

4.2 Regulation of water and nutrient metabolism under temperature changes

Temperature changes regulate tomato water relations largely through root hydraulic function and stomatal behavior. Under suboptimal soil temperature, root hydraulic conductivity and conductance declined, stomatal conductance decreased, and plant biomass was reduced, showing that cool root zones restrict water transport even when aboveground conditions are more favorable (Bristow et al., 2021). Heat stress also altered leaf water relations: high temperature reduced water-use efficiency, while salicylic acid pretreatment improved leaf water potential, osmotic potential, and stomatal function, indicating that water balance is a major component of thermal adaptation (Luo et al., 2023).

Temperature effects on nutrient metabolism are closely linked to photosynthesis and root performance. High temperature reduced nitrogen metabolism through lowered photosynthesis and nutrient loss, while moderate nitrogen supply helped maintain nitrate reductase, glutamine synthetase, soluble protein, and free amino acid levels under thermal stress (Luo et al., 2023). Under suboptimal soil temperature, nutrient uptake was also selectively constrained, with phosphorus uptake identified as especially inadequate because of low solubility and dependence on root surface activity, whereas greater phosphorus uptake was associated with improved photosynthetic performance (Bristow et al., 2021).

4.3 Antioxidant defense and stress adaptation mechanisms

A central consequence of temperature stress in tomato is the overproduction of reactive oxygen species, which disrupts redox balance and damages membranes, proteins, and photosynthetic systems. Heat stress is associated with toxic accumulation of ROS and broad physiological injury, and more general plant evidence shows that high temperature drives ROS overproduction, lipid peroxidation, membrane damage, and impairment of the oxygen-evolving and photochemical systems (Hasanuzzaman et al., 2020; Khan et al., 2024). In tomato exposed to drought, heat, and combined stress, both cultivars showed sharp increases in H₂O₂ and superoxide production, accompanied by higher oxidative damage markers and smaller canopy area and stem diameter under combined stress.

Tomato stress tolerance depends on activating both enzymatic and signaling-based antioxidant defenses. Under cold stress, trehalose pretreatment increased SOD, CAT, APX, and GR-related antioxidant capacity, reduced membrane lipid peroxidation, and acted through an H₂O₂-NO signaling pathway in which NO functioned downstream of H₂O₂ (Liu et al., 2020). Other studies support a similar redox-regulated adaptation model: exogenous ALA increased glutathione- and ascorbate-linked antioxidant defense at low temperature, while in heat stress, tomato thermotolerance was associated with higher APX and SOD activity, HSP40-mediated enzyme protection, and melatonin-related ROS scavenging (Fortunato et al., 2023).

5 Effects of Temperature Regulation on Flowering, Fruit Set and Yield Formation

5.1 Effects on flowering and reproductive development

Temperature regulation is especially critical during the reproductive stage because tomato flowering and fertilization respond to a narrower thermal range than vegetative growth. Optimal daily mean temperature for fruit set is generally around 21°C-24°C, whereas exposure to warmer conditions for successive days or weeks during reproductive growth markedly disrupts fruit set, and in protected cultivation 25°C-26°C appears to be the upper limit for proper fruit set and yield during hot Mediterranean summers. The reproductive damage is expressed through impaired anther and pollen function: mean daily temperatures near 29°C reduce fruit number, fruit set percentage (Dasgan et al., 2021), and fruit weight per plant, largely because elevated temperature disrupts pollen and anther development and lowers pollen viability.

Heat stress affects not only male fertility but the broader sequence of reproductive development from flower formation to post-pollination processes. Long-term moderate heat significantly reduced pollen viability, pollen number, female fertility, seeded-fruit set, and flower number per inflorescence, while only previously identified heat-tolerant cultivars maintained seeded fruit set under stress. Male-sterile experiments further showed that adequate pollen supply alone is not sufficient at high temperature, because as mean daily temperature increased from 25°C to 29°C, fruit set, total fruit number, total fruit weight, and seediness declined due to effects on ovule