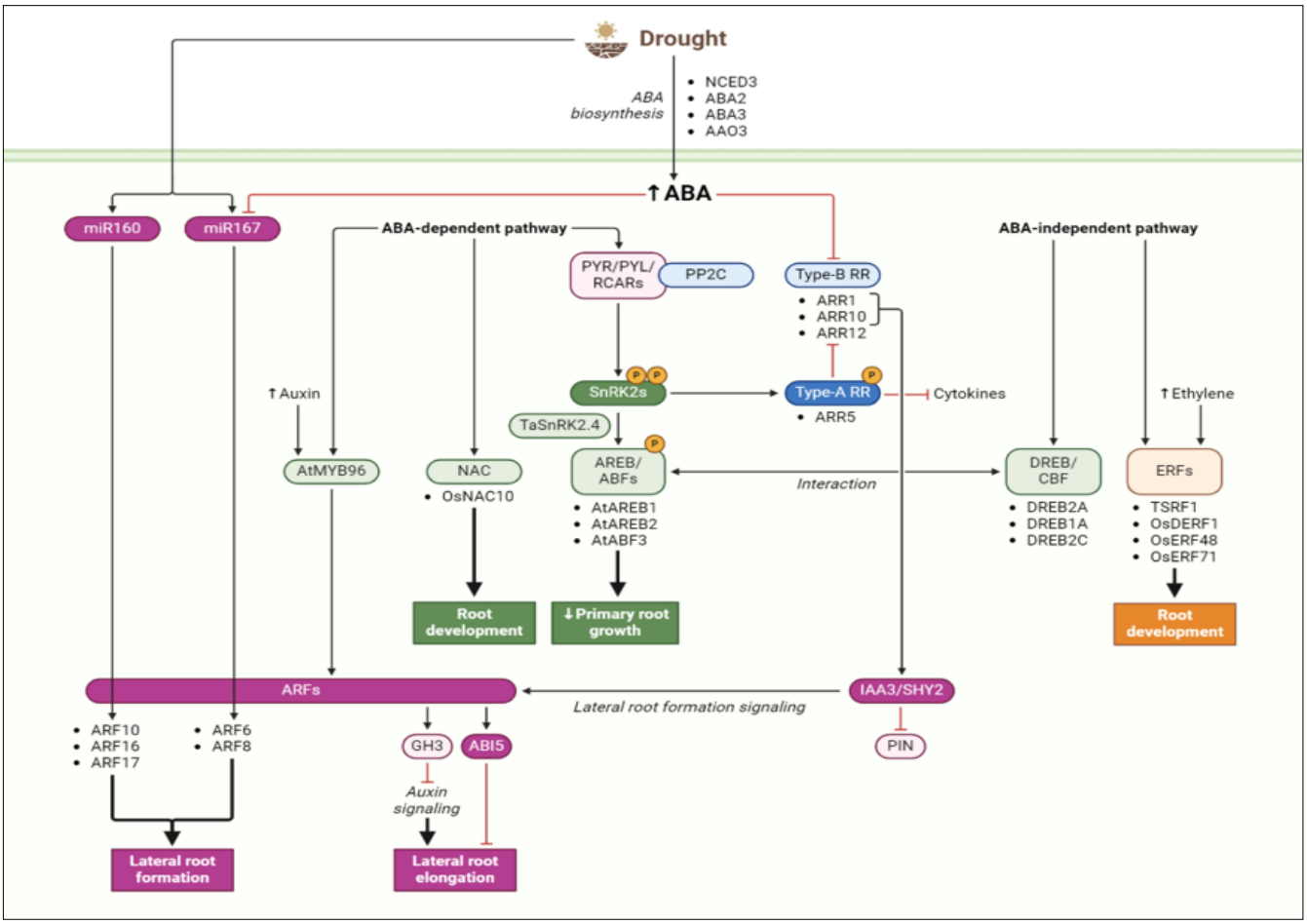

Fig. 2. Schematic representation of water stress-induced hormonal and transcriptional regulation of root development.

Table 3. Morpho-physiological and biochemical responses of tomato under combined drought and high temperature stress

Trait	Response	Reference
Growth (biomass, canopy, leaf area)	Shoot/root dry weight, canopy area and leaf area significantly lower than control and often similar to drought alone	(29,78,96)
Relative water content	Reduction in RWC compared to control	(67)
Chloroplast ultrastructure	Disorganised thylakoids and grana, swollen chloroplasts indicating severe structural damage	(81)
Chlorophyll & carotenoids	Pigments content reduced	(81)
Membrane integrity (thylakoid/leaf)	Increased electrolyte leakage and thylakoid membrane damage, greater under combined drought and high temperature conditions than single stresses	(89,67)
PSII efficiency ($F_v/F_{m,ø}$ PSII, qp)	Decrease in $F_v/F_{m,ø}$ PSII, qp; NPQ increased; PSII damage	(94)
Gas exchange parameter (P_n, g_s, E)	Net photosynthesis, stomatal conductance and transpiration reduced compared to control	(89)
ROS (H_2O_2, superoxide free radicals)	ROS concentration increased	(86)
Lipid peroxidation (MDA)	MDA content increased, indicating enhanced oxidative damage to membranes.	(67)
Enzymatic antioxidants (SOD, APX, CAT, GR)	Activities rise by 2–3 fold; under prolonged combined stress, CAT and POD may be depressed	(94)
Ascorbate-glutathione pool (AsA,GSH)	AsA and GSH concentration increased together with strong upregulation of AsA-GSH pathway transcripts.	(67)
Stress-responsive genes (*DREB*, *LEA*, *HSP70/90*)	*DREB* and *LEA* strongly upregulated under drought and combined stress; *HSP70/90* upregulated under heat and combined stress	(67,97)
Photosynthetic genes (*rbcL, RCA, PSI-P680*)	rbcL and rubisco activase transcripts downregulated, especially under combined	(67)

One study reported that simultaneous exposure of tomato plants to heat and drought stress elicited responses similar to those observed under drought alone, suggesting that drought exerts a dominant influence under combined stress (78). Subsequent studies have documented diverse stomatal behaviours in such conditions, ranging from drought-driven closure to partial or genotype-dependent opening. These differences imply that rather than being cumulative, stomatal control under combined stress is highly context-dependent (28, 78, 85). Thus, a complex pattern of stomatal regulation emerges when both stresses occur simultaneously (85).

Effects on photosynthesis under combined stress

Under heat and drought stress, Photosystem II and chloroplast ultrastructure are severely impaired (86). Drought and heat stresses individually reduced CO_2 diffusional conductance and biochemical processes, respectively. However, under combined stress conditions, mesophyll conductance became the main limiting factor for photosynthesis (7). PSII efficiency (F_v/F_m), quantum yield, photochemical efficiency and gas exchange rates decreased, while non-photochemical quenching increased during combined heat and drought stress (74). Additionally, another study reported that combined stresses caused a significant decline in photosynthetic carbon assimilation under fluctuating light conditions compared with individual stresses (7). Photosynthetic carbon gain under fluctuating light declined by 38 % under drought stress, 73 % under heat stress and 114 % under combined stress, compared with the control. While some studies indicated that drought stress is the primary driver of tomato responses under combined stress conditions, other studies showed synergistic effects that exceed the impact of individual stresses, particularly with respect to mesophyll conductance and photosynthetic carbon assimilation (7, 74, 81). These divergent findings suggested that stress dominance may change depending on experimental conditions, developmental stage as well as stress intensity. Another investigation further showed that different tomato cultivars differ in their sensitivity to heat stress but exhibit similar responses under combined drought and heat stress conditions (81). This indicates that combined stress tolerance is not simply the additive effect of individual stress tolerances.

Net photosynthesis measured per unit leaf area is primarily determined by stomatal conductance, mesophyll conductance, the performance of the photosynthetic machinery (light absorption, electron transport and Calvin cycle activity) and the release of CO_2 through metabolic processes such as photorespiration and dark respiration (80). *In vivo* maximum photochemical efficiency (F_v/F_m)and chlorophyll content are among the best traits for differentiating genotypes under drought and high-temperature stress (28). Stomatal conductance and leaf temperature are useful for studying plant water balance and the capacity to prevent overheating, whereas chlorophyll content and chlorophyll fluorescence provide information on stress-related damage to photosynthetic components and thus on plant heat tolerance (16, 28). In certain cases, stomatal conductance and chlorophyll content have been observed to increase under heat stress, whereas they generally decline under drought stress (28, 81).

Oxidative stress, antioxidant responses and osmoprotectant accumulation

Several studies reported a concurrent increase in ROS and lipid peroxidation, suggesting that antioxidant responses may not be sufficient to completely prevent oxidative damage under severe or prolonged stress, even though antioxidant enzyme activities are frequently elevated under combined heat and drought stress (22, 74, 87). Plants that tolerate stress often accumulate free proline in their cells. This accumulation helps to protect and stabilise the internal environment, as observed in tomatoes under various stress conditions (88). Another study reported that the combination of drought and high-temperature stress leads to greater accumulation of proline, MDA and H_2O_2 and to a significant reduction in RWC and photosynthetic pigments compared with either drought or high-temperature stress alone (75). In this context, proline acts as an osmoprotectant enhancing the plant's ability to cope with osmotic stress.

Molecular and transcriptomic responses to combined stress

In tomato, small RNA deep sequencing identified 335 previously documented miRNAs across 55 distinct miRNA families, along with 430 previously uncharacterized miRNAs. Subsequent differential expression analysis revealed that a subset of these miRNAs showed

significant regulation in response to simultaneous drought and heat stress, underscoring their integral role in orchestrating the plant's molecular and physiological responses to concurrent abiotic stressors (89). Transcriptomic investigations have provided strong evidence that exposure to combined and individual drought and high -temperature stress elicits a coordinated upregulation of antioxidant genes superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), dehydroascorbate Reductase (DHAR) and monodehydroascorbate reductase (MDHAR) and stress-responsive genes (*DREB*, *LEA*, *HSP70* and *HSP90*). The coordinated activation of these gene sets plays an important role in ROS scavenging and reinforcing cellular stress tolerance mechanisms. In contrast, photosynthetic genes, namely *PSIID2*, Ps*aH*, rbcS, rbcL, RCA and PSIP680, were broadly suppressed under combined stress, indicating reduced photosynthetic efficiency and intensified stress-mediated cellular damage (74).

Under high temperature stress, tomato plants coordinate a sophisticated molecular network. This network functions to establish cellular protection, acquired thermotolerance and heat stress memory. At the centre of this response, the receptor-like kinase FERONIA functions as a primary signalling hub. It couples heat-induced Ca^{2+} influx with RBOH1-mediated ROS production. This coupling triggers H_2O_2 generation. Concurrently, the brassinosteroid-regulated transcription factor *BZR1* activates *FER2/3* transcriptionally. This ensures sustained H_2O_2 signalling and robust antioxidant defence under severe thermal stress (90). Once generated, *RBOH1*-derived H_2O_2 acts as a central signalling integrator. It bridges multiple downstream pathways simultaneously. On one hand, it coordinates critical hormonal crosstalk between the brassinosteroid (BR) and ABA signalling axes (91). On the other hand, it directly activates the mitogen-activated protein kinase component MPK1/MAPK1. It also activates key heat shock transcription factors, specifically HsfA1a, HafA2 and HsfB1 (92). This integrated ROS-MAPK-HSF signalling crosstalk is reinforced by a self-sustaining positive feedback loop. This drives robust transcriptional activation of *HSP70* and antioxidant-enzyme-encoding genes. A broader suite of stress-responsive loci is also upregulated. Collectively, these responses safeguard cellular homeostasis under prolonged heat stress (91).

Biomass, yield and photosynthetic limitations under combined stress

Plants under combined drought and heat stress and under individual drought stress showed reduced fresh and dry weight compared with plants subjected to individual heat stress (81). Overall, while drought stress primarily restricts photosynthesis through stomatal closure and heat stress through biochemical impairment of the photosynthetic machinery, combined stress conditions appear to shift the predominant limitation toward mesophyll conductance, highlighting a distinct and non- additive regulatory constraint (7, 28, 93).

One study reported that combined drought and high-temperature stress (ambient + 5 °C, 10 days) imposed during the flowering stage sharply reduced growth, yield and fruit quality in tomato (89). Another study confirmed that combined drought and high temperatures cause the most serious damage to photosynthesis and yield (94). The enhanced abiotic stress tolerance of SlHK2 RNAi plants was associated with increased membrane stability, osmoprotectant accumulation, enhanced antioxidant enzyme activities and protection of photosynthetic machinery, indicating that downregulation of the cytokinin receptor gene SlHK2 improved tolerance to drought, heat and combined stress (95).

Role of endophytic microorganisms in mitigating combined stress

Some endophytic microorganisms help crop plants to adapt to high temperature and drought stress, thereby minimising agricultural losses by enhancing plant's resilience and stress tolerance. One study demonstrated that inoculating tomato plants with arbuscular mycorrhizal fungi (AMF) (*Septoglomus deserticola* and *S. constrictum*) significantly increased tomato shoot and root biomass under combined drought and heat stress (96). Another investigation studied the impact of heat-treated endophytic bacterium LSE01 (HTB) as a fertiliser on plant adaptation to concurrent heat and drought stress (97). The results showed that HTB promoted growth under stress conditions, resulting in larger and heavier fruits while maintaining overall tomato yield. The treatment increased nutritional quality and stress tolerance by elevating vitamin C, sugar and protein levels, strengthening antioxidant defences and reducing stress-induced damage. The treatment further upregulated drought- and heat-responsive genes, improving plant adaptation through modifications in stomatal conductance, morphology, photosynthetic activity and cell wall thickness. This approach shows strong potential for mitigating the adverse effects of heat and drought stress in tomato. It was also reported that combined drought and heat stress did not significantly affect the extent of root colonisation (6). Furthermore, AMF-inoculated plants subjected to stress showed reduced H_2O_2 and MDA levels coupled with altered activities of key defence enzymes-catalase (CAT), peroxidase (POD), polyphenol oxidase (PPO) and glutathione S-transferase (GST)- in both roots and leaves compared to non-mycorrhizal plants.

Conclusion and future perspectives

Combined high-temperature and drought stress causes non-additive and synergistic constraints on tomato. This includes physiological, biochemical and molecular responses that are fundamentally distinct from those exhibited by either stress individually. At the photosynthetic level, mesophyll conductance emerges as the predominant limiting factor under combined stress, shifting the primary constraint away from the stomatal closure that dominates under drought and the biochemical impairment that dominates under heat alone. PSII efficiency, chlorophyll fluorescence and photosynthetic carbon assimilation decline far more severely than predicted by individual stress effects, with reported reductions in carbon gain of up to 114 % relative to the control, substantially exceeding the 38 % and 73 % losses recorded under drought and heat alone, respectively. Oxidative stress is markedly intensified under combined stress conditions, with excessive generation of ROS, malondialdehyde and H_2O_2 frequently exceeding the capacity of antioxidant defence enzymes such as SOD and APX and GR despite their upregulation. Although proline accumulates as a key osmoprotectant, it fails to fully prevent membrane lipid peroxidation under severe or prolonged stress conditions. Stomatal behaviour under combined stress does not follow a simple or cumulative pattern, as drought-induced closure and high-temperature-induced opening interact in a highly genotype- and intensity-dependent manner, highlighting the importance of evaluating leaf temperature and gas exchange parameters together rather than in isolation. Reproductive development is the most critically sensitive stage to combined stress, with pollen viability, anther dehiscence and fertilisation being collectively impaired through the disruption of HSF-HSP regulatory

networks including *HSFA2*, *HSFA3*, *HSP70* and sHSPs, collectively driving yield reductions that exceed those imposed by either stress in isolation, highlighting reproductive stage tolerance as an indispensable target in tomato stress breeding programmes. At the molecular level, ABA signalling functions as a master integrator of both stress responses, with regulatory proteins including *SlWRKY6*, *MYC2*, *SlCIPK7* and HSFs, notably *HSF24* and *HSF30*. This appears to mediate tolerance to both high temperature and drought stress by functioning within interconnected signalling networks. Transcriptomic studies further reveal consistent and widespread suppression of photosynthetic genes coupled with the coordinated upregulation of DREBs, LEAs and HSPs, collectively establishing that combined stress activates a molecularly distinct regulatory programme that cannot be predicted from individual stress responses alone. Encouragingly, biological mitigation strategies utilising AMF and heat-tolerant endophytic bacteria have shown considerable potential in alleviating combined stress effects, with inoculated plants exhibiting notable gains in biomass accumulation, fruit quality and oxidative stress tolerance, pointing to these microbiome-based interventions as accessible and practically viable strategies for field-level stress management in tomato. Despite considerable progress, significant knowledge gaps remain, particularly in field-based mechanistic investigations, reproductive-stage stress physiology, epigenetic regulation and plant-microbiome interactions under combined stress conditions. Addressing these gaps will require the integration of multi-omics approaches, precision genome editing via CRISPR/Cas9 targeting critical regulators such as Rubisco activase and HSFs, introgression of stress tolerant traits from wild Solanum relatives and deployment of high throughput phenotyping platforms for key physiological and biochemical markers, all of which must work in concert to translate fundamental stress biology into the development of climate resilient tomato cultivars capable of maintaining productivity under the growing threat of concurrent high temperature and drought stress conditions.

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Authors' contributions

APR and SA conceptualised the manuscript. APR performed the literature collection and prepared the first draft of the manuscript. DM, DG, TC and SS critically reviewed and provided valuable suggestions for improving the manuscript. APR and SA finalised the manuscript. All authors read and approved the final version prior to submission.

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