

Genomics and Applied Biology

ISSN 1927-5609

Vol.17 No.4 2026



OPEN ACCESS

2026
04

Publisher

BioSci Publisher

Edited by

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Email: edit@gab.bioscipublisher.com

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Genomics and Applied Biology (ISSN 1925-1602) is an open access, peer reviewed journal published online by BioSci Publisher.

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Research Insight

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Effects of Temperature Regulation on Growth and Yield of Tomato

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Received: 02 Jun., 2026

Accepted: 04 Jul., 2026

Published: 15 Jul., 2026

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Preferred citation for this article:

Lin X.X., 2026, Effects of temperature regulation on growth and yield of tomato, Genomics and Applied Biology, 17(4): 200-212 (doi: [10.5376/gab.2026.17.0016](https://doi.org/10.5376/gab.2026.17.0016))

Abstract Temperature is one of the most critical environmental factors regulating tomato (*Solanum lycopersicum* L.) growth, physiological processes, and yield formation. With the increasing frequency of extreme temperature events and the expansion of protected cultivation systems, effective temperature regulation has become essential for achieving stable and high-quality tomato production. This review summarizes the effects and mechanisms of temperature regulation on tomato growth, photosynthesis, reproductive development, fruit quality, and yield formation. Appropriate temperature management promotes seed germination, vegetative growth, root development, and biomass accumulation by optimizing plant metabolic activities and resource utilization efficiency. Temperature regulation also improves photosynthetic performance, antioxidant defense capacity, and nutrient metabolism, thereby enhancing plant adaptation to thermal stress. During reproductive growth, suitable temperature conditions facilitate flowering, pollen viability, fruit set, and fruit expansion, while temperature extremes can cause flower abortion, reduced fruit quality, and yield losses. Furthermore, this review discusses the physiological and molecular mechanisms involved in temperature responses, including hormonal regulation, heat shock proteins, cold-responsive pathways, and temperature-sensitive gene expression. A case study is presented to evaluate the practical effects of different temperature management strategies in greenhouse tomato production. Future research should focus on integrating intelligent environmental control systems, crop growth models, and multi-factor regulation approaches to develop precise and climate-resilient temperature management strategies for sustainable tomato production.

Keywords Temperature regulation; Tomato production; Growth and yield; Thermal stress; Greenhouse cultivation

1 Introduction

Tomato production depends strongly on temperature regulation because tomato is widely cultivated across open-field and greenhouse systems, yet its growth, reproductive success, and fruit quality decline when temperatures move beyond the crop's favorable range. Tomato is one of the world's most important horticultural crops, and rising temperatures are increasingly recognized as a major threat to its productivity under climate change (Luo et al., 2023; Graci and Barone, 2024). This sensitivity is agronomically important because tomato performs best within a relatively narrow thermal window: optimal growth has been placed broadly between 18°C-32°C, while optimal average day and night temperatures for reproductive performance are narrower, around 21°C-30°C and 18°C-21°C, respectively (Luo et al., 2023). As temperatures rise above or fall below these optima, the effects are expressed not only as general stress but also as direct constraints on flowering, fruit set, and marketable yield, making temperature regulation a central component of stable tomato production rather than a secondary environmental concern (Lee et al., 2022).

The importance of regulating temperature is further underscored by evidence that both heat stress and sub-optimal low temperature impair the formation of yield at multiple developmental stages. Temperature has a large effect on all aspects of tomato development, with declining temperatures reducing leaf and truss initiation rates, while sub-optimal conditions also reduce fruit set because of poorer pollen quality. At the high-temperature end, reproductive development is especially vulnerable: exposure above 32/20°C day/night during the reproductive phase reduces fruit set and fruit weight, and temperatures above 35°C can further suppress fruit set and delay normal fruit coloration (Miller et al., 2021; Vijayakumar et al., 2021). These responses explain why temperature regulation is not simply about maintaining vegetative growth, but about protecting the sequence of processes—from floral initiation to successful fertilization and fruit enlargement—that ultimately determines yield.

The relationship between temperature conditions and tomato growth and yield formation is therefore both physiological and developmental. Temperature alters metabolic efficiency, respiration, membrane stability, photosynthesis, and carbon use, and these whole-plant effects interact with stronger reproductive sensitivity during flowering and fruiting (Alsamir et al., 2020; Elazazi et al., 2024). Experimental and modeling studies show that yield losses under heat stress are driven mainly by reductions in fruit number, fruit set, seed set, and individual fruit mass rather than by a simple decline in total biomass. In South Florida simulations, yield decreased as air temperature increased, with losses of 52°C-85% above current conditions, primarily because fruit production declined, even though biomass accumulation and leaf area index increased with temperature (Ayankoji and Morgan, 2020). Likewise, controlled studies of fruit development found that both low (14°C) and high (26°C) temperature regimes tended to produce small parthenocarpic fruits and low fruit yields, while newer modeling work showed that 30-34°C reduces pollen viability, germination, seed set, and fruit mass, and that 14°C lowers yield by reducing both fruit set and fruit size (Zepeda et al., 2026). Together, these findings indicate that tomato yield formation is shaped not only by mean temperature but by the timing, duration, and amplitude of thermal stress, especially during sensitive reproductive stages.

Against this background, the objective of this review is to synthesize current knowledge on how temperature regulation affects tomato growth, reproductive development, and final yield, and to identify practical and biological factors that can improve resilience under fluctuating thermal environments. Recent work has shown that even within commercial greenhouses, local canopy microclimates can vary by up to 3°C in daily average temperature and can measurably influence stem growth, fruit growth, and truss mass, indicating that “temperature regulation” must be understood at the crop-canopy scale rather than only at the level of a central climate setting (Šalagovič et al., 2024). At the same time, advances in genetics and molecular physiology show that thermotolerance can be improved through targeted trait selection and mechanistic understanding: quantitative trait loci linked to fruit set, yield, and soluble solids have been identified under high temperature, and heat-responsive reproductive regulators such as the TSP4a/TSP4b module have been shown to help maintain fruit set and fruit sugar levels under warming conditions (Elazazi et al., 2024; Lu et al., 2025). Accordingly, this review focuses on three linked themes: the importance of temperature regulation in tomato production systems, the mechanisms by which temperature shapes growth and yield formation, and the emerging management, breeding, and monitoring strategies that can support high yield and fruit quality under climate warming.

2 Temperature Requirements and Environmental Regulation in Tomato Production

2.1 Optimal temperature ranges during different growth stages

Tomato temperature requirements vary by developmental stage, and reproductive performance is generally more temperature-sensitive than vegetative growth. Broadly, optimal growth has been placed between 18°C and 32°C, but fruit set and yield respond best within a narrower mean temperature window, with daily average temperatures of 21°C-24°C, 22°C-25°C, or 22°C-26°C repeatedly identified as favorable for reproductive success (Luo et al., 2023). Night temperature is also important during flowering and fruit set, because night temperatures of 15°C-20°C increase marketable yield, while a night temperature of 13°C can still maintain good fruit set under some conditions (Alsamir et al., 2020; Lee et al., 2022).

Stage-specific thresholds further show that tomato should not be managed with a single thermal target throughout the crop cycle. Seedling emergence can already be damaged at 30°C, whereas temperatures above 35°C significantly inhibit germination, vegetative growth, flowering, fruit set, and ripening; by contrast, lower developmental thresholds for tomato are often placed near 15°C, below which growth and development largely cease (Lee et al., 2022). During fruit development, increasing temperature accelerates ripening, with fruits ripening 95, 65, 46, and 42 days after flower opening at 14°C, 18°C, 22°C, and 26°C, respectively, but both high and low temperature regimes also tend to produce small parthenocarpic fruits and lower yields when flower number or fruit set is impaired.

2.2 Effects of temperature fluctuations on plant development

Temperature fluctuations affect tomato development not only through mean temperature but also through the timing, duration, and amplitude of thermal stress. Sub-optimal temperatures reduce leaf and truss initiation rates

and increase the time from anthesis to ripening, while high temperatures above the optimum alter vegetative and reproductive growth, including flower and pollen development, and thereby reduce fruit set and final yield (Graci and Barone, 2024). Experimental evidence also shows that tomato can integrate day-night temperature variation only within limits: early- and late-summer regimes with average day/night temperatures of 28.1°C/24.3°C and 30.1°C/26.5°C supported more clusters, flowers, fruits, and better quality than the hotter 32.4°C/28.5°C mid-summer regime (Talukder et al., 2025).

Short periods of temperature extremes during reproductive stages can be especially damaging because they directly impair pollen quality, seed set, fruit set, and fruit mass. In a controlled modelling study, 30°C and 34°C reduced pollen viability and germination, lowering seed set and fruit mass, while 14°C and 34°C reduced fruit set; the predicted yield loss at 14°C came from both fewer fruits and smaller fruits, whereas at 30°C it came mainly from smaller fruits (Zepeda et al., 2026). Field and greenhouse comparisons likewise showed that yield losses near 70% under high temperature were linked to poorer fruit set, and that maximum or minimum temperature during sensitive reproductive periods can matter more than season-long mean temperature because even short exposure above the optimum can sharply reduce reproductive success (Ro et al., 2021).

2.3 Temperature management strategies in greenhouse tomato production

Greenhouse temperature management should aim to maintain stable crop-level conditions rather than relying only on compartment-wide averages. Commercial greenhouse monitoring has shown spatial temperature gradients of up to 3°C and vapour pressure deficit differences of up to 0.6 kPa within the same canopy, and these local microclimate differences measurably altered stem growth, fruit growth, and truss mass at harvest (Šalagovič et al., 2024). This supports the use of denser sensor networks, because local microclimate effects on plant growth were larger than bulk climate variation recorded by a single central sensor, making whole-greenhouse sensor grids more suitable for climate control than one-point monitoring (Šalagovič et al., 2024).

In hot-season protected cultivation, cooling strategies should be adjusted to reproductive thermal thresholds rather than fixed to a single seasonal set point. Mean daily temperatures of 25°C-26°C appear to be the upper limit for proper fruit set and fruit yield in protected tomato during Mediterranean summer, and reducing mean daily temperature by only 1°C-1.5°C with fogging, together with increasing daytime relative humidity from 50% to 70%, improved pollen viability. Evidence from passive solar greenhouse systems also suggests that low-cost protection can buffer unfavorable field conditions and raise marketable yield, but shading must be used cautiously because although greenhouse production increased yield 1.8-fold over open field, added shading delayed flowering and reduced marketable yield by 48% (Angmo et al., 2021).

3 Effects of Temperature Regulation on Tomato Vegetative Growth

3.1 Effects on seed germination and seedling establishment

Temperature regulation strongly determines the success of tomato seed germination and early seedling establishment because these stages are among the most temperature-sensitive phases of the crop life cycle. Controlled experiments showed that the most suitable germination temperatures were 24°C-28°C, whereas germination rate and seedling vigor declined above 28.5°C, only about half of the seeds germinated at 31.5°C, and no germination occurred at 36°C (Tokić et al., 2023). Classic thermal analysis similarly found that germination occurred between 6.0°C and 37.5°C, with the optimum range for germination kinetics centered around 25.9°C-29.5°C, indicating that both excessively low and excessively high temperatures constrain rapid and uniform emergence.

High temperature not only suppresses germination percentage but can also trigger physiological inhibition that compromises subsequent establishment. In one genetic study, prolonged exposure of imbibed seeds to elevated temperature induced thermo-dormancy in the cultivar 'Moneymaker', with induction beginning after about 33 h and germination falling to 0% after roughly 100 h of exposure. Variety comparisons also showed that 33°C significantly reduced germination rate, vigor, germination index, and vitality index, and that early seedling roots were inhibited more strongly than shoots, with larger effects in less thermotolerant genotypes.

3.2 Effects on plant morphology and biomass accumulation

Temperature regulation also reshapes tomato morphology during vegetative growth, often by altering elongation patterns, leaf traits, and whole-plant partitioning. Seedlings developed at 28.5°C and 31.5°C showed significant hypocotyl elongation, while stronger heat exposure caused more severe visible injury, including chlorosis, leaf wilting, and stem bending in both seedlings and adult plants (Tokić et al., 2023). Under greenhouse lighting systems with different thermal properties, warmer leaf conditions were associated with thinner and smaller leaves and with a higher fraction of biomass allocated to vegetative tissues, indicating that temperature interacts with canopy energy balance to shape plant form and dry-matter distribution.

Biomass accumulation responds to temperature in a more complex way than morphology because higher temperature can stimulate growth processes while reducing final dry matter if respiratory or assimilate costs become too high. In growth-chamber experiments, a daily mean temperature of 30°C increased relative growth rate, net assimilation rate, and leaf area ratio, and gas-exchange at the later stage was about twice that at 20°C (Yamaura et al., 2021). However, the same study found that total dry matter was lower at 30°C and that non-structural carbohydrate accumulation in leaves and stems decreased, showing that supra-optimal temperature can accelerate carbon use and short-term growth while limiting biomass storage and final vegetative accumulation (Yamaura et al., 2021).

3.3 Effects on root development and nutrient uptake

Root systems are highly temperature-sensitive, and both low and high root-zone temperatures restrict root development and nutrient capture. Under heat stress, tomato seedlings showed inhibited primary root length at both 37°C and 45°C, while lateral root number was significantly suppressed under 37°C, demonstrating that root architecture is modified even before severe aboveground damage becomes apparent (Tokić et al., 2023). Low root-zone temperature had similarly negative effects: at 7°C and 13°C, root development was delayed and the number and diameter of ducts in root and stem were reduced, which limited mineral absorption and transport capacity (Miao et al., 2023).

Temperature effects on roots translate directly into nutrient uptake efficiency and shoot nutrition. Across six root-zone temperature treatments, nutrient uptake for most mineral elements peaked at 26.7°C, and root dry weight, shoot dry weight, shoot growth, plant height, and water use all peaked near 25°C, indicating a clear physiological optimum for root-mediated support of vegetative growth (Tindall et al., 1990). Additional evidence from low-temperature and nutrient-composition studies showed that increasing root temperature increased shoot total N, P, Mg, and K, whereas low root temperature caused nitrate and potassium to accumulate in roots because ion translocation was hindered, helping explain why cool root zones slow tomato growth even when nutrients are supplied adequately.

4 Effects of Temperature Regulation on Photosynthesis and Physiological Processes

4.1 Temperature effects on photosynthetic performance

Temperature regulation directly controls tomato photosynthetic capacity because both chilling and heat stress impair the efficiency of the photosynthetic apparatus. Under sub-optimal temperature, tomato showed reduced chlorophyll content and declines in Y(II), Fv/Fm, qP, and ETR, with larger reductions in the cold-sensitive cultivar than in the tolerant one, indicating that genotype influences the extent of photochemical damage (Gao and Wu, 2024). Heat stress similarly depressed gas exchange and photosynthesis by lowering P_{Nmax} and SPAD values, while increases in internal CO₂ concentration indicated that the limitation was mainly non-stomatal and associated with photosystem and Rubisco impairment (Luo et al., 2023).

Evidence from fluorescence-based studies shows that temperature stress acts strongly on electron transport, especially within PSII. In tomato leaf and fruit, OJIP fluorescence parameters clearly distinguished heat from chilling injury, and heat had a greater effect on the PSII electron transport chain than chilling, with fruit tissues showing stronger changes than leaves. Day/night temperature regime also matters: at the fruiting stage, positive DIF increased chlorophyll content, net photosynthetic rate, stomatal conductance, Fv/Fm, and ϕ PSII, whereas negative DIF reduced these traits and increased non-photochemical quenching.

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

development and post-pollen production processes, with sharp losses already evident from 25°C to 26°C and from 28°C to 29°C (Fortunato et al., 2023) (Figure 1).

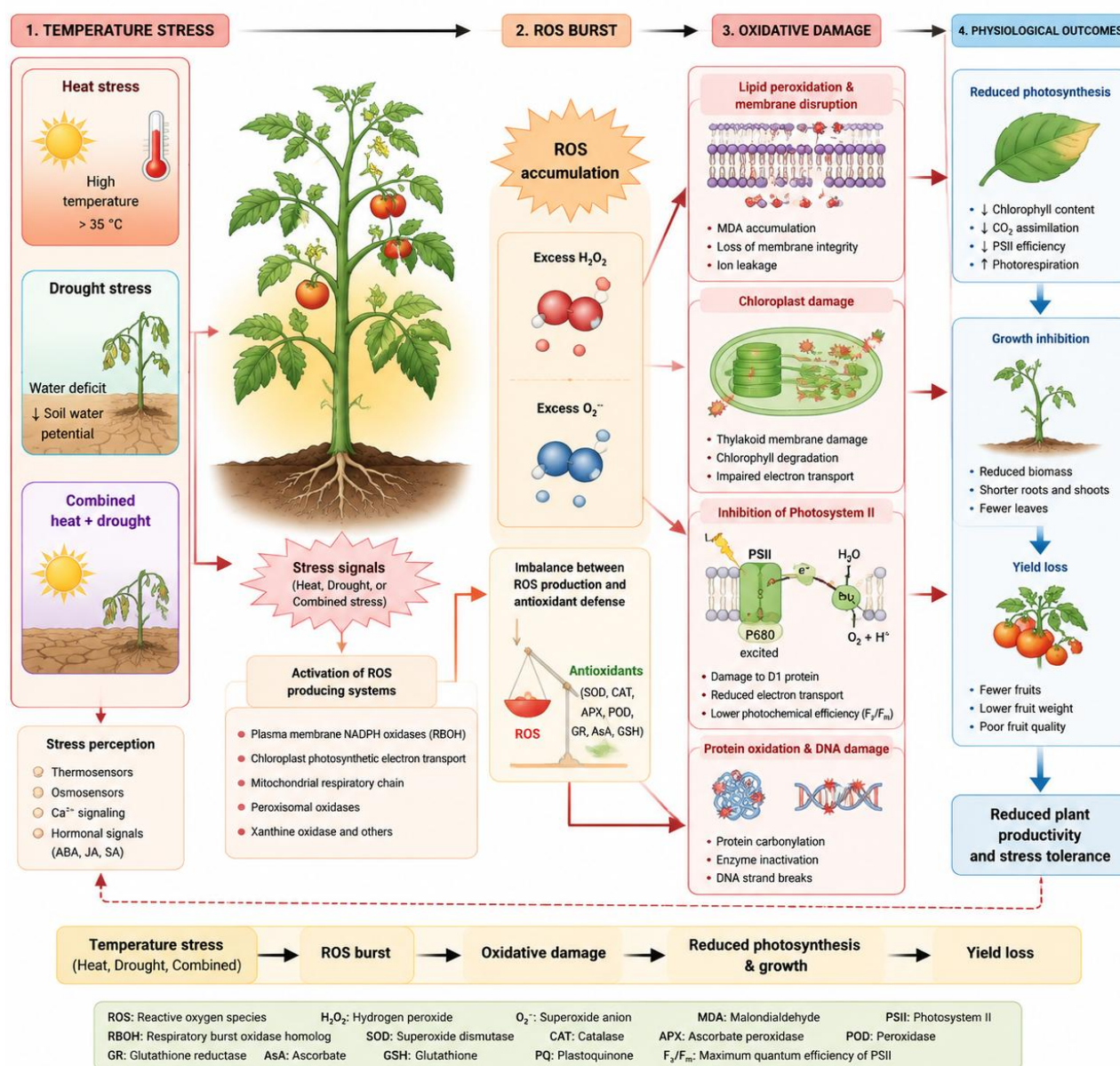


Figure 1 Mechanistic overview of temperature stress-induced reactive oxygen species (ROS) accumulation and antioxidant defense activation in tomato plants

5.2 Effects on fruit development and yield components

Temperature regulation strongly influences yield formation by altering fruit set, fruit number, seed formation, fruit growth rate, and fruit mass. In male-fertile tomatoes, a daily mean temperature of 29°C reduced fruit number, fruit weight per plant, and seed number per fruit to 10%, 6.4%, and 16.4% of the values observed at 25°C, showing how rapidly yield can collapse when reproductive heat stress persists. Genotype comparisons under elevated temperature likewise found that fruit number per plant, fruit set percentage, average fruit weight, and yield per plant all declined with rising temperature, although the extent of reduction differed among cultivars, indicating substantial genetic variation in reproductive heat tolerance (Vijayakumar et al., 2021).

Fruit development after set is also temperature-sensitive, and the direction of the response depends on both developmental stage and the thermal regime. Controlled-environment studies showed that fruits ripened much faster as temperature rose from 14°C to 26°C, but both low and high regimes tended to produce small

parthenocarpic fruits, and the combination of poor fruit set at 26°C, fewer flowers, and altered fruit growth resulted in low yield. Temperature also modifies the cellular basis of fruit growth: although fruit growth rate was lower at 20/20°C than at warmer regimes, final fruit size was maintained by compensation between cell number and cell size, whereas heavier fruit load reduced fruit size mainly by slowing cell expansion rather than by reducing cell number.

5.3 Effects on fruit quality characteristics

Temperature regulation affects tomato fruit quality as strongly as it affects yield, but the response is trait-specific. Elevated temperature often increases total soluble solids, titratable acidity, and ascorbic acid, while decreasing lycopene, and high-temperature field screening further showed increases in soluble solids, acidity, total phenols, and vitamin C in tolerant genotypes, with concurrent decreases in pH, electrical conductivity, flavonoids, lycopene, and β -carotene (Vijayakumar et al., 2021). These quality shifts indicate that heat does not uniformly degrade composition; instead, it tends to re-balance primary and secondary metabolites, sometimes improving acidity- or vitamin-related traits while reducing carotenoid-based color and nutritional value.

The effect of temperature on fruit quality also depends on developmental stage, humidity, and the specific metabolite considered. Increasing fruit temperature from 21°C-26°C reduced total carotene without affecting lycopene, whereas a further rise from 27°C-32°C reduced ascorbate, lycopene, and precursor contents but increased rutin, caffeic acid derivatives, and glucosides, showing that antioxidant pathways are highly temperature-sensitive. Under combined high temperature and high relative humidity, enzyme activities linked to sucrose breakdown and organic acid metabolism shifted in ways that reduced soluble sugar, vitamin C, total sugar, and the sugar/acid ratio, while increasing titratable acidity; notably, 32°C with 70% relative humidity was identified as the best condition for maintaining fruit quality during the reproductive period under high-temperature stress (Zheng et al., 2022).

6 Physiological and Molecular Mechanisms of Temperature Regulation Effects

6.1 Hormonal regulation under temperature stress

Temperature stress in tomato triggers broad hormonal reprogramming rather than a single-pathway response. Across heat-stress studies, hormone-associated genes are repeatedly among the temperature-responsive transcripts, and genotype-dependent thermotolerance is linked in part to differential regulation of auxin- and ethylene-related genes (Hu et al., 2020). Brassinosteroid signaling appears to be one important branch of this response, because BR treatment in tomato increases RBOH1 expression and apoplastic H₂O₂, while silencing RBOH1 compromises heat tolerance (Li et al., 2021).

Hormonal regulation also integrates developmental temperature responses and cross-stress protection. Day-night temperature difference regulates stem elongation through changes in gibberellin and IAA biosynthesis, with negative DIF suppressing both hormone levels and elongation-related gene expression (Ohtaka et al., 2020). Under extreme temperatures, strigolactones act upstream of ABA-dependent protection, since heat and cold induce strigolactone biosynthesis genes, and ABA deficiency abolishes strigolactone-induced transcription of HSP70, CBF1, and antioxidant-related genes (Chi et al., 2021).

6.2 Heat and cold stress response pathways

The core heat stress response in tomato is organized around HSF-HSP networks that preserve protein homeostasis and cellular survival. Hsfs control transcriptional reprogramming at high temperature and activate canonical HSR genes, especially heat shock proteins, which function as molecular chaperones to prevent protein misfolding and aggregation. Within tomato, HsfA1 has a uniquely central role, because plants with HsfA1 cosuppression become extremely heat-sensitive and fail to induce normal synthesis of chaperones and other Hsfs under elevated temperature.

Cold and heat pathways also intersect with ROS and kinase signaling, but the specific regulators differ by stress type. In heat-stressed tomato, SIMAPK3 acts as a negative regulator of thermotolerance, since knockout mutants show less wilting and membrane damage, lower ROS, and higher antioxidant enzyme activity together with

increased HSF and HSP expression. Under chilling, tomato appears to use more than the classical CBF route alone: SIGRAS4 promotes chilling tolerance by directly activating many cold-response targets and SICBF promoters, while functioning as a distinct regulon that operates independently of the ICE1-CBF pathway (Liu et al., 2020).

6.3 Molecular regulation of temperature-responsive genes

Temperature-responsive gene regulation in tomato combines conserved stress modules with substantial genotype- and tissue-specific variation. In seedlings, most heat stress transcription factors and HSP genes respond similarly across genotypes, but hormone- and RNA-related regulators such as HsfA6b show differential expression associated with thermotolerance (Hu et al., 2020). In reproductive tissues, heat-stressed microspores upregulate small HSPs, HSP70, HSP90, HSFA2, and HSFA3, while tolerant microspores show higher basal expression of several protective genes before stress, consistent with a primed thermotolerance state (Frank et al., 2009).

Recent genomic studies show that these responses are organized into complex regulatory networks rather than isolated genes. In tomato flower buds, co-expression analysis under heat identified novel HSR-related transcription factors such as SIWRKY75, SIMYB117, and SINAM, and experimentally validated HSF-regulated targets including SIGrpE, SIERDJ3A, SITIL, and SIPOM1 (Li et al., 2023). Genetic mapping and transcriptomics further indicate that heat tolerance is polygenic, with major QTL regions enriched for plant hormone signaling, MAPK signaling, sugar metabolism, and fatty acid metabolism, and with tolerant genotypes showing more gene upregulation than sensitive genotypes under heat stress.

7 Case Study: Effects of Temperature Regulation Strategies on Greenhouse Tomato Production

7.1 Experimental background and temperature management treatments

Recent greenhouse case studies have tested temperature regulation through both structural control and targeted thermal treatments rather than by relying on ambient protection alone. In commercial and research settings, treatments included multi-point canopy monitoring to detect spatial thermal gradients, geothermal pipe heating with water temperatures of 25°C, 35°C, and 45°C against an unheated control, and comparisons between regulated greenhouse environments and more variable open-field conditions (Ouyang et al., 2022; Šalagovič et al., 2024). These designs reflect a common experimental logic: quantify how precisely managed air or root-zone temperature modifies crop performance relative to uncontrolled or weakly controlled systems.

Other studies used dynamic or stage-specific strategies that more closely resemble practical greenhouse decision-making. A low pre-night temperature integration strategy imposed 9.4°C, 11.3°C, 13.3°C, and 15.1°C pulses for the first 3 h of the night while keeping the same 24-h mean temperature, whereas root-zone regulation trials combined daytime air temperatures of 20°C, 25°C, 30°C, and 35°C with root-zone settings of 15°C, 20°C, 25°C, and 30°C to identify efficient combinations for early growth (Ju et al., 2023). Additional greenhouse studies also evaluated heat mitigation through micro-spray plus drip irrigation, and precision control through sensor placement near the ground, canopy, and roof, showing that temperature management treatments increasingly integrate climate control with real-time monitoring and automated adjustment (Figure 2) (Xue et al., 2023; Zhang et al., 2024).

7.2 Effects of temperature regulation on growth and physiological responses

Temperature regulation consistently altered vegetative growth and physiological activity in greenhouse tomatoes. Soil warming significantly affected plant height, leaf area index, assimilation rate, leaf temperature, chlorophyll, and dry matter accumulation, and across two years the strongest treatment ranked T3 > T2 > T1 > control for most growth and physiological indicators (Ouyang et al., 2022). Root-zone regulation produced similarly clear effects during early growth, with 20°C-25°C root-zone settings generally supporting favorable crop growth rate and relative growth rate across several air temperature regimes (Ju et al., 2023).

Heat mitigation strategies also improved physiological resilience when greenhouse temperatures became excessive. Under high-temperature greenhouse conditions, micro-spray reduced average daily air temperature by about 0.76°C-0.8°C and leaf temperature by 4.6°C-4.9°C, while increasing photosynthetic rate, PSII efficiency,

and stomatal conductance relative to drip irrigation alone (Xue et al., 2023). At the same time, genotype-focused greenhouse screening showed that high temperature depressed photosynthesis, chlorophyll, proline balance, and vegetative traits such as plant height and shoot and root fresh weight, confirming that the value of temperature regulation depends partly on cultivar heat tolerance (Rajametov et al., 2021).

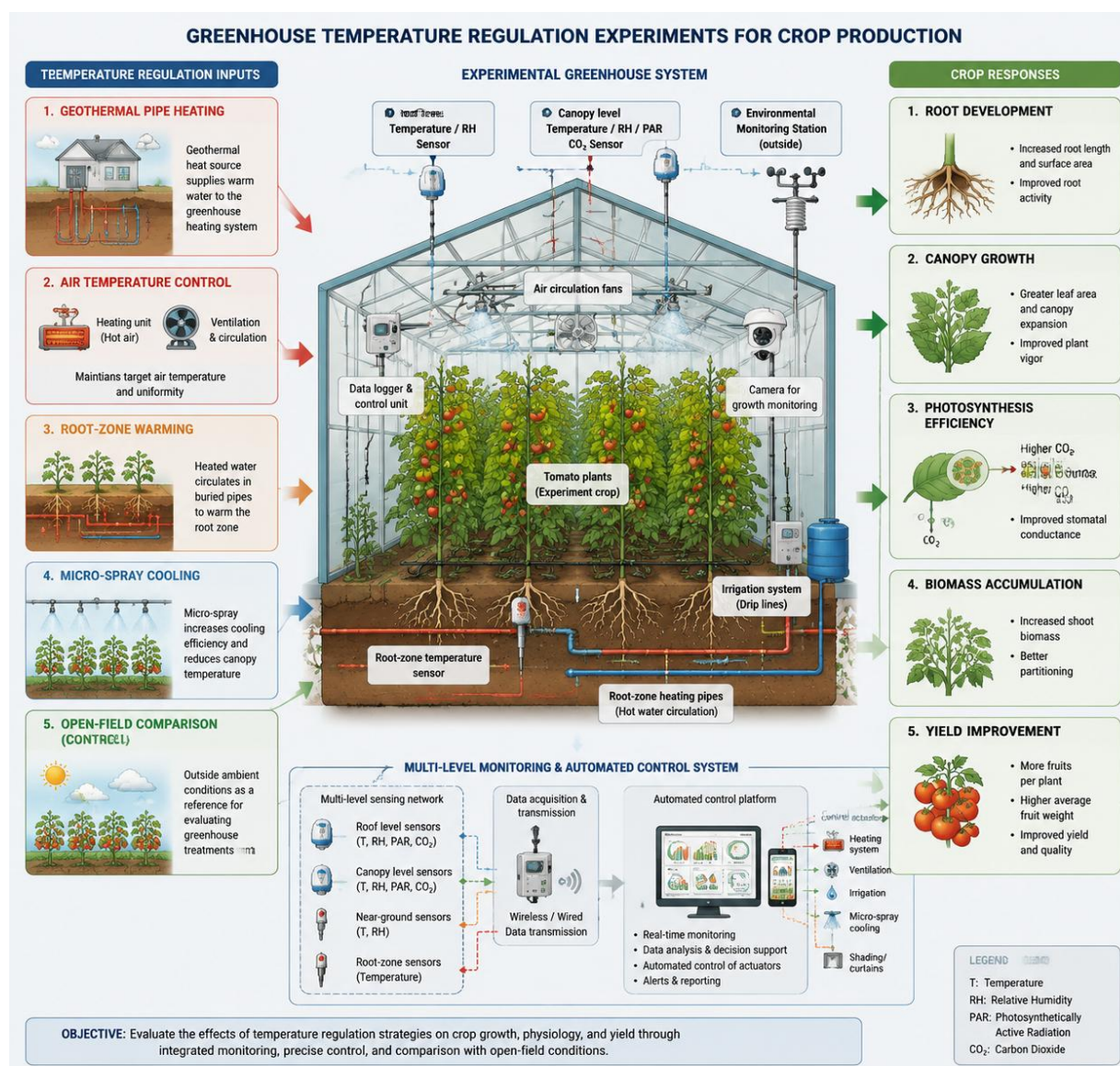


Figure 2 Experimental framework for evaluating greenhouse temperature regulation strategies and their effects on crop growth performance

7.3 Effects on yield performance and economic benefits

The yield effects of greenhouse temperature regulation were substantial, but they depended on how effectively the strategy stabilized the crop microclimate. In a greenhouse versus open-field comparison, weekly temperature variation was only about $\pm 1.0^{\circ}\text{C}$ in the greenhouse versus $\pm 10.2^{\circ}\text{C}$ in the open field, and the more stable greenhouse environment produced higher yields while reducing the risk of total crop loss (Efeta et al., 2025). In another greenhouse study, passive solar protection increased marketable tomato yield by 1.8-fold over open-field production, although adding shade delayed flowering and reduced marketable yield by 48%, showing that not every cooling-oriented intervention improves productivity (Angmo et al., 2021).

More intensive regulation strategies also translated into measurable yield and economic gains. Geothermal soil warming increased yield by about 18.2%-18.6% and water productivity by 32.6%-33.5%, with optimal soil temperatures estimated at 26.1°C in spring/summer and 20.6°C in autumn/winter (Ouyang et al., 2022). Economic

case evidence from overwinter tomato production in North China further showed that soft-shell solar greenhouses raised average daily temperature by 10°C-15°C, reduced low-temperature stress duration by 25%, and improved net returns when combined with variety optimization and scenario-based sales, indicating that greenhouse temperature regulation can generate both biological and commercial benefits when paired with cultivar and market strategy (Liu et al., 2025).

8 Conclusions and Future Perspectives

Temperature exerts a pervasive influence on tomato performance because developmental, physiological, and reproductive processes respond differently to thermal conditions across the crop cycle. Tomato is sensitive to temperatures below 12°C and above 32°C, and high temperature particularly decreases fruit yield while also altering multiple physiological traits and fruit quality attributes. Reviews of sub-optimal and supra-optimal conditions further show that cooler conditions can slow leaf and truss initiation, increase leaf thickness, reduce relative growth rate, and impair pollen quality, whereas warmer conditions can accelerate early development yet compromise later vegetative growth, fruit set, and seasonal yield stability. The overall yield outcome reflects the integration of many distinct temperature-sensitive processes rather than a single limiting trait. High temperature negatively affects both vegetative growth and reproductive development, leading to losses in fruit set, yield, and quality, while genotype-dependent differences in pollen viability, photosynthesis, and fruit-setting ability explain why some cultivars perform better under stress than others. Experimental and field-based evidence also indicates that elevated temperature can reduce fruit number, fruit weight, and marketable quality, although moderate chilling in some systems can induce acclimation and preserve yield, highlighting that the effect of temperature regulation depends on stress intensity, duration, and developmental stage.

Future research in temperature-controlled tomato production should move beyond describing stress injury and focus on predictive, trait-based, and mechanistic strategies for intervention. High-throughput phenotyping, including thermal infrared, hyperspectral, and chlorophyll fluorescence imaging, now offers non-destructive ways to detect heat-response traits, while GWAS and integrated genomics can identify markers for targeted breeding of thermotolerant cultivars. At the same time, molecular research increasingly supports the use of candidate genes related to flowering, pollen development, fruit set, heat shock responses, and epigenetic regulation as practical targets for breeding under recurrent heat stress. A second priority is to connect crop genetics with greenhouse engineering and climate-control technologies at commercial scale. Survey evidence from 326 ha of high-tech hydroponic greenhouses exposed to extreme summer heat showed that even advanced systems suffered yield loss and rising water, fertilizer, and electricity use, indicating that current climate-control capacity is often insufficient under future warming. Research should therefore test combinations of improved cooling, renewable-energy integration, season shifting, and heat-resilient varieties, while also evaluating emerging interventions such as prime editing, which increased tomato yield by 33% under heat stress without fruit-quality penalties through heat-responsive regulation of source-sink relations.

The implications for sustainable tomato production are both agronomic and systemic. Climate warming is projected to reduce processing tomato production in major producing regions by about 6% by 2050, with some leading areas facing additional water constraints, which implies that climate resilience will depend not only on plant tolerance but also on regional shifts in production systems and resource availability. In greenhouse systems, adaptation will require integrated approaches that combine structural innovations, precision irrigation, decision-support tools, and climate-resilient cultivars, because elevated temperature increasingly acts together with high radiation, water shortage, and vapor pressure deficits rather than in isolation. Sustainable and climate-resilient tomato production will therefore depend on combining biological resilience with technological and management innovation. Multidisciplinary strategies that unite breeding, genetic engineering, physiological knowledge, agronomic adjustment, precision monitoring, and beneficial microorganisms are increasingly viewed as essential for maintaining yield and food security under climate change. For tomato specifically, advanced ventilation, shading, renewable-energy-supported climate buffering, and cultivar selection for reproductive heat tolerance appear especially important because stable temperature and humidity are central to fruit set, lycopene formation, and marketable yield preservation in warmer production environments.

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Research Insight

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Effects of Planting Density on Yield Formation in Pepper

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Received: 10 Jun., 2026

Accepted: 14 Jul., 2026

Published: 26 Jul., 2026

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Preferred citation for this article:Yan J.Q., 2026, Effects of planting density on yield formation in pepper, Genomics and Applied Biology, 17(4): 213-225 (doi: [10.5376/gab.2026.17.0017](https://doi.org/10.5376/gab.2026.17.0017))

Abstract Planting density is a critical agronomic factor regulating crop population structure, resource utilization, and yield formation in pepper (*Capsicum annuum* L.) production. Improper planting density can lead to excessive competition for light, water, and nutrients, resulting in reduced photosynthetic efficiency, imbalanced biomass allocation, and unstable yield performance. This review summarizes the effects and underlying mechanisms of planting density on pepper growth, physiological processes, yield components, and fruit quality. Changes in planting density influence canopy architecture, leaf area index, light interception, root development, and microclimatic conditions, thereby affecting carbon assimilation and resource acquisition. Moderate planting density optimizes source–sink relationships, improves photosynthetic capacity, enhances nutrient and water use efficiency, and promotes reproductive development, including flowering, fruit setting, and fruit expansion. Excessive density often causes canopy shading, increased disease risks, and reduced individual plant productivity, whereas insufficient density limits land resource utilization and decreases population yield potential. Furthermore, this review discusses the physiological, ecological, and molecular mechanisms involved in density-induced adaptation, as well as strategies integrating planting density with irrigation, fertilization, and precision agriculture technologies. A case study is presented to demonstrate the practical application of density optimization for improving pepper yield formation and production efficiency. Future research should focus on developing dynamic density management strategies based on cultivar characteristics, environmental conditions, and intelligent agricultural technologies to achieve sustainable and high-yield pepper production.

Keywords Planting density; Pepper production; Yield formation; Canopy architecture; Resource use efficiency

1 Introduction

Pepper is an economically important vegetable crop in which yield and fruit quality depend strongly on how efficiently light, space, water, and nutrients are captured and converted into marketable fruit. Within this production system, planting density is one of the most practical management variables because it directly determines canopy structure, radiation interception, and the intensity of competition among neighboring plants. Recent agronomic work in pepper has therefore treated density management as a central component of yield improvement strategies rather than as a simple spacing decision. In field and protected systems alike, increasing density can improve land-use efficiency and raise output per unit area, especially when it is coordinated with cultivar choice and nutrient supply (Tian et al., 2024). In organic sweet pepper, higher planting density has likewise been proposed as a way to reduce production costs and increase fruit production within limited physical space, highlighting its relevance not only for biological productivity but also for production economics and system sustainability (Silva et al., 2021).

The relationship between planting density and pepper yield formation is complex because yield per unit land area and yield per plant do not respond in the same way. Multiple studies show that as density increases, total yield per hectare often rises, whereas individual plant performance tends to decline because each plant has access to fewer resources. In sweet pepper grown under field conditions, increasing plant density reduced fruit weight, fruit volume, and yield per plant, yet total yield per hectare still increased, indicating a compensatory population effect (Aminifard et al., 2012). Comparable patterns were reported in paprika pepper, where yield per hectare increased mainly because fruit number per unit area increased with density, while fruit number and dry fruit weight per plant declined and gains became marginal beyond very high densities, suggesting the existence of an agronomic optimum rather than an unlimited positive response.

Yield formation under different planting densities is further mediated by changes in crop architecture, dry matter accumulation, and assimilate partitioning. Evidence from bell pepper indicates that higher population density increases fruit yield per land area and that node number is a major yield component underlying density responses, pointing to structural adjustment of the plant population as a key mechanism of productivity change. Greenhouse research also shows that density alters leaf area index, canopy interception of photosynthetically active radiation, and dry matter partitioning between vegetative and reproductive organs; specifically, leaf dry matter partition increases and fruit dry matter partition decreases as density rises, while harvest index remains closely related to cumulative intercepted radiation. Together, these findings suggest that pepper yield formation under density stress depends not only on plant number, but also on how effectively the crop canopy captures light and directs assimilates toward fruit production.

Against this background, a review of planting density effects on yield formation in pepper is timely because published results indicate both broad agreement and important context dependence across cultivars, production systems, and target quality traits. For example, organic protected cultivation showed that higher densities increased yield and shortened the production cycle without necessarily reducing fruit size or quality in some genotypes, with the highest yields occurring at 6 to 8 plants/m² depending on genotype (Silva et al., 2021). In greenhouse bell pepper, marketable yield responded positively and linearly to increased density even though fruit set per plant declined, reinforcing that optimal density must be defined at the crop-population level rather than at the single-plant level. Therefore, the objective of this review is to synthesize current evidence on the importance of planting density management in pepper production, clarify the mechanisms linking density to yield formation, and identify how density interacts with genotype, canopy traits, and cultivation environment to shape both productivity and fruit quality.

2 Planting Density Regulation and Population Structure of Pepper

2.1 Canopy architecture and light interception

Planting density directly regulates pepper population structure by changing canopy closure, leaf area development, and the spatial pattern through which incoming radiation is distributed within the crop. In greenhouse sweet pepper, canopy light interception increased progressively after planting and reached about 92% at maturity, showing that dense, trained pepper stands can capture most incident radiation once the canopy is fully developed. Density also shapes canopy size through its effect on leaf area index, which follows a logistic increase after planting and reaches density-dependent maxima under protected cultivation. Together, these results indicate that population density is not simply a numerical stand attribute, but a structural regulator of canopy formation that determines how quickly pepper crops occupy space and intercept available light.

The effect of density on light interception depends not only on plant number but also on canopy geometry and within-row shading. In glasshouse pepper, light transmission below the canopy varied strongly by position and time of day, with much less light beneath rows than in the gaps between them, indicating that denser canopies create pronounced internal light gradients. At the same time, studies of pepper growth under modified light environments show that reduced light promotes taller plants and wider crowns through increases in canopy spread and branching, which helps explain why density-driven crowding often induces architectural adjustment as plants compete for radiation (Febrianto et al., 2024). Thus, the influence of planting density on pepper light capture operates through both canopy closure and plastic changes in plant architecture.

2.2 Plant growth and biomass accumulation

Planting density alters the balance between individual plant growth and biomass production per unit land area. Field evidence in sweet pepper shows that increasing density reduces vegetative growth traits such as lateral stem number and leaf dry matter, while also lowering fruit weight and yield per plant, even though total yield per hectare increases (Aminifard et al., 2012). A similar trade-off was reported under open-field conditions in another pepper study, where higher densities produced taller plants and greater total fruit production, whereas lower densities improved yield per plant and the proportion of marketable fruit. These findings show that density intensifies competition among neighboring plants, shifting performance away from individual vigor and toward collective productivity per unit area.

Density effects on biomass accumulation are also expressed through growth rate, assimilate partitioning, and the yield components that support fruit production. In bell pepper, higher population densities decreased absolute growth rate but still increased shoot biomass accumulation per unit land area, and fruit yield per land area rose consistently with density. Greenhouse modeling work further showed that crop biomass per unit area was positively related to intercepted photosynthetically active radiation, while increasing density raised dry matter partitioning to leaves and reduced partitioning to fruits. This means that the biomass response to density is governed not only by plant competition, but also by how the denser canopy redistributes assimilates between vegetative and reproductive sinks during yield formation.

2.3 Root system development

Planting density is also expected to regulate pepper population structure belowground by modifying the space available for root expansion and the intensity of competition for water and nutrients. Although direct pepper evidence remains limited, broader plant studies consistently show that increasing density constrains root structural development. In Chinese fir, average root length and root volume were significantly greater at low and intermediate densities than at high density, indicating that crowded stands suppress root development through reduced growing space and stronger competition (Farooq et al., 2019). Similarly, rice grown at higher planting density showed a higher top-root ratio and a greater concentration of roots in the surface soil layer, indicating that root growth became relatively inferior to shoot growth and that root distribution shifted under crowding. These patterns provide a useful framework for interpreting likely root responses of pepper under dense planting.

Available pepper studies support the view that belowground responses contribute to density effects on aboveground growth and yield, even when root traits are not the primary target. In intercropped bell pepper, reduced biomass and yield were interpreted partly as consequences of stronger belowground competition for nutrients, especially under high-density conditions where nitrogen competition becomes more intense (Sandhu et al., 2021). Separate greenhouse work in sweet pepper showed that root length density is sensitive to soil physical conditions, confirming that pepper root proliferation responds measurably to changes in the rooting environment even when total dry matter production is not significantly altered (Grasso et al., 2021). Therefore, the influence of planting density on pepper root development likely operates through reduced root expansion, altered spatial distribution, and stronger competition for belowground resources, all of which can feed back on canopy growth and yield formation.

3 Effects of Planting Density on Photosynthesis and Resource Utilization

3.1 Photosynthetic characteristics

Planting density modifies pepper photosynthesis first through its effects on canopy development and the internal light environment. In bell pepper, leaf area index is a core variable for estimating canopy photosynthetic rate, and the light-intensity ratio between the upper and lower canopy declines exponentially as LAI increases, indicating that denser canopies generate stronger vertical light attenuation and less favorable light conditions for lower leaves (Lee et al., 2020). Glasshouse pepper studies similarly show that increasing plant density raises leaf area index at fruiting level but reduces photosynthetically active radiation within the canopy, confirming that the photosynthetic response to density is governed by the trade-off between greater light capture at the population level and deeper self-shading within the stand.

Once density exceeds the range that maintains balanced canopy light distribution, photosynthetic efficiency tends to decline even when total intercepted radiation increases. In maize, higher planting density significantly increased leaf area index and intercepted photosynthetically active radiation, but simultaneously reduced net photosynthetic rate, stomatal conductance, and chlorophyll content, and these changes were identified as key mechanisms behind lower productivity at excessive density (Zhang et al., 2021). Pepper evidence points in the same direction: high plant density creates poor light conditions in the middle and lower canopy through mutual shading, whereas supplemental interlighting improves vertical light distribution and increases canopy light use efficiency, showing that density stress acts largely through deterioration of within-canopy photosynthetic conditions rather than through reduced land-area light capture alone (Kwon et al., 2023).

3.2 Water and nutrient use efficiency

The effect of planting density on water and nutrient use efficiency is not monotonic, because denser stands can improve resource capture per unit area while also intensifying competition among neighboring plants. In chili pepper under precision fertigation, higher densities up to 106,666 plants/ha increased total yield and had positive effects on water use efficiency, nitrogen use efficiency, and phosphorus use efficiency, even though individual plant performance declined (Susila et al., 2025). Across crops more broadly, optimized rather than maximal density tends to give the best integrated outcome; in rainfed maize, increasing density improved leaf area index and intercepted radiation, but precipitation use efficiency, radiation use efficiency, and nitrogen use efficiency followed a parabolic response, indicating that excessive crowding raises resource demand faster than resource conversion efficiency (Zhang et al., 2021).

Resource-use responses also depend on how density changes canopy cover, transpiration, and nutrient acquisition pathways. In sweet pepper grown under greenhouse conditions, improvement of canopy light distribution by interlighting increased both light use efficiency and water use efficiency, because dry matter and fruit yield increased faster than water consumption, suggesting that density-related inefficiencies can be partly offset when more of the canopy remains photosynthetically productive (Kwon et al., 2023). Root-based studies from other crops further show that increasing planting density can shift water uptake toward the topsoil and alter the balance between water consumption and productivity, while higher density in wheat often improves nitrogen uptake per unit area but can reduce water use efficiency when evapotranspiration rises without sufficient yield compensation (Gao et al., 2022; Zhou et al., 2026).

3.3 Carbon allocation and assimilate distribution

Under density stress, yield formation depends not only on carbon assimilation but also on how efficiently assimilates are distributed between vegetative and reproductive sinks. In high-density maize, superior hybrids maintained higher net photosynthetic rate, stronger sucrose-metabolizing enzyme activity in grains, and greater leaf carbon transport efficiency, which increased the proportion of grain in total dry matter under crowded conditions (Ren et al., 2022). A broader synthesis of cereal physiology reaches the same conclusion: improvements in photosynthesis do not necessarily increase yield unless carbon allocation and sink utilization remain coordinated, because inadequate sugar transport to sinks can negate gains in source activity under stressful field conditions (Liang et al., 2023).

For pepper, available evidence suggests that density-induced shading and nutrient competition likely reshape assimilate partitioning in analogous ways. In *Capsicum*, specific leaf area responds strongly to both shading and nitrogen supply, with shading increasing SLA and nitrogen-driven metabolic changes modifying leaf thickness and density, indicating that source-leaf structure and carbon economy are highly sensitive to the same resource gradients intensified by dense planting (De Ávila Silva et al., 2021). Stress studies in other crops also show that when source limitation develops, carbon allocation can be redirected away from reproductive sinks toward survival-oriented organs such as roots, while post-anthesis yield loss is closely tied to reduced late photosynthesis and altered remobilization of stored carbohydrates, supporting the view that excessive pepper density may depress yield by disrupting assimilate flow as much as by reducing instantaneous photosynthesis (Rubia et al., 2025; Yang and Liang, 2025).

4 Effects of Planting Density on Yield Formation Components of Pepper

4.1 Flowering, fruit set, and reproductive development

Planting density affects pepper reproductive development mainly by altering the source–sink balance that supports young reproductive organs. In sweet pepper, reducing source strength through high plant density increases flower and fruit abortion linearly, and the first week after anthesis is the most abortion-sensitive stage. A broader review reaches the same conclusion that lower planting density increases assimilate availability per plant and reduces reproductive abortion, whereas abortion remains especially high in very young buds, buds near anthesis, and fruits up to 14 days after anthesis.

The effect of density on flowering time itself appears weaker and more variable than its effect on subsequent fruit retention. In open-field pepper, higher density did not significantly change flowering time, although it tended to increase yield in the first harvest and in total production. Likewise, in chilli pepper, planting density showed no significant effect on most reproductive timing and yield-related traits other than plant height, indicating that temperature, genotype, and sowing date can override density effects on flowering and fruit set under some field conditions (Mends-Cole et al., 2019).

4.2 Yield components and final yield formation

Planting density consistently shifts pepper yield formation from per-plant performance toward per-area productivity. In sweet pepper, increasing density reduced fruit volume, fruit weight, and yield per plant, but total yield per hectare still increased, with the highest yield recorded at the closest spacing tested (Aminifard et al., 2012). Direct-seeded paprika pepper showed the same pattern: fruit number and dry fruit weight per plant declined as density increased, while yield per hectare rose because the number of fruits per unit area increased.

The yield response is not unlimited, and several studies indicate a density optimum beyond which competition suppresses final production gains. In chili pepper, increasing plant population from 20,000 to 30,000 plants/ha raised total fruit yield by 52.58%, but yield then declined by 34.09% at 40,000 plants/ha (Setiawati et al., 2022). Bell pepper trials across five densities also found that fruit yield per land area increased with density, and yield-component analysis identified node number as the component most responsive to population density, linking final yield gains to structural changes in reproductive site formation.

4.3 Fruit quality characteristics

The interaction between planting density and fruit quality is genotype- and trait-dependent rather than uniform across pepper types. In an organic protected system, higher density increased yield and shortened the crop cycle without impairing fruit size or quality in the ‘TE 300’ and ‘Timor’ genotypes, although ‘Mallorca’ responded less favorably at densities above 4 plants/m² for fruit mass (Silva et al., 2021). Glasshouse pepper showed similarly limited density effects on commercial quality traits, with fruit weight, length, diameter, volume, dry matter, soluble solids, and flesh pH unaffected by plant density and shoot number.

Other quality traits respond more sensitively to denser planting, especially in pungent or processing peppers. In paprika pepper, pigment content declined linearly as density increased even though moisture content at harvest remained unchanged, so the agronomic optimum was defined by both yield and color retention. In field-grown pungent pepper, the spacing that produced the highest yield per area also increased capsaicin and dihydrocapsaicin content, while Jalapeño pepper maintained fruit quality under denser planting even as acidity-related traits shifted modestly (Paulus et al., 2015; Ragassi et al., 2019).

5 Physiological and Ecological Mechanisms Underlying Density-Driven Yield Formation

5.1 Hormonal regulation and plant developmental responses

Planting density changes pepper development by altering the hormonal control of shoot expansion, root growth, and the transition between vegetative and reproductive growth. In *Capsicum*, plant architecture traits such as plant height and leaf size are tightly linked to endogenous hormone regulation, and transcriptome analysis has identified differential expression in auxin, gibberellin, cytokinin, abscisic acid, jasmonic acid, ethylene, and salicylic acid signaling pathways associated with structural variation (Xing et al., 2024). More generally, auxin and cytokinin act as a central antagonistic pair in regulating the shoot-to-root growth ratio, with cytokinin favoring shoot growth and limiting root growth, whereas auxin promotes root development and improves adaptation to water and nutrient limitation, a balance that is directly relevant when higher density intensifies above- and belowground competition (Kurepa and Smalle, 2022).

Hormonal effects on developmental plasticity also extend to reproductive allocation and stress buffering in pepper. Under salinity, contrasting rootstock-mediated yield responses in pepper were associated with shifts in hormonal balance, with higher leaf cytokinin concentrations clustering with productivity traits and the ethylene precursor ACC showing the opposite pattern, indicating that hormonal rebalancing can sustain fruit production under stress

(Gálvez et al., 2021). At the organ level, pepper fruit size depends strongly on early auxin and cytokinin accumulation that promotes rapid cell division, while high gibberellin accumulation supports later pericarp cell elongation and expansion, showing how hormone-regulated developmental processes can translate canopy resource status into final yield components (Figure 1) (Tang et al., 2025).

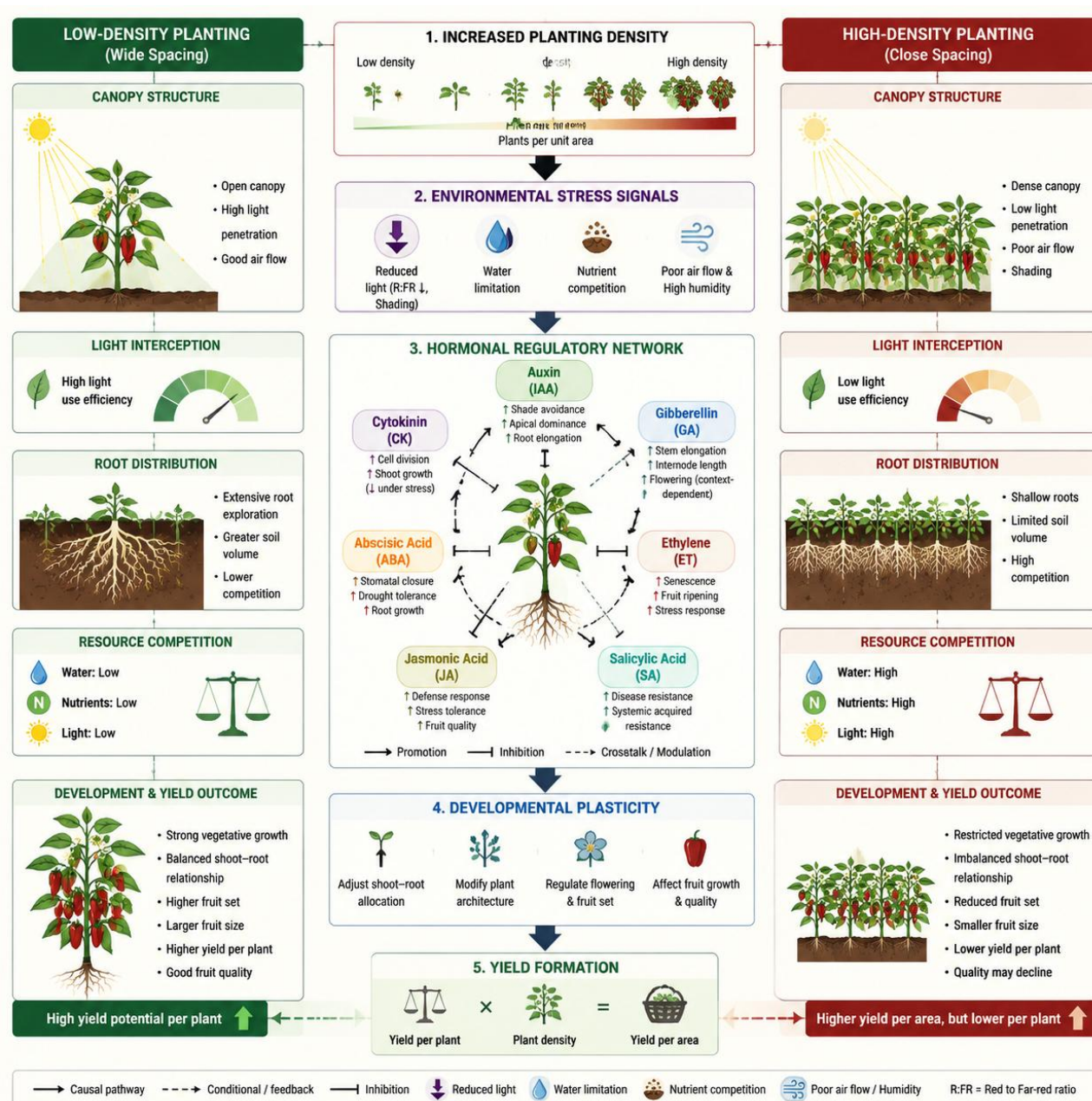


Figure 1 Conceptual model illustrating the regulation of pepper (*Capsicum annuum* L.) development by planting density-mediated hormonal pathways

5.2 Microclimate changes within pepper populations

Density-driven yield formation is also mediated by microclimate changes within the crop stand, especially shifts in light, temperature, and humidity. Studies on pepper-related systems show that denser or more shaded canopies reduce irradiance and temperature while increasing relative humidity, thereby creating a cooler but less illuminated internal environment (Oliosi et al., 2021). This general canopy effect is consistent with broader microclimate evidence showing that higher crown density is strongly associated with lower light intensity and temperature and with higher humidity, which helps explain why dense pepper populations often experience reduced evaporative demand but greater within-canopy shading (Kartika and Marjenah, 2023).

The agronomic consequence of these microclimate shifts depends on their intensity and spatial distribution. In Mediterranean photovoltaic cultivation, pepper experienced lower solar radiation near structures, along with reduced air temperature, lower wind speed, higher relative humidity, and lower evapotranspirative demand, yet these modified conditions were still associated with reduced shoot and fruit fresh weight in some zones, indicating that microclimate amelioration can become light limitation when shading is excessive (Tucci et al., 2025). Controlled-environment evidence likewise shows that in high-density production systems, close canopy positioning to light sources can disturb canopy temperature, humidity, and airflow uniformity, reinforcing that dense stands change not only mean microclimate but also its spatial heterogeneity, which can affect crop performance (Yu et al., 2023).

5.3 Molecular responses to density stress

At the molecular level, density stress in pepper is likely expressed through regulatory networks that are also activated by drought, heat, salinity, and osmotic imbalance, because crowding modifies light capture, water relations, and resource competition in parallel ways. Large-scale transcriptome profiling in *Capsicum annuum* across heat, cold, salinity, and osmotic treatments generated time-resolved gene expression datasets specifically intended to identify complex stress-response networks and breeding-relevant traits (Kang et al., 2020). Complementing this, a deep RNA-seq analysis across 425 pepper samples identified 1,642,007 alternative splicing events and 4,354 differential alternative splicing genes associated with environmental stressors, tissues, and signaling molecules, indicating that transcript diversification is a major component of pepper stress adaptation (Kim et al., 2024).

Specific gene families further clarify how pepper may adapt to density-related stress. In hot pepper, SR genes contain cis-elements related to abiotic stress responses, and most CaSR genes showed alternative splicing under both normal and stress conditions, supporting a role for splice regulation in environmental adaptation (Li et al., 2025). HD-Zip transcription factors and SnRK2 kinases provide additional evidence of integrative stress signaling in *Capsicum*: CaHD-Zip promoters are enriched in light-, hormone-, and stress-responsive elements, while CcSnRK2.5 enhanced drought tolerance through ABA-responsive regulation and reduced water loss, suggesting that density stress adaptation likely depends on coordinated transcriptional and hormonal control rather than on a single pathway (Wang et al., 2025; Shu et al., 2026).

6 Optimization Strategies for Planting Density Management in Pepper Production

6.1 Optimal density by cultivation system

Optimal planting density in pepper depends on cultivation system, genotype, and the trade-off between per-plant performance and yield per unit area. In protected organic sweet pepper, the highest total yield occurred at 8 plants/m² for ‘TE 300’ and ‘Timor’ and at 6 plants/m² for ‘Mallorca’, while higher density also shortened the production cycle without reducing fruit quality in two of the three genotypes (Silva et al., 2021). Under unheated greenhouse conditions, planting arrangement also changed fruit morphology, with tighter configurations producing taller plants and thinner fruits, which shows that the best density in protected cultivation must be defined jointly by yield and market traits (Xushvaqtov et al., 2024).

Open-field studies point to a similar pattern: intermediate or moderately high density is usually optimal, whereas excessive crowding reduces returns. In bell pepper, 42,000 plants/ha produced the best yield without significant quality penalties. In field-grown chili pepper, both 50,000 plants/ha and 30,000 plants/ha were identified as practical optima in different environments, indicating that recommended density should be adjusted to local climate, seedling age, and management level rather than fixed as a universal value (Setiawati et al., 2022).

6.2 Density with irrigation and fertilization

Density optimization is more effective when coordinated with irrigation and fertilizer supply, because crowding raises competition for water and nutrients even when land productivity increases. A two-year pepper study showed that integrated management combining a suitable planting density, high-yielding cultivars, and reasonable nitrogen management was a practical route to higher yield and quality, and the densest tested spacing (0.4 m × 0.6 m) increased aboveground dry matter and yield (Tian et al., 2024). Separate field evidence likewise found a

significant density $\times$ nitrogen interaction for fruit volume and fruit weight, confirming that density recommendations should be linked to fertilizer regime rather than chosen independently (Aminifard et al., 2012).

Recent irrigation studies reinforce that the best density is the one matched to a specific water-delivery system. Under automated protected cultivation, sensor-based irrigation at 75% available soil moisture combined with 125% recommended fertilizer produced 60,089 kg/ha and the highest water and nutrient use efficiencies (Ningoji et al., 2024). In precision-fertigated chili pepper, higher densities up to 106,666 plants/ha increased total yield and improved WUE, NUE, and PUE, but double drip lines raised yield while reducing water use efficiency, showing that irrigation layout can shift the agronomic optimum for density (Susila et al., 2025).

6.3 Precision technologies

Precision agriculture offers a way to regulate planting density more dynamically by linking stand establishment, canopy monitoring, and input delivery to spatial variability within the crop. In greenhouse pepper, sensor networks and machine-learning-based control systems are being developed to improve decision-making, resource use, and sustainability, while fertigation regimes tailored to crop response already improve productivity under monitored microclimate conditions (Fadare et al., 2025). More broadly in vegetable systems, integrating weather stations, soil sensors, and remote sensing into decision-support systems helps farmers evaluate crop growth, yield potential, and resource use, which is directly relevant for refining density management over time (Chaudhari et al., 2024).

Remote sensing and automation are especially useful for translating density management from fixed spacing recommendations into site-specific regulation. Remote sensing in precision agriculture supports crop monitoring, irrigation management, nutrient application, and yield prediction, and UAV platforms are increasingly favored because they provide high-resolution imagery needed for practical management decisions (Sishodia et al., 2020). In parallel, automated seeding and transplanting systems can improve the uniformity of plant spacing and reduce labor costs, which makes them a practical tool for achieving target pepper populations more accurately than manual establishment (Chaudhari et al., 2024).

7 Case Study: Effects of Different Planting Densities on Pepper Yield Formation

7.1 Experimental background and planting density treatments

Pepper density case studies have been conducted across open-field, greenhouse, protected organic, and soilless production systems, and they consistently use multi-level density gradients to quantify how stand structure affects yield formation. In protected organic sweet pepper, experiments compared three genotypes at 2, 4, 6, and 8 plants/m² in a duplicated randomized complete block design, while bell pepper trials in Canada tested 1.4, 1.9, 2.8, 5.6, and 11.1 plants/m² under mulch and row-cover conditions to capture both density and microenvironment effects (Silva et al., 2021). These designs are useful as case-study models because they span both moderate and very high densities and therefore allow identification of the point where greater land occupancy ceases to improve biological or commercial performance.

Other studies show that density treatments are also shaped by establishment method and local production practice. In field-grown sweet pepper, four spacing combinations—20 $\times$ 50, 30 $\times$ 50, 20 $\times$ 100, and 30 $\times$ 100 cm—were combined with nitrogen treatments, whereas direct-seeded paprika pepper was thinned to a very broad density range from 13,333 to more than 500,000 plants/ha, enabling evaluation of both yield and color responses under commercial-scale plant populations (Figure 2) (Aminifard et al., 2012). Together, these case studies show that meaningful density evaluation in pepper requires treatment ranges wide enough to detect not only yield increases at low-to-moderate crowding but also the threshold where competition begins to offset further gains.

7.2 Responses of growth characteristics and yield components

Across case studies, increasing planting density generally shifts pepper growth toward greater population productivity but weaker individual plant performance. In sweet pepper, higher density reduced vegetative and reproductive traits at the plant level, including lateral stem number, leaf dry matter, fruit volume, fruit weight, and yield per plant, even though total yield per hectare increased (Aminifard et al., 2012). A similar pattern was

observed in paprika pepper, where fruit number and dry fruit weight per plant declined as population increased, while yield per hectare rose because fruit number per unit area increased. This confirms that density-driven yield formation depends less on maximizing the performance of each plant than on increasing the number of productive units occupying a given area.

Experimental framework: Planting density gradient of sweet pepper (*Capsicum annuum* L.) across production systems

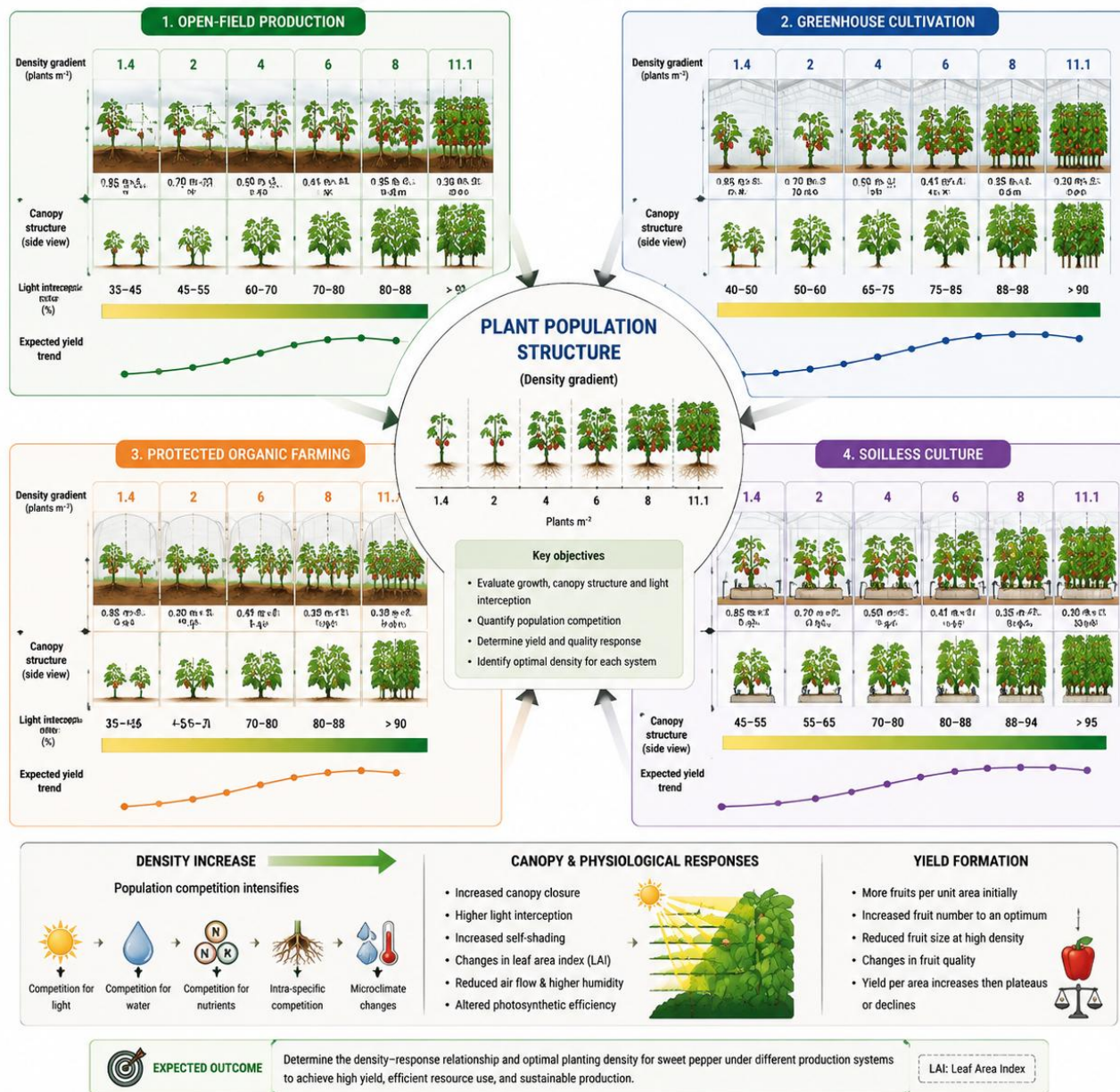


Figure 2 Conceptual framework of pepper density experiments across different production systems

Not all responses are linear, and several case studies identify clear biological limits to crowding. In chili pepper, raising density from 20,000 to 30,000 plants/ha increased total fruit yield by 52.58%, but increasing to 40,000 plants ha⁻¹ caused yield to decline by 34.09%, showing that excessive competition can reverse the yield advantage of denser planting (Setiawati et al., 2022). Greenhouse bell pepper supports the same interpretation at the reproductive level: marketable yield increased linearly with density, but fruit set per plant decreased linearly as density increased, indicating that total yield gains arise from stand-level compensation rather than improved reproductive success of individual plants.

7.3 Optimal density and production implications

The optimal planting density in pepper is therefore context-specific, but most case studies favor an intermediate-to-moderately high density rather than the lowest or most crowded treatment. In bell pepper grown in the Caspian Sea region, 42,000 plants/ha produced the best yield without significant quality penalties, while a more recent field study in the Northern Guinea Savannah identified 50,000 plants/ha as the best compromise between plant competition and land-use efficiency. These findings suggest that the agronomic optimum is usually the density that preserves enough per-plant growth to maintain fruit size and reproductive function while still increasing fruit number per unit area.

Production implications also depend on genotype and cultivation system. In protected organic cultivation, the best total yields were obtained at 8 plants/m² for 'TE 300' and 'Timor' and 6 plants/m² for 'Mallorca', showing that cultivar-specific adaptation to crowding is a practical determinant of density recommendations (Silva et al., 2021). In glasshouse pepper, 80 × 15 cm with two shoots per plant was suggested for maximum yield, whereas 80 × 30 cm with three shoots per plant was considered more economical when seed cost was high, indicating that density optimization should be integrated with pruning strategy and production costs rather than based on spacing alone. Overall, pepper yield formation is best supported by densities that intensify land use without pushing the crop into excessive competition, and the exact optimum should be calibrated to genotype, establishment method, and management system.

8 Conclusions and Future Perspectives

Across pepper systems, higher planting density generally increases total yield per hectare by increasing fruit number per unit area, even though fruit number or fruit mass per plant declines. In sweet pepper, greater density reduced fruit volume, fruit weight, and yield per plant but increased total yield, while in direct-seeded paprika pepper the yield gain from density was specifically driven by more fruits per hectare. This positive response is not unlimited, and most studies support an intermediate or moderately high density rather than maximum crowding. Chili pepper yield increased by 52.58% when population rose from 20,000 to 30,000 plants/ha but declined by 34.09% at 40,000 plants/ha, and a separate field study identified 50,000 plants/ha as the best balance between plant competition and land-use efficiency.

Density effects on yield formation also depend on genotype and cultivation system because varieties differ in their tolerance to competition and their ability to maintain fruit quality. In protected organic production, 'TE 300' maintained yield per plant across 2-8 plants/m² and, together with 'Timor', achieved its highest total yield at 8 plants/m², while 'Mallorca' performed best at 6 plants/m². At the physiological level, density influences yield formation through canopy light interception, resource competition, and reproductive success. Higher density increased leaf area index but reduced photosynthetically active radiation within the canopy in glasshouse pepper, and in sweet pepper reduced source strength was directly associated with higher flower and fruit abortion.

Future density research in pepper should move from single-factor spacing trials toward integrated designs that test density together with cultivar choice, fertilization, irrigation, and establishment traits. A recent two-year field experiment showed that suitable density, high-yield cultivars, and optimal nitrogen management jointly improved yield, nutrient uptake, and quality, while another study showed significant interactions between plant density and nitrogen for fruit volume and fruit weight. More work is also needed on density responses under advanced production systems, where the economic optimum may differ from the biological optimum. In greenhouse pepper, 80 × 15 cm with two shoots per plant was suggested for maximum yield, but 80 × 30 cm with three shoots per plant could be more economical when seed is expensive, and 3D ray-tracing models have been proposed to determine stem density and supplemental lighting levels during cultivation.

A second research priority is to improve site-specific density management using sensing and geospatial tools. Precision approaches that integrate soil attributes with NDVI can delineate management zones for more efficient decision-making, and automated sensor-driven irrigation and fertigation already improve pepper growth, yield, and resource-use efficiency under protected cultivation. Future studies should also expand the trait set used to define optimum density beyond yield alone to include harvestability, weed suppression, and quality preservation.

Higher density improved plant architecture and the percentage of marketable fruit for mechanical harvest in New Mexico green chile, whereas a moderate density of 37,037 plants ha⁻¹ in chili pepper improved yield while also providing moderate weed suppression.

For sustainable pepper production, the main implication is that optimized density can increase land productivity without proportionally increasing resource use, but only when density remains within the crop's tolerance range. Under precision fertigation, higher chili densities up to 106,666 plants ha⁻¹ increased total yield and had positive effects on water, nitrogen, and phosphorus use efficiency, while in rainfed maize moderate density rather than excessive density improved yield stability and resource-use efficiency, offering a useful principle for pepper systems. Sustainability also depends on matching density to microclimate management and climate stress adaptation. Moderate shading improved pepper productivity in some environments, but increasing shade intensity to 60% could reduce fruit yield or fruit number, showing that dense canopies and protective structures must be managed to avoid turning stress protection into light limitation. At the production-system level, density optimization can support profitability, labor efficiency, and lower input waste when paired with modern management. Mechanized pepper systems showed that reduced planting density improved working conditions while maintaining strong productivity in some settings, and sustainability assessment of greenhouse pepper in southeastern Spain found that a high-productivity system can remain environmentally and economically robust when adapted to changing inputs and resistant cultivars.

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Research Insight

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Influence of Light Management on Fruit Quality and Sugar Accumulation in Strawberry

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Received: 16 Jun., 2026

Accepted: 25 Jul., 2026

Published: 07 Aug., 2026

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Preferred citation for this article:

Shen J.Y., 2026, Influence of light management on fruit quality and sugar accumulation in strawberry, Genomics and Applied Biology, 17(4): 226-239 (doi: [10.5376/gab.2026.17.0018](https://doi.org/10.5376/gab.2026.17.0018))

Abstract Light is a critical environmental factor regulating strawberry growth, fruit development, and quality formation. With the expansion of protected cultivation systems, optimizing light management has become an effective strategy for improving fruit yield and enhancing nutritional and sensory attributes. This review summarizes recent advances in the effects of light intensity, photoperiod, light quality, and canopy light distribution on strawberry fruit quality and sugar accumulation. Light regulation influences photosynthetic carbon assimilation, carbohydrate transport, and source-sink relationships, thereby affecting the accumulation of soluble sugars, organic acids, anthocyanins, and flavor compounds. Artificial lighting technologies, particularly LED supplemental lighting, provide precise control of spectral composition and light dosage, promoting photosynthetic efficiency and improving fruit sweetness under low-light conditions. In addition, canopy management practices, including leaf removal, planting density optimization, and reflective mulching, enhance light interception and improve fruit uniformity. At the physiological and molecular levels, light signals regulate sugar metabolism-related enzymes, photosynthetic pathways, and hormone interactions through photoreceptors and transcriptional networks. Case studies demonstrate that optimized light environments can significantly enhance strawberry fruit quality in greenhouse production. Future research should focus on integrating intelligent sensing technologies, environmental modeling, and multi-factor regulation to establish precise and sustainable light management systems for high-quality strawberry production.

Keywords Strawberry; Light management; Fruit quality; Sugar accumulation; LED supplemental lighting

1 Introduction

Strawberry (*Fragaria* × *ananassa* Duch.) is one of the world's most important and widely consumed fruit crops, valued not only for its economic significance but also for its sensory and nutritional attributes, including sweetness, color, aroma, vitamins, fiber, and antioxidant compounds. Current production systems are under increasing pressure to deliver fruit that satisfies consumer expectations for appearance, flavor, firmness, and health-promoting value while remaining profitable under climate instability, pest pressure, and protected-cropping constraints. For this reason, improvement of fruit quality has become a central goal in strawberry research and industry, alongside yield stability and postharvest performance. Sweetness is especially important because it strongly influences consumer acceptance and marketability, yet it is a complex trait shaped by both genotype and environment. Recent advances in breeding and molecular research have improved understanding of quality-related traits, but practical crop-management tools are still needed to consistently enhance sweetness and overall fruit quality under commercial conditions (Hernández-Martínez et al., 2023).

Among environmental factors, light is one of the most decisive regulators of strawberry growth, flowering, ripening, and metabolite accumulation. Light does not act only as an energy source for photosynthesis; its intensity, duration, and spectral composition also function as developmental signals that influence plant architecture, floral induction, fruit coloration, sugar accumulation, and the synthesis of phenolics and other secondary metabolites. In strawberry, inadequate or suboptimal light conditions can reduce fruit quality, causing poor coloration and weaker accumulation of desirable compounds, whereas suitable light exposure promotes soluble sugars and anthocyanins in ripening fruit. Mechanistically, light-mediated quality formation is linked to regulation of photoreceptors and downstream transcriptional networks that control biosynthetic genes associated

with sugar and pigment metabolism. Thus, the strawberry light environment is directly relevant to both source activity in leaves and sink metabolism in fruits, making it a key target for quality-oriented crop management (Warner et al., 2021).

Research over the last decade has shown that light management can be used strategically to improve strawberry production in greenhouses and controlled environments, particularly where winter radiation is limited or canopy structure creates local shading. Supplemental LED lighting has received the greatest attention because it allows precise control of wavelength, intensity, and photoperiod, and different spectra can produce distinct outcomes. Red light often promotes productivity and anthocyanin accumulation, while blue light can enhance certain quality traits and, in some systems, increase soluble sugar content. Combined red-blue lighting has also been reported to improve soluble solids, anthocyanin concentration, and vegetative performance, although cultivar dependence remains an important limitation. In addition, newer work suggests that far-red or other spectrum adjustments can further alter flowering, biomass partitioning, fruit yield, and sweetness. Collectively, these findings indicate that light management is no longer a purely supplemental practice for maintaining growth, but an active production tool for steering fruit quality formation in strawberry (Lauria et al., 2023; Ries and Park, 2024).

Despite this progress, important gaps remain in understanding how light management specifically influences sugar accumulation while simultaneously affecting other fruit-quality components. Available studies show that supplemental lighting can increase total sugar, glucose, and fructose concentrations, and can also modify soluble solids, acidity, polyphenols, and anthocyanins, but responses vary with season, cultivar, irrigation status, and the precise light regime applied. Moreover, the physiological and molecular coordination between carbon assimilation, carbohydrate transport, ripening metabolism, and light signaling has not yet been fully resolved for strawberry production systems. Therefore, a focused synthesis of current knowledge is needed to clarify how light intensity, spectral composition, and light-management strategies shape fruit quality, with particular emphasis on sugar accumulation. The objective of this paper is to examine the influence of light management on strawberry fruit quality and sweetness-related traits, summarize current research progress, and provide a basis for optimizing lighting strategies in modern strawberry cultivation (Qiu et al., 2023; Xu et al., 2023).

2.Light Characteristics and Their Effects on Strawberry Photosynthetic Performance

2.1 Effects of light intensity on photosynthesis and carbon assimilation

Light intensity is a primary determinant of strawberry photosynthetic performance because it directly affects carbon fixation, stomatal behavior, and assimilate supply. Under greenhouse shading, reduced irradiance decreased photosynthetic rate, stomatal conductance, sugar accumulation, and marketable fruit yield, showing that inadequate light restricts both source activity and carbon allocation to developing sinks (Choi, 2021). Similar responses were observed during transplant production in LED systems, where increasing intensity within an effective range enhanced stomatal conductance, net photosynthetic rate, and dry matter accumulation, confirming that carbon assimilation improves as photon supply approaches the cultivar's physiological requirement.

However, the effect of intensity is not simply linear, because optimal ranges differ with developmental stage and production environment. During runner propagation, unrooted plants performed best at $90 \mu\text{mol m}^{-2} \text{s}^{-1}$ during rooting, whereas rooted seedlings responded positively up to $270 \mu\text{mol m}^{-2} \text{s}^{-1}$, with no further growth improvement at $360 \mu\text{mol m}^{-2} \text{s}^{-1}$, indicating saturation of biomass gain at higher irradiance. Recent controlled-environment work also showed that moderate supplemental illumination directed to the abaxial leaf surface increased CO_2 assimilation, fruit yield, and fruit quality with greater energy efficiency than equivalent adaxial lighting, emphasizing that both light dose and light distribution influence whole-canopy carbon gain (Wang et al., 2026).

2.2 Influence of photoperiod on vegetative growth and reproductive development

Photoperiod modifies strawberry growth by changing the daily duration of carbon acquisition and by regulating the timing of developmental transitions. In indoor sole-source systems, extending the photoperiod from 12 to 16 h accelerated flowering by 17-21 days, advanced first harvest, and increased fruit production by 372%–989%, while increases in PPFD mainly enhanced vegetative biomass, indicating that day length can dominate reproductive

output even when light intensity is adequate (Park et al., 2023). This interaction between light duration and growth is reinforced by recent synthesis work showing that PPFD and photoperiod act synergistically in controlled production, although cultivar-specific sensitivity remains an important constraint on universal lighting prescriptions (Wang et al., 2025).

Photoperiodic regulation also acts through flowering and vegetative signaling pathways that differ among strawberry types and developmental stages. In seasonal flowering cultivars, long days induce FaCO responses yet can delay flowering through repression pathways involving FaTFL1, while FaSOC1 functions as a strong repressor of flowering and promoter of vegetative growth (Muñoz-Avila et al., 2022). After floral initiation, photoperiod continues to shape reproductive progression: in ‘Akihime’, long-day treatment delayed the first inflorescence but increased flower number in the secondary inflorescence and accelerated later fruit maturation, showing that post-flowering photoperiod can redistribute reproductive timing rather than simply promote or inhibit it (Ren et al., 2024).

2.3 Regulation of light quality on plant morphology and physiological responses

Light quality regulates strawberry morphology and physiology by altering chlorophyll formation, stomatal behavior, photochemistry, and downstream metabolic programming. Under different LED spectra, strawberry leaves showed significant changes in chlorophyll content, minimal fluorescence, and net photosynthetic rate, and transcriptomic analysis linked these responses to pathways related to photosynthesis, carbon fixation, chlorophyll metabolism, and hormone biosynthesis (Li et al., 2024). Spectral composition also affected propagation-stage morphology: adding green or far-red light to red-blue backgrounds increased shoot multiplication and plant height, while green light enhanced chlorophyll biosynthesis and far-red stimulated photomorphogenesis-related gene expression (Li et al., 2025).

Different wavebands, however, do not contribute equally to photosynthetic efficiency, and narrow spectra can produce contrasting physiological outcomes. White supplemental light supported higher photosynthesis after prolonged exposure, whereas monochromatic red and blue reduced maximal photosynthetic rate and increased superoxide formation, suggesting that broader spectra better sustain leaf function over time (Lauria et al., 2023). At the leaf level, blue and green light increased intercellular CO₂ concentration and transpiration through stronger stomatal opening, while red light more strongly promoted photochemical reactions and CO₂ fixation, indicating that balanced spectral combinations are more effective than single wavelengths for coordinating morphology with carbon assimilation.

3 Mechanisms of Light Regulation on Strawberry Fruit Quality Formation

3.1 Regulation of light environment on fruit growth and development

Light regulates strawberry fruit growth and development by controlling both whole-plant carbon supply and ripening-related signaling. When light intensity is reduced, strawberry plants show lower photosynthetic rate, stomatal conductance, sugar accumulation, and fruit yield, indicating that insufficient irradiance restricts assimilate production needed for fruit expansion and maturation (Choi, 2021). In contrast, supplemental LED lighting in commercial systems generally increases yield and can accelerate maturation-related changes in fruit quality, showing that managed light environments can shift fruit development toward earlier and more productive harvests (Figure 1) (Tang et al., 2023; Pérez-Romero et al., 2024).

Beyond total irradiance, spectral composition shapes developmental timing and fruit formation through photoreceptor-mediated pathways. Additional far-red light accelerates flower and fruit formation and increases soluble sugar, whereas low red:blue ratios alter metabolite composition without strongly changing fruit set, suggesting that developmental and quality responses can be partially uncoupled (Li et al., 2025). At the molecular level, light signaling also acts as a brake-or-release system during ripening, because COP1 suppresses fruit quality formation by destabilizing HY5-, RIF-, and MYB10-dependent downstream regulators, while light relieves this repression and promotes visible changes in fruit color and shape (Bi et al., 2025).

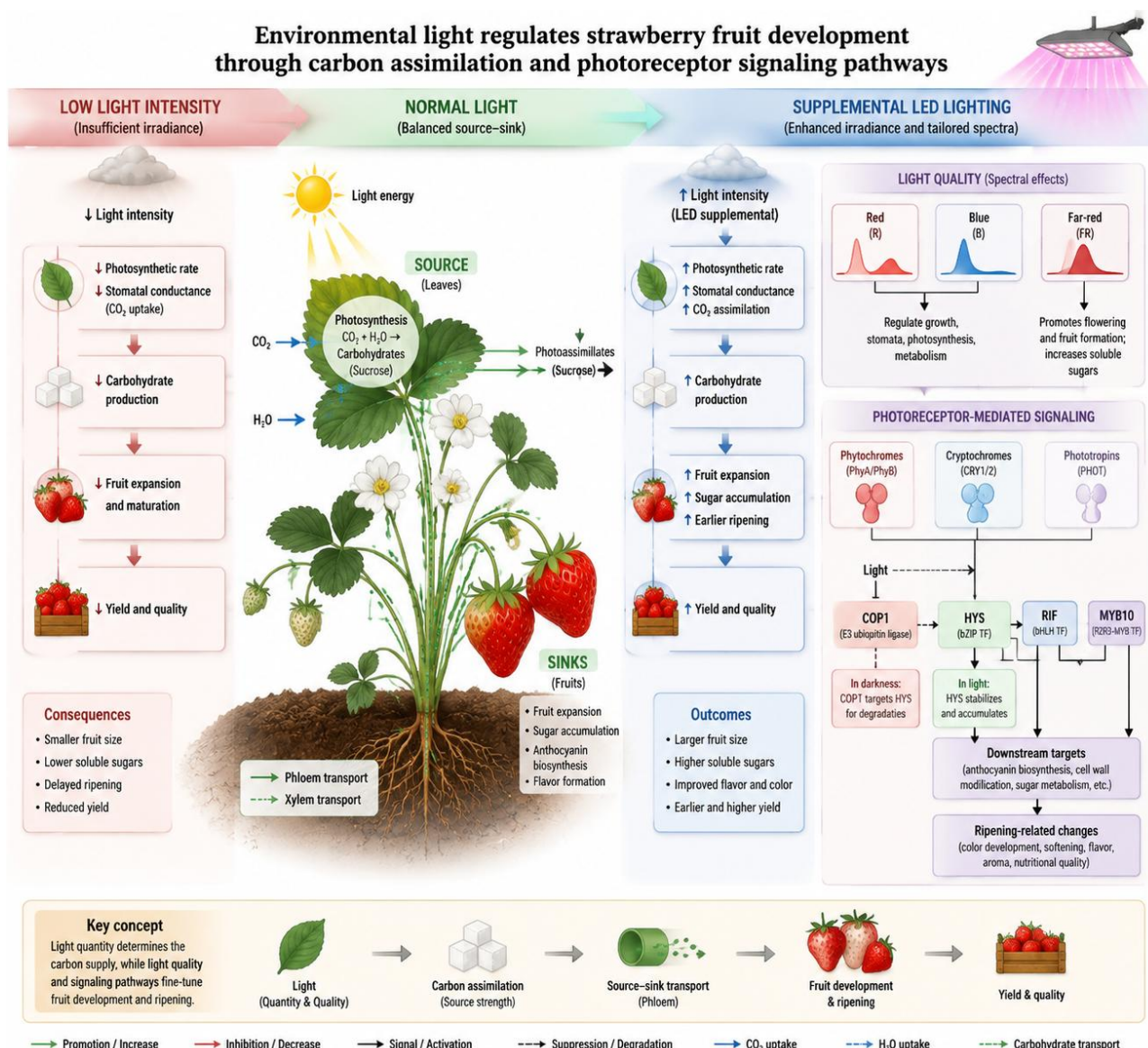


Figure 1 Mechanistic framework illustrating how light quantity and quality regulate strawberry fruit growth, carbon allocation, and ripening processes

Light management also modifies fruit growth indirectly by changing source-sink balance under greenhouse stress or resource limitation. Supplemental light combined with elevated CO₂ increases yield across the production season and improves sweetness, supporting the view that fruit development responds strongly when carbon acquisition is simultaneously enhanced by atmospheric and radiative inputs (Qiu et al., 2023). Similarly, under full or deficit irrigation, supplemental light improves fruit size and elevates quality-related metabolites, indicating that light can partially buffer suboptimal water conditions during fruit development (Xu et al., 2023).

Recent synthesis work indicates that light effects on fruit growth are stage-specific rather than uniform across the crop cycle. Phase-specific strategies that adjust spectral composition from vegetative growth to flowering and maturation appear to improve quality formation more effectively than static lighting, because the developmental roles of light differ across fruit set, enlargement, and ripening (Warner et al., 2021; Wang et al., 2025). This helps explain why responses vary across cultivars and experiments: light acts through interacting effects of wavelength, developmental stage, and preharvest versus postharvest exposure rather than through a single universal mechanism (Warner et al., 2021).

3.2 Effects of light on sugar accumulation and carbohydrate metabolism

Light promotes sugar accumulation in strawberry fruit at both physiological and molecular levels. Dark-treated fruit fail to accumulate sugars normally, whereas light-treated fruit show increased soluble sugar levels together with stabilization of FvMYB10, indicating that ripening-associated sugar accumulation depends on active light signaling. In greenhouse production, supplemental light increases total sugar, glucose, and fructose concentrations, especially late in the season, confirming that improved carbohydrate status under better light translates into sweeter fruit (Xu et al., 2023).

This regulation is mediated by specific photoreceptors and downstream metabolic genes. Blue-light receptors FvCRY1 and FvCRY2 directly promote anthocyanin and sugar accumulation, and their overexpression increases soluble solids, glucose, and fructose together with higher expression of FvINV and FvSFP9, linking light perception directly to carbohydrate metabolism and transport (Zhang et al., 2025). A parallel negative pathway is mediated by COP1, which represses sugar accumulation by inhibiting HY5-, RIF-, and MYB10-regulated transcriptional activation of downstream biosynthetic genes (Bi et al., 2025).

Spectral quality also changes the balance among carbohydrate-related metabolites. Red-light supplementation alters inositol metabolism and affects compounds such as D-mannose-6-phosphate, sorbitol, and inositol, while transcriptomic enrichment in galactose metabolism suggests that red light reshapes broader carbohydrate networks beyond simple soluble sugar accumulation. Consistent with this, recent review evidence indicates that spectral optimization can balance sucrose-to-hexose partitioning through FaSPS1-related regulation, providing a mechanistic explanation for why different light recipes produce different sweetness outcomes (Wang et al., 2025).

Not all light treatments increase sugars in the same way, and responses can depend on treatment context. In detached fruit, most red-, blue-, and white-light treatments decreased the TSS/TA ratio and the soluble sugar/acid ratio, especially when sucrose was added exogenously, indicating that postharvest or detached-ripening responses can differ from whole-plant preharvest lighting effects (Jiang et al., 2023). Likewise, some commercial greenhouse experiments found that supplemental spectra changed individual sugars by sampling date without altering Brix overall, so sugar regulation by light appears to be dynamic and environment-dependent rather than uniform across all systems (Pérez-Romero et al., 2024; Roosta et al., 2024).

3.3 Light-induced regulation of organic acids, anthocyanins and flavor compounds

Light has especially strong effects on anthocyanin accumulation, which is one of the clearest mechanisms by which it improves strawberry fruit quality. Light is essential for anthocyanin accumulation in ripening fruit, and dual red and blue irradiation appears to optimally activate the flavonoid pathway by co-upregulating structural genes such as CHS, F3H, DFR, and ANS together with regulatory factors including FaMYB10 and FaHY5 (Wang et al., 2025). Blue light tends to induce upstream phenylpropanoid enzymes, whereas red light enhances proanthocyanidin production, showing that different wavebands regulate distinct branches of secondary metabolism rather than producing identical quality responses (Lauria et al., 2023; Wang et al., 2025).

Experimental studies broadly support the quality benefits of preharvest supplemental lighting, although the specific metabolite profile depends on the spectrum. Red light improves productivity and promotes anthocyanin accumulation in fruit, while blue, red, and red/blue combinations also increase anthocyanin concentration across cultivars, indicating that multiple spectra can stimulate pigmentation but with different strengths and accompanying effects on other metabolites (Lauria et al., 2023; Roosta et al., 2024). Under stress conditions, red and blue-red light also raise fruit anthocyanin levels, suggesting that light quality can preserve or enhance color development even when salinity or alkalinity constrains normal metabolism.

Light also regulates acidity and volatile flavor formation, which are critical for perceived eating quality. Supplemental light can increase titratable acids in some greenhouse systems, whereas LED supplementation combined with elevated CO₂ decreases titratable acidity, showing that acid responses are not uniform and depend on the broader production environment (Qiu et al., 2023; Tang et al., 2023). For aroma, red light promotes synthesis of furanones and esters, and blue or red postharvest LED exposure increases key aroma-related volatile esters, supporting a persistent light-triggered effect on flavor chemistry (Farneti et al., 2025; Wang et al., 2025).

Postharvest evidence further shows that light can continue regulating quality after harvest. Continuous red LED during storage increases anthocyanin and TSS while preserving firmness and reducing weight loss, whereas brief early LED exposure enhances anthocyanins and aroma-related VOCs during subsequent storage without major color changes, indicating that strawberries retain light responsiveness after picking (Farneti et al., 2025). Overall, light-induced fruit quality formation in strawberry reflects an integrated response in which photoreceptors, transcription factors, carbohydrate metabolism, pigment biosynthesis, acid balance, and volatile production are coordinately modulated by the intensity, duration, and spectrum of the light environment.

4. Artificial Light Supplementation Strategies in Strawberry Cultivation

4.1 Application of LED supplemental lighting in strawberry production

LED supplemental lighting has become a central strategy in strawberry production because it can compensate for low winter radiation and improve both productivity and fruit quality in protected systems. Across greenhouse studies, supplemental LEDs increased vegetative growth, marketable yield, soluble solids, and overall berry quality, especially during off-season production when natural light is limiting (Stuemky and Uchanski, 2020). Similar benefits were observed across multiple cultivars grown under different spectra, where artificial LED light enhanced early yield, increased total soluble solids, and raised anthocyanin concentrations, indicating that supplemental lighting can improve both commercial output and quality traits relevant to consumer acceptance (Roosta et al., 2024).

The effectiveness of LED supplementation depends on spectral design and production context rather than simply adding photons. In plastic greenhouse cultivation, ambient light supplemented with blue or blue-plus-red LEDs produced higher fruit output, whereas red or blue-plus-red supplementation promoted greater accumulation of organic acids and phenolic compounds, showing that different spectra can target yield and quality differently. In commercial and research greenhouses, blue and red LED combinations also increased flowering substantially and reduced second-quality fruit without compromising overall quality, supporting their practical use for improving production uniformity and marketable fruit proportion.

4.2 Effects of light duration and intensity regulation on yield and quality

Regulation of light duration and intensity is a major determinant of how effectively supplemental lighting translates into yield and fruit quality. In indoor strawberry production, extending the photoperiod from 12 to 16 h accelerated flowering and first harvest and increased fruit production by 372%–989%, while increasing PPFD mainly promoted vegetative growth and had comparatively little effect on fruit production, indicating that photoperiod can dominate reproductive performance in some systems (Park et al., 2023). Evidence from multi-tier vertical systems also showed that both light intensity and duration increased yield, and that longer lighting duration increased sugar content, although the economic return remained constrained by electricity cost (Swann et al., 2021).

Optimal duration and intensity are not universal, because cultivar and cultivation system alter the response. In forcing culture, a 12-h LED photoperiod increased leaf photosynthesis, accelerated flower bud differentiation, improved fruit quality, and produced the highest marketable yield, whereas longer than 12 h inhibited later floral development and reduced total yield. By contrast, under time-differential supplemental lighting in soilless greenhouse culture, the combination of lower supplemental intensity at $132 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a 16-h photoperiod produced the highest fruit yield and improved water and fertilizer use efficiency, showing that longer duration with moderate intensity can outperform higher-intensity strategies in other environments.

4.3 Integration of supplemental lighting with greenhouse environmental control

Supplemental lighting is most effective when integrated with broader greenhouse environmental control rather than used as an isolated input. Combining LED supplemental light with elevated CO_2 increased light-saturated photosynthetic rate, leaf area index, biomass, and yield, and also improved soluble sugar content while reducing titratable acidity, demonstrating a clear synergy between radiative and atmospheric management (Qiu et al., 2023). At the seasonal scale, this combined treatment raised yield by 51.3%, exceeding the effects of either elevated CO_2 or LED lighting alone, and therefore represents a strong strategy for improving winter-to-spring greenhouse productivity and sweetness (Qiu et al., 2023).

Integration with temperature and greenhouse control systems is equally important. In a subtropical forcing system, controlled-environment greenhouses increased yield relative to conventional houses, and adding daytime LED supplemental lighting produced a further increase, especially during winter periods of persistent cloudiness and low solar radiation, although benefits became limited in spring under high external radiation (Nakayama and Nakazawa, 2023). More intensive combinational control that included supplemental lighting, elevated CO₂, and regulated air temperature accelerated flowering, increased fruit number, and, when paired with movable beds and higher planting density, achieved more than a twofold increase in yield per unit land area, underscoring that lighting delivers its greatest value when embedded in whole-system greenhouse optimization.

5 Canopy Light Management and Cultivation Practices

5.1 Effects of leaf removal and canopy structure optimization

Canopy structure strongly determines how much radiation reaches strawberry leaves and fruits, and fruit quality changes measurably with fruit light exposure. Under field conditions, light incidence altered flavor and antioxidant content, and the response was genotype-dependent, indicating that canopy-opening practices such as leaf removal are most likely to be effective when they improve fruit exposure without overexposing sensitive cultivars. The same study found that cultivars with larger canopies compensated by producing longer peduncles, which helped maintain a similar proportion of exposed fruits despite canopy-size differences, showing that canopy architecture itself is a plastic determinant of fruit light interception.

Broader photobiology evidence supports canopy optimization as a quality-management tool because strawberry responses depend on how light is distributed through the plant rather than on total irradiance alone. Controlled-environment studies summarized in recent review work show that tailored light strategies can optimize fruit production and consumer-desired quality traits, while wavelength-specific effects on flavonoids vary enough that better canopy light penetration should be paired with spectral management rather than treated as a stand-alone intervention (Warner et al., 2021). This logic is reinforced by shading experiments showing that low light reduces photosynthetic rate, sugar synthesis, and commercial fruit yield, implying that canopy-thinning practices that relieve self-shading can improve assimilate supply to fruit as long as total leaf area is not excessively reduced (Choi, 2021).

5.2 Influence of plant density and training systems on light distribution

Plant density is one of the clearest cultivation variables affecting canopy light distribution in strawberry, and its effects extend to photosynthesis, fruit quality, and profitability. In southern Brazil, plant spacing altered photosynthetic efficiency, production, fruit quality, and economic return, with 5-15 cm spacing providing a practical compromise for the high-quality cultivar ‘Pircinque’. In alpine mountain production, lower density increased aboveground biomass, leaf photosynthetic rate, and the number of crowns and flower trusses per plant, while fruits from low density also showed a higher color index, consistent with improved within-canopy light penetration (Soppelsa et al., 2023).

Higher density, however, often increases yield per unit land area even when individual plants receive less light and produce smaller fruit. A recent review found positive linear relationships between density and hectare-scale yield across annual hill culture, protected systems, and matted rows, with no clear upper limit imposed by light competition in most experiments, likely because inter-row spacing still allowed acceptable interception (Menzel, 2024). In hydroponic and vertical systems, higher planting density similarly reduced yield per plant but increased yield per square meter, while light limitation inside vertical structures remained a key reason why optimum density depends on greenhouse irradiance and system configuration.

5.3 Application of reflective mulching and light redistribution materials

Reflective mulches and light-redistribution materials improve the light environment around the lower canopy and fruiting zone, where direct interception is often limited. In one of the clearest demonstrations, strawberries ripened over red mulch were about 20% larger and had higher sugar-to-organic-acid ratios and higher concentrations of favorable aroma compounds than fruit over black mulch, indicating that reflected red and far-red light can directly improve flavor-related chemistry. Highly reflective polythene mulches also increased growth and yield through

greater fruit size and number, while raising total ellagic acid and ascorbic acid concentrations, showing that reflected PAR can enhance both productivity and bioactive quality traits.

More recent work shows that the effect of mulch-based light management depends on the optical properties of the material used. In greenhouse winter production, white reflective mulch reflected far more PAR than red, olive, or black mulch and supported consistent saleable berry production, suggesting that highly reflective surfaces are useful where ambient light is seasonally limiting. Other light-redistribution materials have also shown strong promise: red light-selective plastic film improved photosynthetic performance, fruit weight, total sugar, and anthocyanin content, while rare-earth photoconversion films increased net CO₂ assimilation, soluble solids, soluble sugar, vitamin C, flavonoids, and yield by modifying spectrum, temperature, and greenhouse light transmission (Peng et al., 2020; Zhao et al., 2025).

6 Molecular and Physiological Mechanisms Underlying Light-Induced Sugar Accumulation

6.1 Regulation of photosynthetic carbon fixation pathways

Light-induced sugar accumulation in strawberry begins with enhanced source activity and more efficient allocation of newly fixed carbon from leaves to fruit. When light intensity declines, strawberry plants show lower photosynthetic rate, stomatal conductance, and sugar accumulation, indicating that reduced carbon fixation at the source directly limits the carbohydrate supply available for developing fruit (Choi, 2021). At the same time, greater daylight integrals increase the rate and amount of photosynthate translocation into individual fruits, showing that stronger leaf assimilation under longer light exposure improves sink loading as well as source production.

The fate of this additional carbon depends on how strawberry leaves partition assimilates between transportable sugars and temporary storage pools. Under high photosynthetic activity, carbon is first allocated to sucrose, but once leaf sucrose concentration exceeds storage capacity, excess carbon is diverted into starch, indicating that starch functions as an overflow product rather than the primary export form (Nakai et al., 2023). More broadly, fruit sugar accumulation depends on coordinated regulation of sugar transporters and metabolic enzymes that govern long-distance translocation, sink unloading, and post-translational control of carbohydrate metabolism, so light-driven increases in fixation must ultimately be coupled to these downstream allocation processes to raise fruit sweetness (Ren et al., 2023).

6.2 Light signaling pathways involved in fruit development

Beyond its role in carbon supply, light also acts as a developmental signal that directly regulates strawberry fruit maturation and sugar-related gene expression. Light-treated fruits accumulate more soluble sugar than dark-treated fruits, and this response is accompanied by stabilization of the ripening regulator FvMYB10, indicating that light promotes sugar accumulation partly through transcriptional and post-translational control during ripening. Blue-light receptors FvCRY1 and FvCRY2 provide a more direct mechanism, because their overexpression increases soluble sugar content and they bind promoters of sugar metabolism genes such as FvSFP9 and FvINV, with blue light enhancing their transcriptional activation capacity (Zhang et al., 2025).

Light signaling in fruit development also includes repressive modules that prevent sugar accumulation when photomorphogenic signaling is attenuated. FvCOP1 acts as a molecular brake by suppressing sugars, anthocyanins, and flavonoids through inhibition of downstream transcriptional activation mediated by FvHY5, FvRIF, and FvMYB10, and by ubiquitinating these regulators to reduce their stability (Bi et al., 2025). Far-red signaling likely contributes as well, because FxAPHY15 is strongly responsive to far-red light and peaks transcriptionally during the fruit turning stage while interacting with PIF3-related regulatory networks, supporting a role for phytochrome-mediated signaling in the transition from vegetative growth to fruit maturation.

6.3 Interaction between light signals and hormonal regulation

Light-induced sugar accumulation is closely integrated with hormone signaling, especially the balance between abscisic acid and auxin during ripening. Fruit grown under light accumulates more ABA than bagged fruit, whereas dark treatment delays sugar accumulation and softening, indicating that light promotes ripening in part by

sustaining ABA-associated developmental progression (Sun et al., 2024). Mechanistically, blue or red light combined with sucrose promotes detached ripening by increasing ABI4 expression, decreasing SnRK2.6 expression, and suppressing AUX/IAA11 and ARF6, consistent with activation of ABA signaling alongside inhibition of auxin signaling (Jiang et al., 2023).

This hormonal crosstalk extends to direct control of sugar transport and signaling outputs. ABA regulates sugar accumulation through the FaRIPK1-FaTCP7-FaSTP13/FaSPT module, in which ABA-enhanced FaRIPK1 interaction with FaTCP7 relieves repression of sugar transporter genes and thereby promotes soluble sugar accumulation during ripening. Light and ABA also converge, but not identically, on downstream ripening regulators: both induce FaMYB10 and enhance anthocyanin accumulation, yet their effects are additive rather than strictly linear, indicating partly independent pathways that intersect at common transcriptional targets controlling fruit maturation and quality formation.

7 Case Studies: Application of Light Management Technologies in Strawberry Production

7.1 LED spectrum optimization for improving strawberry sugar content and fruit quality

Case studies of LED spectrum optimization show that spectral composition can be used to target both sugar accumulation and visual fruit quality in greenhouse strawberries. In a four-cultivar greenhouse experiment, blue, red, and red/blue supplemental lighting all increased early fruit yield in most cultivars, while supplemental light also raised total soluble solids and anthocyanin concentration, indicating that spectrum selection can simultaneously improve sweetness-related and pigmentation traits (Roosta et al., 2024). A complementary preharvest study found that red LED supplementation produced the highest productivity and selectively enhanced anthocyanin accumulation, whereas blue and green light preferentially increased other primary and secondary metabolites, showing that different spectra shift fruit quality in different biochemical directions (Lauria et al., 2023).

Recent synthesis studies suggest that the most effective strategy is not a fixed wavelength but a phase-specific spectral program matched to crop development. Red-blue combinations are reported to improve photosynthetic efficiency and accelerate fruit maturation when applied at moderate photon flux and long daily duration, while dynamic spectral adjustment across vegetative growth, flowering, and maturation is proposed to better coordinate yield formation with sugar and anthocyanin accumulation (Wang et al., 2025). More broadly, controlled-environment evidence indicates that manipulating light intensity and spectral composition can substantially modify strawberry secondary metabolism and fruit antioxidant properties, although blue-light effects remain less consistent across studies than responses to mixed or red-dominant spectra (Figure 2) (Warner et al., 2021).

7.2 Supplemental lighting in greenhouse strawberry production under low-light conditions

Under winter and spring greenhouse conditions, supplemental lighting consistently improves strawberry growth and fruit quality when natural radiation is inadequate. A commercial greenhouse study using an hourly light integral strategy showed that supplemental LEDs increased daily light integral to about 10 mol m⁻² d⁻¹, raised canopy temperature by 1 °C-2 °C, and improved net photosynthetic rate, fruit yield per plant, soluble solids, and sugar-acid ratio, demonstrating that real-time light compensation can directly enhance both productivity and eating quality (Yang et al., 2024). Similar benefits were observed in a subtropical forcing system, where daytime LED lighting further improved dry matter accumulation and yield during cloudy winter periods, although the yield advantage became limited in spring when solar radiation was already high (Nakayama and Nakazawa, 2023).

Case studies also show that supplemental lighting is most effective when integrated with other greenhouse controls. In autumn-to-spring production, the combination of elevated CO₂ and LED supplemental light increased photosynthetic capacity, biomass, and yield, while also improving fruit soluble sugar content and reducing titratable acidity across the growth cycle (Qiu et al., 2023). Under full and deficit irrigation, supplemental lighting likewise increased fruit polyphenols early in the season and total sugar, glucose, and fructose later in the season, indicating that added light can stabilize or improve fruit quality even when water management differs (Xu et al., 2023).

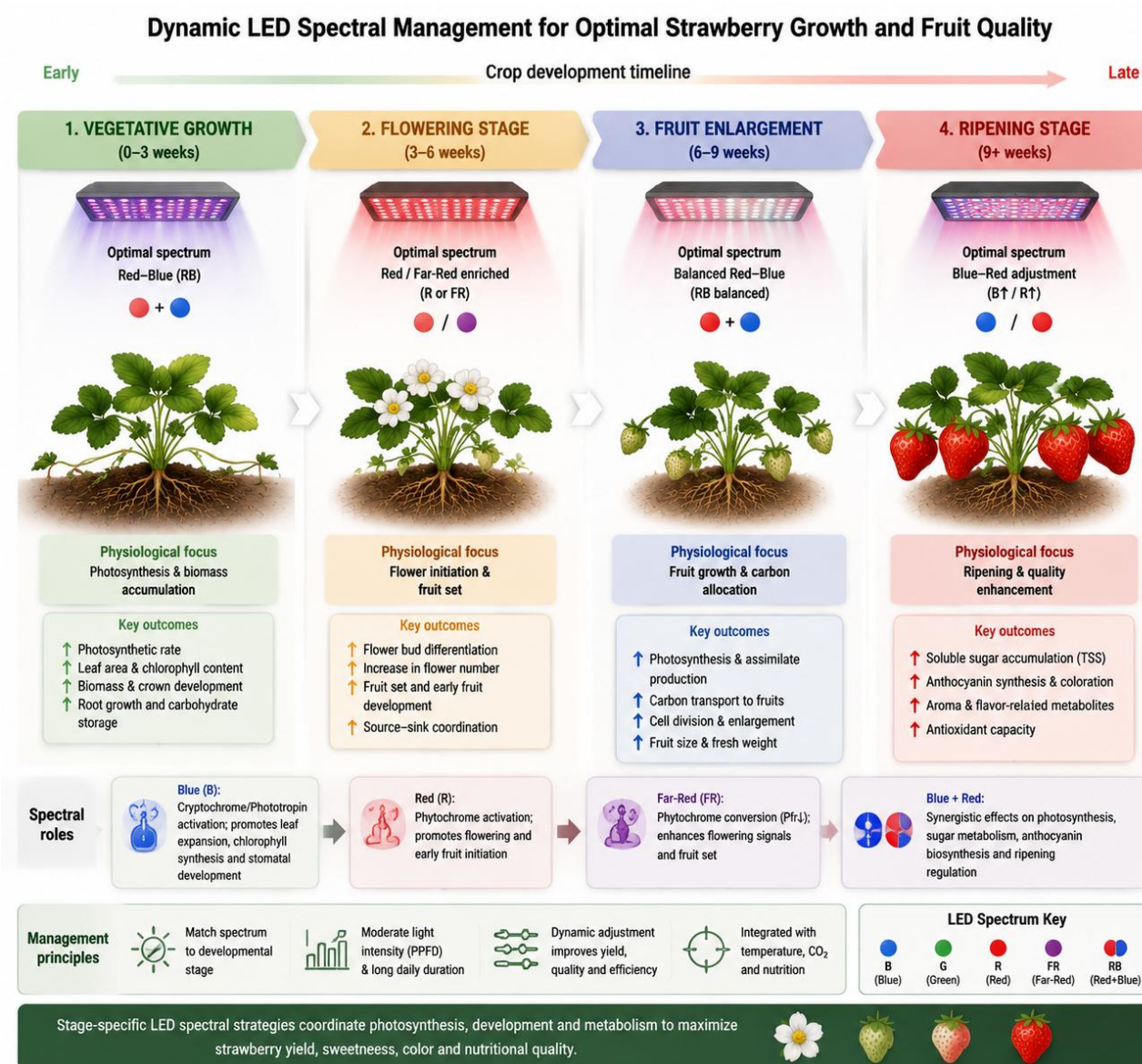


Figure 2 Developmental stage-specific LED spectral management strategy for optimizing strawberry yield and fruit quality

7.3 Canopy light optimization through leaf management and reflective mulching

Canopy light optimization depends both on plant architecture and on practices that increase fruit-zone light exposure. Field evidence shows that fruit light exposure changes strawberry flavor and antioxidant content, and that the magnitude of this response is cultivar-dependent, suggesting that leaf removal or canopy opening should be calibrated to genotype rather than applied uniformly. The same work found that cultivars maintained similar proportions of exposed fruit despite canopy-size differences by adjusting peduncle length, which highlights that canopy architecture itself influences how effectively management can redistribute light to the fruiting zone.

Reflective mulches provide a more direct case study of canopy light redistribution by increasing upward-reflected radiation into shaded fruit and lower canopy positions. In strawberry, highly reflective mulches increased growth and yield through larger fruit size and fruit number, and also increased ellagic acid and ascorbic acid concentrations, showing that improved reflected PAR can enhance both production and nutraceutical quality. More recent evidence indicates that mulch choice also affects fruit biochemical quality during ripening, with silver-black mulch outperforming paddy straw, black, and red mulches for fruit color and compositional traits, supporting reflective mulch as a practical tool for improving canopy light distribution and final fruit quality (Supreetha et al., 2024).

8 Future Perspectives and Conclusions

Future strawberry production will likely move from fixed supplemental lighting schedules to precision systems that regulate spectrum, intensity, and timing in response to plant demand and greenhouse conditions. Recent work on controlled environments identifies optimized spectral quality and spatial distribution as a promising route to improve yield, fruit quality, and resource-use efficiency, while emphasizing that dynamic and spatially adaptive lighting solutions will be essential for modern sustainable horticulture. This direction is reinforced by broader photobiology reviews showing that LEDs allow growers to tailor spectrum and intensity to crop needs and developmental stages, creating a practical basis for more precise regulation of strawberry growth and quality.

A second priority is the development of sensor-based and model-driven lighting control. Hourly light integral control has already shown that real-time monitoring of PPFD and temperature can determine when supplemental lighting should be applied or withheld, improving yield, soluble solids, and sugar-acid ratio under commercial greenhouse conditions. More advanced frameworks are now pointing toward remote monitoring, weather-linked forecasting, and centralized smart control, suggesting that future strawberry systems will combine sensor networks with predictive algorithms to regulate light proactively rather than reactively.

Stage-specific lighting is another major future direction because strawberry responses differ across vegetative growth, flowering, fruit development, and postharvest storage. Recent synthesis work argues that current reviews have often treated only part of the crop cycle and that a full developmental framework is needed to design stage-specific lighting strategies that improve both yield and quality. Consistent with this view, earlier review evidence identified unresolved questions on cultivar-dependent wavelength effects, blue:red ratios during vegetative and flowering phases, and flavonoid retention during storage and transport, all of which remain highly relevant for precision recipe design.

An additional frontier is dynamic lighting aligned with biological rhythms rather than static daily light delivery. Recent review evidence on circadian regulation shows that spectrum-tunable LEDs can now enable real-time control of light quality, intensity, and timing, and that dynamically combining these factors can coordinate biological rhythms with light-energy use more effectively than simple adjustments of intensity or spectrum alone. This suggests that future strawberry lighting systems should not only meet daily photon targets, but also test whether circadian-aligned light programs can improve sugar accumulation, metabolite balance, and energy efficiency in ways that fixed schedules cannot.

Future light management strategies will also need to fit within broader sustainability goals, because greenhouse production is energy-intensive and lighting is one of its most consequential inputs. Energy reviews show that greenhouses have substantial energy consumption and greenhouse gas emissions, and that energy-saving strategies in design and operation are therefore essential for sustainable crop production. Within that context, light regulation should be evaluated not only by its effect on yield and quality, but also by its contribution to whole-system energy conservation, carbon footprint, and environmental performance.

Low-carbon optimization provides a concrete framework for this integration. Multi-objective modeling work shows that supplemental lighting can be regulated against both photosynthetic performance and carbon-emission targets, reducing carbon emissions by as much as 14.85% while maintaining 95.49% of the net photosynthetic rate relative to light-saturation objectives. For strawberry systems, this implies that future lighting recipes should be selected by balancing fruit quality gains against electricity demand and carbon cost, rather than simply maximizing photon delivery.

Sustainable integration also includes combining light regulation with other resource-management practices. In greenhouse strawberry, supplemental light increased fruit polyphenols and sugars under both full and deficit irrigation, and the combination of silicate spray with LED lighting was recommended as a route to produce high-quality fruit while allowing deficit irrigation for water conservation. More broadly, informed management of sunlight through materials, structures, and monitoring can improve food quality and yield while potentially reducing water, energy, and pesticide use, indicating that artificial and natural light management should be treated as part of the same sustainability framework.

Another important sustainability perspective is that targeted light regulation may reduce dependence on chemical inputs and labor-intensive corrective practices. Preharvest red LED light has been shown to increase fruit yield and quality while improving tolerance to *Botrytis cinerea*, supporting the possibility that optimized light environments could contribute to future reductions in agrochemical use. At the industry level, broader strawberry production reviews also emphasize that future commercial systems will rely on new technologies, protected-environment systems, and management innovations to maintain high-quality production under mounting climatic and biological pressures.

The accumulated evidence indicates that light management is already a powerful tool for improving strawberry yield, sugar accumulation, pigmentation, and overall fruit quality, but the next advance will depend on moving from empirical recipes to mechanism-guided control. Existing reviews agree that artificial lighting can optimize fruit production and sensory quality, yet also stress that information remains limited on how specific light properties shape productivity and secondary metabolite accumulation in strawberry. Recent biotechnology-focused synthesis reaches a similar conclusion by emphasizing that strawberry quality formation is shaped by interactions among developmental stage, stress, and external regulation, and that modern tools such as omics, LED regulation, and gene-based approaches now offer a stronger basis for targeted intervention.

Several research gaps stand out clearly. One is the need for more work on underexplored spectral regions and treatment windows, especially preharvest UV-A, preharvest UV-C, and cultivar-by-temperature interactions under visible spectra. Another is the need for longer-term validation, because recent controlled-environment engineering work explicitly calls for studies on scalability across environments and long-term effects on plant health, yield stability, nutritional quality, and flavor characteristics.

Postharvest performance should also become a more central research target, because fruit quality benefits produced before harvest are only valuable if they persist through storage and transport. Current synthesis highlights rapid postharvest deterioration as a major constraint in strawberry and calls for more development of green prevention and control measures to support disease-free, high-quality fruit. This complements earlier calls to monitor flavonoid degradation after harvest and determine how long light-induced benefits are retained during storage and distribution.

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Review Article

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Seasonal Management Strategies for Improving Honey Production

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Received: 26 Jun., 2026

Accepted: 31 Jul., 2026

Published: 15 Aug., 2026

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Preferred citation for this article:

Xu J.J., 2026, Seasonal management strategies for improving honey production, Genomics and Applied Biology, 17(4): 240-253 (doi: [10.5376/gab.2026.17.0019](https://doi.org/10.5376/gab.2026.17.0019))

Abstract Honey production is strongly influenced by seasonal variations in floral resources, climatic conditions, and honeybee colony dynamics. Effective seasonal management strategies are essential for maintaining colony strength, optimizing foraging activity, and improving honey yield and quality. This review summarizes the key seasonal management approaches for enhancing honey production, including colony development regulation, nutritional supplementation, environmental adaptation, disease control, and advanced beekeeping technologies. During spring, stimulating colony expansion, preventing swarming, and synchronizing colony growth with major nectar flows are critical for maximizing honey collection. In summer, temperature regulation, supplementary feeding, and pest management help reduce heat stress and maintain colony productivity. Autumn and winter management focus on strengthening colonies, improving overwintering survival, and preparing for the next production cycle. Furthermore, precision beekeeping technologies, including environmental monitoring, intelligent hive systems, and data-driven management, provide new opportunities for optimizing seasonal decisions. Case studies of commercial honey production demonstrate that integrated seasonal strategies can significantly improve honey yield by coordinating colony development with nectar availability. Future research should focus on climate-smart beekeeping systems, genetic improvement, and the integration of artificial intelligence technologies to achieve sustainable and efficient honey production under changing environmental conditions.

Keywords Honey production; Seasonal management; Honeybee colony dynamics; Nectar flow; Precision beekeeping

1 Introduction

Modern apiculture depends on more than maintaining bee colonies alive; it requires aligning colony management with the annual biological cycle of the hive and the environmental conditions that shape nectar and pollen flows. Honey bee health and productivity are strongly linked to management practices, and large evidence syntheses show that colony management is one of the most frequently studied applied themes in beekeeping, alongside pathogen control (Gratzer et al., 2025). This importance is especially clear in regions where honey production remains below potential despite favorable ecological conditions, because low yields are often tied to suboptimal colony management, limited technical adoption, and weak alignment between beekeeping operations and seasonal resource availability (Nganso et al., 2024). Seasonal management therefore matters not only for colony survival, but also for profitability, pollination service continuity, and the efficient conversion of floral resources into marketable honey. At the biological level, colonies shift between summer and winter physiological states, and successful overwintering depends on seasonal transitions in brood rearing, nutrient storage, and the production of long-lived winter bees adapted to thermoregulation and spring restart (Knoll et al., 2020). For this reason, seasonal hive management is best understood as a strategic framework that coordinates feeding, colony strength, queen status, disease prevention, and harvest timing with predictable seasonal transitions in colony metabolism and resource use.

The relationship between seasonal environmental change and honey production is direct, multidimensional, and increasingly unstable under contemporary climate conditions. Beekeeping is one of the most weather-sensitive agricultural activities, and honey yield responds to short-term effects on bee flight and foraging as well as longer-term seasonal effects on plant phenology and blooming dynamics (Vincze et al., 2024). Seasonal conditions influence not only nectar secretion and foraging opportunities, but also colony growth, because the amount, richness, and diversity of pollen collected by honey bees vary significantly across seasons and are

positively associated with brood development and colony performance. These relationships help explain why climate anomalies can sharply reduce production: in a Mediterranean monitoring study, drought and high temperatures shortened flowering by three weeks, reduced hive weight gain from 18.92 kg to 7.67 kg between years, and increased food stress while altering pollen spectrum and honey characteristics. Seasonal stress also carries over into winter survival, as warmer and drier conditions in the preceding year have been linked to increased winter mortality, highlighting that honey production is shaped not only by harvest-season conditions, but also by how colonies enter and endure the non-productive season.

These environmental pressures make adaptive seasonal management a primary requirement for modern beekeeping. Modeling and survey studies indicate that seasonality affects colony dynamics through changes in foraging behavior, resource access, brood production, and lifespan, while climate change is altering the timing and severity of these seasonal processes in ways that can increase losses or weaken spring colonies (Chen et al., 2025). Warmer autumns and winters can extend late-season flight, skew colony age structure toward older bees, and raise the risk of spring failure, which means overwintering strategies developed under historically colder conditions may no longer remain adequate in many regions (Rajagopalan et al., 2024). At the practical level, this has shifted attention toward interventions such as seasonal feeding, improved queen and comb management, stronger autumn preparation, and in some contexts relocation, cold storage, water supplementation, or shade management to buffer climate stress. Research from Kenya likewise suggests that management can partly mitigate climate effects, with water supplementation associated with lower livestock decrease during the dry and hot season, reinforcing the view that seasonal strategies must increasingly function as climate-adaptation tools rather than routine calendar tasks.

Against this background, the objective of research on seasonal hive management is shifting from documenting losses toward developing predictive, regionally adapted, and evidence-based strategies to improve both colony resilience and honey yield. Recent studies show that productivity is influenced by multiple interacting factors, including hive number, harvest frequency, beekeeper experience, weather, and management intensity, while machine learning and remote monitoring tools are beginning to identify winter climatic variables and in-hive indicators that can forecast production outcomes and guide timely interventions. Parallel work using environmental and machine-learning models finds that winter temperature, humidity, wind, pressure, and vegetation signals can predict honey production classes and support targeted responses such as adjusted feeding or supplementary heating (Ramirez-Diaz et al., 2025). Even so, the literature remains uneven: reviews highlight regional gaps, strong dependence on local environmental context, and the need for broader integration of floral diversity, pest pressure, and management variables into decision-support frameworks (Gratzer et al., 2025). Accordingly, this paper positions seasonal management as an integrative concept linking colony biology, environmental variability, and applied beekeeping practice, with the aim of clarifying how season-specific interventions can be used to improve honey production under increasingly variable ecological conditions.

2 Seasonal Dynamics of Honeybee Colonies and Honey Production

2.1 Seasonal changes in colony population development

Honeybee colony population development follows a pronounced seasonal cycle driven by brood rearing, food availability, and queen laying dynamics. Modeling and empirical studies agree that colony populations fluctuate periodically across the year, with brood and adult populations typically increasing through spring and early summer when pollen and nectar are abundant, then declining after mid-summer as environmental conditions and forage become less favorable (Chen et al., 2025). Field observations in southwestern Saudi Arabia similarly showed that adult bee populations were highest from early March to late June, while brood populations peaked from February to June, confirming that seasonal colony expansion is closely synchronized with the main flowering period.

Seasonal transitions also shape colony physiology and overwintering capacity, not just colony size. Colonies shift from short-lived summer workers to long-lived winter bees, and this transition is strongly associated with reduced brood rearing in autumn and declining pollen supply, which helps colonies survive winter and resume brood

production in the next cycle (Knoll et al., 2020). At the same time, simulation studies indicate that seasonality in queen egg-laying rate can either support or suppress colony survival, and brood-based indicators can reveal stress from spring and autumn forage gaps earlier than adult bee abundance or honey reserves alone.

2.2 Influence of seasonal floral resources on honey yield

Seasonal variation in floral resources directly affects honey production because nectar and pollen availability determine both foraging opportunity and colony nutritional status. Large-scale floral resource datasets show that flowering phenology, nectar output, pollen production, and sugar availability vary through the year and can be quantified on a daily basis, making seasonal resource continuity a central determinant of potential honey yield. In farmed landscapes, nectar supply shows strong seasonal fluctuations, with major peaks in May and July but clear deficit periods in March, June, and late summer, indicating that the timing of forage availability can constrain honey production even where total annual floral resources appear adequate.

Seasonal honey yield also depends on the diversity and composition of flowering plants available to colonies. In semi-arid Tanzania, the number of foraging bees varied significantly among months in parallel with flower abundance, and foraging increased with plant diversity, supporting the view that diverse plant communities sustain more continuous honey production across the year (Mramba, 2025). More region-specific studies reach the same conclusion: linden species can substantially improve nectar and pollen supply in June and July, but their short flowering periods and year-to-year shifts in flowering onset mean that complementary plant species are needed to stabilize seasonal resource availability and reduce fluctuations in honey flow.

2.3 Seasonal environmental factors affecting foraging behavior

Seasonal environmental conditions strongly regulate honeybee foraging behavior, and weather effects are often immediate enough to alter daily nectar and pollen intake. Honeybee activity is more sensitive to weather variation than bumblebee activity, and predictive modeling shows that most observed variation in bee egress rate can be explained by temperature and solar radiation, highlighting how closely foraging depends on short-term atmospheric conditions. Review evidence further indicates that temperature and light intensity are generally positively associated with nectar collection, whereas rainfall, humidity, and wind reduce collection efficiency, so seasonal weather patterns influence honey production through both bee behavior and floral nectar secretion (Vincze et al., 2024).

The effects of environmental conditions on foraging also vary by season and time of day. In Egypt, honeybees showed a bimodal daily foraging rhythm, significant temperature dependence, and the highest seasonal abundance of foragers in spring, with effective flight occurring within a microclimatic window of about 20 °C-28 °C. Autumn observations in Chandigarh likewise found that pollen foraging peaked around midday under moderate temperatures and then declined later in the afternoon, while the main pollen source near the colonies strongly shaped the daily pattern of activity, illustrating how local forage and season-specific weather interact to determine field performance.

3 Spring Management Strategies for Enhancing Honey Production

3.1 Early spring colony recovery and population expansion

Early spring colony recovery depends first on rebuilding brood production before the main nectar flow begins. Spring pollen supplementation consistently advances brood rearing and increases early worker production, with supplemented colonies starting brood rearing earlier and producing more workers by late April or early May than pollen-limited colonies. This nutritional effect is especially important when natural pollen is scarce, because unsupplemented colonies in pollen-poor environments rear less brood and later enter the season with smaller adult populations (Figure 1) (Hoover et al., 2022; Ulgezen et al., 2025).

Targeted feeding before or at the start of spring also improves colony build-up at the whole-colony level. Late-winter supplemental feeding increased net hive weight, bee numbers, and brood cell numbers by April, showing that early nutritional support can accelerate spring development under commercial conditions. More recent field evidence similarly found that a pollen substitute diet can improve early-spring population growth,

capped brood area, colony weight, and vitellogenin-linked nutritional status, although natural pollen still remains nutritionally superior to any artificial replacement.

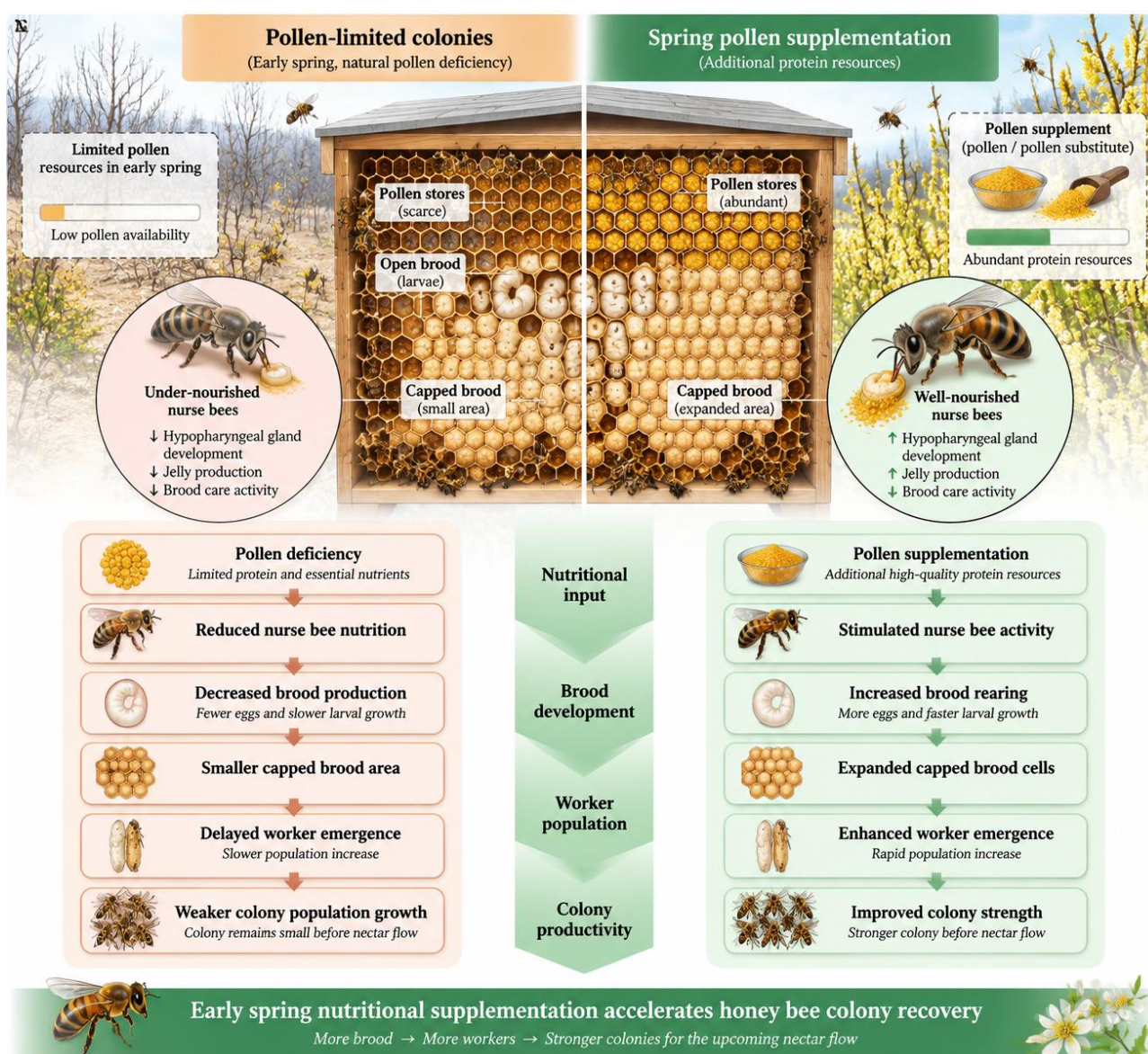


Figure 1 summarizes the nutritional mechanism underlying early spring colony recovery. When pollen availability is limited, nurse bees experience insufficient protein intake, resulting in reduced brood production and delayed worker population expansion

3.2 Swarm prevention and colony strength optimization

Swarm prevention is a core spring management objective because swarming reflects strong colony growth but usually diverts bees away from harvestable honey production. In managed systems, swarming is generally undesirable because it reduces colony productive capacity and can directly lower honey yield if the departing swarm is lost (Puškadija et al., 2023). Proactive swarm-season management therefore aims to maintain large but controlled colonies, allowing beekeepers to preserve strong field populations while retaining the option to make splits and increase profitability.

Colony strength optimization in spring also requires controlling biological stressors that weaken expanding populations. Evidence syntheses show that swarm control, methods of starting new colonies, and regular Varroa management all contribute to lower colony losses, and no single intervention is sufficient without integration into broader colony management (Gratzer et al., 2025). Experimental work supports this integrated view: colonies managed under best-management-practice systems had lower Varroa infestation, lower viral infection, and lower

mortality, while prolonged time above the economic mite threshold was associated with increased viral infection and mortality.

3.3 Preparation for major nectar flow periods

Preparing colonies for major nectar flows requires aligning spring population growth with upcoming resource availability rather than maximizing short-term harvest too early. Colonies need abundant pollen and nectar in spring to rebuild food stores, support brood production, and increase population, and their ability to exploit these spring resources helps determine later seasonal success. This timing is environmentally sensitive, because brood rearing in early spring is regulated by both temperature and photoperiod, and mismatches between these cues and floral availability could impair colony growth as seasonal patterns shift (Ulgezen et al., 2025). Preparation for nectar flow also depends on avoiding management decisions that weaken brood production before mass flowering. In intensive farmland systems, favoring honey storage over brood production in spring intensified later pollen shortage effects, and colonies managed this way ultimately produced less honey during the sunflower flow and had lower overwinter survival. Accordingly, avoiding or limiting spring honey harvest can improve later productivity, while colonies established with greater early-season brood resources are more capable of producing honey during the main summer nectar flow (Puškadija et al., 2023).

4 Summer Management Strategies Under High Temperature Conditions

4.1 Temperature regulation and hive microclimate control

Summer management under high temperature conditions begins with maintaining a stable hive microclimate, because brood development depends on narrow thermal limits and colonies experience physiological stress when those limits are exceeded. The brood chamber should be kept near 33 °C-35 °C, while temperatures above 38 °C increase metabolic damage risk, making thermoregulation a central management priority during hot weather. At the colony level, honey bees buffer heat through coordinated behavioral mechanisms, including fanning, evaporative cooling, and adjustments in bee density, but these mechanisms require labor and can divert effort from foraging and brood care. Field evidence shows that external hive conditions strongly influence summer performance. In hotter months, shaded colonies outperformed unshaded colonies because unshaded hives experienced elevated temperature stress that reduced foraging activity, pollen collection, colony growth, and honey production, supporting the practical use of summer shading in hot climates (Taha et al., 2026). Extreme heat can also exceed the effective limits of colony thermoregulation: when maximal shaded air temperatures intermittently exceeded 40 °C, greater within-hive temperature fluctuations were associated with declining colony populations, even though average brood temperatures remained near the optimal range (Chen et al., 2025).

High summer temperatures also threaten queen performance, not just worker activity and brood growth. Queen sperm viability appears safe within an approximate 15 °C-38 °C range, and exposure outside that window can contribute to fertility loss associated with queen failure, which makes temperature control during both field management and queen transport important in hot seasons. More broadly, recent heat-stress synthesis indicates that high temperatures inhibit foraging, fecundity, and normal thermoregulation while also increasing susceptibility to disease and parasites, reinforcing the need to pair microclimate control with broader summer colony support. A practical implication is that summer microclimate management should combine site selection, shading, ventilation, and water availability rather than relying on hive placement alone. Honeybee colonies maintain brood temperature through an interlaced set of physiological and behavioral responses across a wide environmental range, but that resilience is graded rather than unlimited, so management that reduces heat load helps preserve colony labor for nectar collection and brood maintenance. This is especially relevant as temperature is a major determinant of colony behavior, physiology, and performance under fluctuating climatic conditions, making summer microclimate regulation a direct route to sustaining productivity (Taha et al., 2026).

4.2 Nutrition supplementation and colony maintenance

Summer nutrition management is most important during nectar and pollen dearth, when high temperatures and forage scarcity jointly suppress brood rearing and colony growth. Reviews of honeybee nutrition emphasize that seasonal scarcity of bee flora reduces brood rearing, honey production, and overall colony development, and that

proper colony management during dearth periods is therefore essential for maintaining productive colonies. Artificial feeding is used as an alternative to migration during such periods, with the goal of maintaining colony parameters well enough to take advantage of the next floral-rich season, although no universally accepted standard commercial diet yet exists (Paray et al., 2020). Experimental studies support the value of supplementation in summer and autumn. Colonies fed liquid and protein supplements showed improved open brood area, sealed brood area, bee density, and honey area, with the strongest responses reported for super-protein supplementation (Nafi and Ghani, 2024). Commercial feeding trials likewise found that two pollen-containing diets produced the largest colonies and the heaviest bees, while some pollen-free diets still outperformed sugar-only feeding, indicating that diet formulation matters but that supplementation can remain beneficial even when pollen is absent from the recipe (Ricigliano et al., 2022).

Nutritional support in summer also has important health implications because poor forage quality can amplify pathogen pressure and weaken later recovery. Colonies under nutritional stress had lower brood and adult bee populations and higher *Nosema* infection levels than supplemented colonies, and these deficits persisted into spring, showing that inadequate nutrition can create both short- and long-term losses in colony strength. More broadly, nutritional stress and *Nosema* together had severe effects on colony strength, supporting the view that summer feeding is not only a productivity measure but also part of preventive colony health management. For colony maintenance, the key aim of summer feeding is to stabilize brood production, worker condition, and food reserves until natural forage improves. During periods of adverse weather and restricted foraging, egg laying and brood rearing decrease, but their extent depends partly on stored food availability, which is why supplementary diets are used to buffer the colony through stressful conditions (Paray et al., 2020). Optimizing diet composition remains an active area of research, because essential amino acid balance, rather than crude macronutrient content alone, appears to predict bee weight and later colony size more reliably (Ricigliano et al., 2022).

4.3 Disease and pest management during summer

Summer disease and pest management is dominated by control of *Varroa destructor*, because mite populations can rise rapidly during brood-rearing periods and compromise the bees that must survive into autumn and winter. Seasonal field studies show that mite populations rebound faster after summer and fall treatments than after winter or spring treatments, often exceeding the economic threshold in less than three months, which makes close summer monitoring especially important. This seasonal timing matters because in temperate climates *Varroa* populations peak around August, and mites parasitizing late-summer brood damage the developing winter bees that determine colony survival in the following season (Plamondon et al., 2024). Integrated pest management is therefore more effective than relying on a single treatment. *Varroa* control efficacy varies with season, temperature, humidity, colony condition, and local context, so no single strategy works for every beekeeper, and treatment choice should be matched to the specific management situation (Jack and Ellis, 2021). In Europe, seasonal brood interruption has shown strong potential as a long-term *Varroa* strategy, and its consistent use may even reduce dependence on winter treatments while supporting more sustainable control.

Recent summer-treatment trials reinforce the value of intervening before winter bees are produced. In Canada, a Formic Pro summer treatment tended to reduce *Varroa* infestation below the fall economic threshold and significantly reduced colony mortality, even though colony-level viral loads did not decline (Plamondon et al., 2024). In mild-climate systems, combining oxalic acid vaporization with a forced summer brood break increased mite mortality fivefold and significantly reduced mite populations, offering an additional nonwinter control option when brood is otherwise continuously present. Summer pathogen management should also include attention to *Nosema ceranae*, whose seasonal dynamics overlap with colony growth and food stress. Infection, prevalence, and spore viability are highest in spring and summer, and high infection levels are associated with reduced bee populations and food stores, indicating that summer colony maintenance should include surveillance for this pathogen where it is locally important. Because *N. ceranae* shows high pathogenicity during spring and summer and is associated with poor colony growth, integrated measures such as supplemental feeding, sanitation, selective breeding, and timely treatment can support better colony condition through the hottest part of the season (Emsen et al., 2020).

5 Autumn and Winter Management for Sustainable Honey Production

5.1 Autumn colony recovery and winter preparation

Autumn management should prioritize producing a strong overwintering population, because colonies survive winter through the transition from short-lived summer workers to long-lived winter bees. This transition is closely associated with declining brood rearing and falling pollen supply in autumn, which helps generate the diutinus workers needed for winter survival and spring restart (Knoll et al., 2020). Colony condition entering winter also matters at the whole-hive level, since overwintering success depends on multiple interacting environmental, physiological, and social factors rather than any single preparation step. In practical terms, autumn preparation should aim to ensure adequate colony size, food reserves, and queen quality before temperatures fall. Recent synthesis suggests that a colony entering winter should weigh at least about 20 kg in autumn and contain roughly 4,000-5,000 bees, while survey evidence shows that young queens are associated with better colony survival and fewer queen-related losses (Oberreiter and Brodschneider, 2020). Autumn decisions should also account for within-colony cues that affect the timing of winter-bee production, since late-summer requeening shifted the appearance of winter bees later than in unrequened control colonies.

Autumn recovery also depends on controlling late-season biological stress before colonies enter the most vulnerable part of the year. Disease and pest pressure must be controlled before overwintering, and Varroa is especially damaging because it both vectors viruses and reduces fat stores in pre-winter bees (St. Clair et al., 2022). Observational evidence further shows that colonies with many bees showing crippled or deformed wings during the foraging season had higher winter losses, making visible late-season brood-health problems an important warning signal (Oberreiter and Brodschneider, 2020). Management quality in autumn appears to translate into measurable differences in winter survivorship, although optimal practice varies by region and operation type. Across U.S. survey data, higher-quality management was associated with lower winter mortality, and modest improvements in practice still produced meaningful survival gains. That regional variation matters, because stressors, winter severity, and even the performance of specific practices differ across climates and seasons, so autumn preparation is most effective when adapted to local conditions rather than treated as a fixed checklist (Steinhauer et al., 2021).

5.2 Winter hive protection and energy conservation

Winter hive protection is fundamentally an energy management problem, because honey bees do not hibernate and must consume stored food to produce heat while confined in the hive. Colonies rely on clustered workers feeding on finite stores to maintain a stable internal temperature through winter, which is why this season is often the highest-risk period for colony survival. At the mechanistic level, winter thermal stability depends not only on insulation by the cluster mantle but also on active endothermic heat production by core bees, showing that colony heating carries a real metabolic cost. Because winter thermoregulation is energetically expensive, preserving food stores is central to sustainable management. Adequate nutritional reserves are required for colonies to thermoregulate effectively, and colonies with at least 30 kg of honey stores in a temperate Pennsylvania climate had a 95% chance of surviving winter (St. Clair et al., 2022). More broadly, winter survival depends on both the availability of honey reserves and the colony's ability to consume them, while average winter mass loss indicates a steady seasonal drain on stored energy.

Physical hive protection can reduce that energetic burden, although its benefits depend on context. In a randomized field experiment, covered colonies consumed less food and had 22.5% higher survival than uncovered colonies when other recommended overwintering practices were already in place (St. Clair et al., 2022). Material choice also affects the winter microclimate, as polyurethane hives maintained higher inner temperatures and more optimal relative humidity than wooden hives, supporting the idea that better insulation can reduce the energy required for thermoregulation. Winter monitoring should increasingly focus on integrative colony traits rather than simple survival checks. Population size, social thermoregulation, and honey reserves appear to function as key predictors of overwintering failure, and tracking these traits may provide early warning of collapse before visible mortality occurs. Precision monitoring is especially promising here, because current information technologies could extend from honey-flow surveillance into winter tracking of temperature and other indicators linked to colony status.

5.3 Spring transition management after overwintering

Management after overwintering should focus on the risky transition from a broodless or brood-restricted winter state to renewed brood production. In temperate regions, this late-winter to early-spring period appears to be one of the colony's most vulnerable phases because resources remain scarce just as brood rearing begins to raise nutritional demand. This seasonal transition differs fundamentally from autumn, because autumn reduces brood and produces winter bees, whereas early spring rapidly increases brood rearing under still-limited resource conditions (Ulgezen et al., 2025). The timing of brood onset is therefore a critical management concern after winter. Colonies resume brood rearing in late winter to build a worker force for spring bloom, but premature brood onset can deplete energy reserves and increase stress, whereas late onset reduces the colony's ability to exploit early floral resources. Experimental evidence indicates that brood onset is mainly driven by increasing temperature and modulated by photoperiod, suggesting that abnormal warming patterns could shift spring colony phenology in maladaptive ways.

Spring transition management should therefore balance rapid recovery with conservation of the remaining winter buffer. The shift from a broodless state to brood rearing increases resource demand while temperatures may still fluctuate, and severe winter depletion makes this transition especially dangerous because the energetic cost of brood initiation draws from limited stores that cannot easily be replenished (Ulgezen et al., 2025). More generally, surviving winter bees must both forage and rear the first new brood in spring, so successful post-winter management depends on preserving enough population strength and stored energy to support both tasks simultaneously. A practical implication is that post-overwintering management should rely on close observation of colony thermoregulation and brood status, not just external weather cues. Stable high comb temperatures and low daily temperature amplitudes within the winter cluster are reliable indicators of brood rearing activity, allowing less invasive detection of spring buildup. This is useful because the timing of spring brood reactivation strongly influences later growth, reproduction, and survival, so early recognition of mistimed or weak colony buildup can support better intervention decisions.

6 Advanced Management Technologies for Improving Honey Yield

6.1 Precision beekeeping and environmental monitoring technologies

Precision beekeeping is designed to monitor individual colonies in ways that reduce resource use and strengthen productivity, making it especially relevant for managing seasonal variation in honey flows and colony stress (Catania and Vallone, 2020). Recent reviews add that smart hives can remotely provide real-time information, reduce the need for frequent physical inspections, and lower colony disturbance while still supporting management decisions (Hadjur et al., 2022). The most useful environmental monitoring variables are hive weight, internal temperature, humidity, and external weather conditions, because these measurements track nectar intake, reserve consumption, and thermoregulatory status (Cecchi et al., 2020). Continuous weight monitoring can identify the beginning and end of nectar flow, while internal temperature patterns can reveal reduced thermoregulation and the need for timely intervention (Alleri et al., 2023).

Field applications show that these systems can detect direct environmental effects on honey production. In one precision apiculture platform, a drop in external temperature coincided with a short period of no honey production, and wind peaks above 5 m s⁻¹ were also associated with reduced production (Catania and Vallone, 2020). More broadly, sensor fusion approaches that combine hive and environmental data can provide insight into colony status, colony-environment interaction, and climatic influences on performance (Cecchi et al., 2020). Advanced systems increasingly integrate sensor outputs with inspection data and beekeeper actions to improve forecasting rather than only description. Healthy Colony Checklist models combine sensor streams, meteorological data, and field inspections, while digital systems can also record management events such as feeding, harvesting, and disease treatments to better interpret colony responses (Alleri et al., 2023). This makes precision beekeeping useful not only for detecting problems, but also for aligning interventions with seasonal nectar flows and reducing unnecessary apiary visits (Hadjur et al., 2022).

6.2 Nutritional regulation and functional feed application

Nutritional regulation has become more important because forage shortages are increasingly common, and supplemental feeding is now a routine management input during dearth or stressful production periods (Ricigliano et al., 2022; Bogaert et al., 2025). Reviews indicate that artificial feeding can serve as an alternative to migration and help maintain colony parameters well enough to benefit from the next floral-rich season, although no universally accepted balanced commercial diet yet exists (Paray et al., 2020). Experimental feeding studies show that diet composition strongly affects colony performance. In commercial colonies under extended forage dearth, artificial feed improved colony performance and health, and pollen-containing diets produced the largest colonies and the heaviest bees (Ricigliano et al., 2022). Other trials likewise found that soybean-enriched pollen substitute diets increased brood area, bee strength, foraging efficiency, and honey yield relative to control feeding (Ullah et al., 2021).

Current evidence also suggests that feed quality depends on specific nutrient balance rather than crude protein content alone. In one commercial study, diet macronutrient content was not correlated with colony size or health biomarkers, whereas essential amino acid deficiencies relative to leucine were associated with lower bee weight and smaller colonies. This supports a shift from generic supplementation toward functional feed design based on bioactive nutrient requirements and operation-specific goals (Ricigliano et al., 2022). Newer work indicates that nutritionally complete pollen-replacing diets can support brood production for much longer than standard commercial feeds when natural pollen is absent. A complete diet supported continuous brood production from May to October, whereas colonies on a commercial diet declined sharply in brood production after 36 days and died out. The same study identified isofucosterol as a critical micronutrient, because omitting it significantly reduced brood production and caused adult neuromuscular dysfunction (Bogaert et al., 2025).

6.3 Genetic improvement and queen bee management

Genetic improvement is increasingly treated as a practical management technology because it supports colony productivity, health, and adaptation while preserving locally suitable bee stocks (Maucourt et al., 2021). Modern breeding programs rely on breeding value estimation because environmental conditions strongly mask colony phenotype, so queen selection must separate hereditary merit from apiary effects.

Long-term breeding data show that this approach can improve commercially relevant traits. In a Canadian selection program, progress averaged 0.63 kg per year for honey production and 164 brood cells per year for spring development (Maucourt et al., 2021). Large-scale European breeding data similarly indicate considerable gains in honey yield and other desirable traits after the adoption of BLUP-based evaluation, without increased inbreeding coefficients.

Queen management is central to translating genetic gain into field performance because breeding success depends on accurate selection, standardized testing, and mating control. Standard methods emphasize that ranking queens by breeding value is the basis for improvement, and that controlled mating remains a major challenge because queens naturally mate with many drones over long distances. Queen and drone rearing, artificial insemination, and controlled mating stations therefore remain major tools for adapting colonies to changing environments, pests, and production demands.

Genomic tools now extend this framework by improving selection accuracy and supporting diversity management. Large-scale genomic prediction increased breeding value accuracy for honey yield compared with pedigree-based evaluation, and routine queen genotyping can also verify subspecies identity and monitor genetic diversity within breeding populations (Bernstein et al., 2022). Even so, evidence for molecular selection remains stronger for productivity and workability traits than for disease-related traits, so phenotypic testing still needs to be paired with genetic data across diverse environments.

7 Case Studies: Seasonal Management Practices in Commercial Honey Production

7.1 Spring management for maximizing acacia honey production

In acacia-based systems, spring management is most effective when colony buildup is completed before the short major bloom, because acacia often serves as the primary honey source and rewards strong colonies entering

bloom at peak population. Evidence from spring feeding studies supports this strategy: colonies supplemented in spring began brood rearing earlier and produced more workers by late April or early May, while feeding with stimulatory syrup from late March to the start of white acacia flowering increased colony strength, brood rearing, and honey productivity under weak supporting forage conditions. Management during the acacia period should also avoid overexploiting colonies before subsequent flows, because intensive use for spring-summer honey collection can slow brood growth and weaken later performance. This trade-off appears in commercial feeding and migration systems as well: colonies stimulated in late March and moved first to rapeseed and then to acacia produced 14.67% to 45.49% higher profit, but broader farmland evidence shows that maximizing spring honey production at the expense of brood can reduce later honey yield and halve overwinter survival.

7.2 Summer stress management in honeybee colonies

Summer case studies show that heat stress management is fundamentally a labor-allocation problem inside the colony, because workers shift toward cooling behaviors such as fanning and water collection when ambient temperature rises. Colony-level tracking further shows that heat stress increases overall activity and causes bees to reorganize away from the brood area, indicating that summer management should reduce heat load before thermoregulation begins to compete with normal colony tasks (Figure 2).

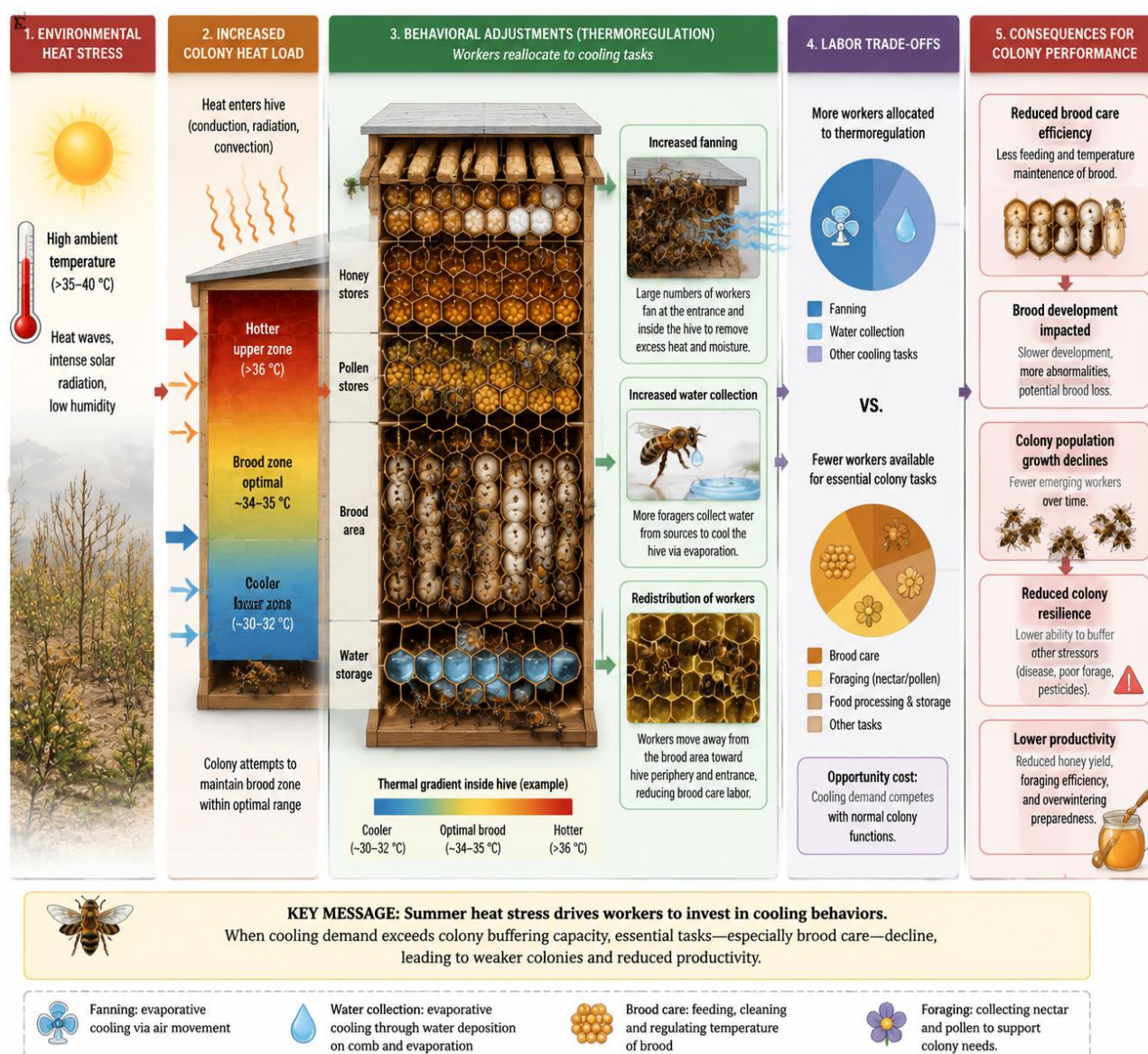


Figure 2 Mechanistic framework illustrating labor reallocation and colony-level consequences of summer heat stress in honey bees

The production consequences of severe summer heat depend on whether colony thermoregulation remains effective. Under simulated heat waves, colonies increased foraging by about 70% and shifted effort toward water collection without reducing nectar and pollen flow, but this likely relied on recruiting backup workers and could reduce buffering capacity against additional stressors. Under more extreme field conditions, maximal temperatures above 40 °C and greater within-hive thermal fluctuations were associated with declining colony populations, while fan-based cooling alone reduced internal temperature by only 1 °C-2 °C and produced minimal summer performance gains, suggesting that passive ventilation by itself is often insufficient in very hot climates (Chen et al., 2025).

7.3 Integrated seasonal management in migratory beekeeping systems

Migratory beekeeping systems illustrate how seasonal management can increase honey yield when colony movement is synchronized with floral phenology across regions. By definition, migratory beekeeping is the seasonal transport of hives, traditionally used to maximize honey production by exploiting differences in flowering time across altitudes and latitudes (Martínez-López et al., 2022). Recent field surveys from Himachal Pradesh similarly found that well-planned floral calendars and flexible migration reduced feed requirements during long dearth periods, while strategic seasonal movement increased honey yield and profitability across apiary sizes.

The main limitation is that migratory gain depends on integrated health and resource management, not movement alone. In commercial systems, summer honey production was the only clearly profitable activity once management and overwintering costs were included, and greater summer and fall forage availability was identified as part of the solution for both honey yield and overwinter survival. At the same time, migratory operations differ sharply in nutrition, pesticide exposure, transport stress, queen replacement, and pathogen control, and these factors can increase pathogen prevalence if not actively managed across the season (Martínez-López et al., 2022).

8 Future Perspectives and Conclusions

Future climate-smart beekeeping systems will need to manage colonies around season-specific climate risks rather than relying on fixed calendars, because weather effects on survival and productivity vary strongly by season and location. Recent modeling further suggests that warmer autumns and winters can extend flight activity, skew overwintering colonies toward older bees, and increase spring failure risk, which means adaptive overwintering strategies will become more important as climates warm. A practical climate-smart direction is to combine landscape management with adaptive in-hive interventions. Landscape evidence shows that grassy-herbaceous land can buffer the negative effects of warm, wet climates on summer nectar intake, while surveys from hot, dry regions indicate that water supplementation can reduce seasonal livestock decrease by up to 10%. Additional adaptation options already identified by beekeepers include apiary relocation, shade provision, and supplementary feeding, but these strategies appear to work best when matched to local climatic stressors rather than applied uniformly.

Climate-smart systems will also need stronger winter adaptation protocols, because both unusually warm and unusually cold winters can increase colony loss. Cold storage is one promising option: simulations indicate it could reduce overwintering losses under future warming, and field data suggest it can be a viable, lower-cost strategy for maintaining colony survival under warmer fall conditions. Beekeeper adaptation remains constrained by information gaps and institutional support, especially in regions where climate impacts are already evident but extension systems are weak. This makes place-based management frameworks a priority for future development, since the main reported drivers of honey decline differ across regions, from drought and irregular flowering to temperature extremes and pest pressure.

Digital technologies are likely to become central to seasonal hive management because precision beekeeping already supports remote, optimized monitoring of colony conditions and faster responses to internal stress signals. Current systems can continuously track hive weight, temperature, humidity, sound, and related environmental variables, giving beekeepers a more complete view of colony state without disruptive inspections. The strongest

near-term direction is multimodal sensing linked to predictive decision support. Reviews indicate that single parameters are informative but that simultaneous monitoring of multiple variables gives a fuller picture of colony status, and smart-beehive research is now moving from basic reporting toward predictive analytics and behavioral inference. Future systems are therefore expected to combine multiple sensor types with embedded machine learning, anomaly detection, and open benchmarking datasets to improve real-time forecasting across seasons.

Field studies already show that digital monitoring can translate into production-relevant decisions. Precision apiculture platforms have linked drops in honey production to lower external temperature and strong wind events, and they can identify the start and end of production, guide supering decisions, and warn of swarming risk. Broader IoT syntheses similarly conclude that continuous remote data streams support early problem detection, more targeted interventions, and better resource efficiency than routine inspection alone. The main barriers are no longer proof of concept, but deployment and usability. Current reviews emphasize the need for real-world validation, beekeeper-centered design, cost-effectiveness, and stronger collaboration between engineers and domain experts if smart hive systems are to scale beyond fragmented pilot studies (Šabić et al., 2025). Adoption will also depend on solving implementation costs, data security, and beekeeper training, since these remain recognized obstacles to integrating IoT tools into conventional practice.

The main conclusion across this literature is that sustainable honey production will depend on integrated seasonal management, not isolated practices, because colony health and productivity reflect interacting effects of climate, forage, pests, and beekeeper decisions. Large observational datasets further show that better overall management is associated with lower winter losses, even though no set of practices eliminates all risk (Steinhauer et al., 2021).

A clear research priority is improving evidence for region-specific forage resilience. Recent African work shows that forage availability is shaped by both season and land use, with agricultural lowlands offering fewer and less diverse resources during dry periods, while exotic plants now dominate much of the recorded diet. Future work should therefore compare the nutritional value of native and exotic forage across seasons and test how forage design can support colony productivity under climate change. Another priority is building more robust evidence pipelines for management innovation. Existing practice reviews show that most field interventions have focused on Varroa and late-season management, while also identifying major regional research gaps that limit evidence-based advisory services. Research infrastructure itself also needs attention, because methods that extend winter experimentation can alter learning and thermoregulation, making validation under realistic colony conditions essential.

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Review Article

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Effects of Fruit Thinning on Yield and Quality of Loquat

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Received: 13 Jul., 2026

Accepted: 17 Aug., 2026

Published: 29 Aug., 2026

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Preferred citation for this article:Zhang G.S., 2026, Effects of fruit thinning on yield and quality of loquat, Genomics and Applied Biology, 17(4): 254-268 (doi: [10.5376/gab.2026.17.0020](https://doi.org/10.5376/gab.2026.17.0020))

Abstract Fruit thinning is an important horticultural practice for regulating fruit load, improving resource allocation, and enhancing fruit yield stability and quality in loquat (*Eriobotrya japonica* Lindl.) production. Excessive fruit setting often leads to intense competition for assimilates, resulting in reduced fruit size, uneven development, and inferior commercial value. This review summarizes recent advances in the effects of fruit thinning on loquat yield formation, fruit quality improvement, and physiological regulation mechanisms. Fruit thinning can optimize the source-sink relationship by reducing fruit competition, increasing individual fruit weight, improving external appearance, and promoting the accumulation of soluble sugars, organic acids, vitamins, and bioactive compounds. Furthermore, thinning regulates photosynthetic performance, hormone metabolism, and carbon-nitrogen balance, thereby facilitating fruit expansion and quality formation. The effects of thinning intensity and timing vary among cultivars and cultivation environments, highlighting the need for precise management strategies. Case studies demonstrate that the integration of fruit thinning with fertilization, irrigation, canopy management, and digital orchard technologies can significantly enhance production efficiency and economic benefits. Future research should focus on developing cultivar-specific thinning models, exploring molecular mechanisms underlying fruit load regulation, and applying precision agriculture technologies to achieve sustainable and high-quality loquat production.

Keywords Fruit thinning; Loquat (*Eriobotrya japonica*); Yield regulation; Fruit quality; Source-sink relationship

1 Introduction

Loquat (*Eriobotrya japonica* Lindl.) is a subtropical evergreen fruit tree native to China and now cultivated commercially in more than 30 countries, including production regions in the Mediterranean, Australia, and Central Europe (Shafiq et al., 2025). Its fruit is valued for attractive flavor, juiciness, and a rich nutritional profile that includes carotenoids, phenolics, vitamins, minerals, and other bioactive compounds, which has increased both consumer interest and research attention. At the same time, the crop remains underexploited relative to its biological and commercial potential, with the fruit still consumed mainly fresh and lacking extensive industrial utilization (Shah et al., 2023). In several producing regions, growers have increasingly recognized the economic importance of loquat and expanded commercial orchards, yet productivity and fruit marketability remain constrained by cultivar characteristics, environmental adaptation, and postharvest fragility. Many traditional loquat cultivars bear relatively small fruit and produce lower yields than major rosaceous fruit crops such as apple, pear, and peach, which has slowed wider industry expansion and intensified demand for practical orchard management strategies that can improve fruit size and output without waiting for long breeding cycles. Market acceptance of loquat depends strongly on visual and eating quality, and fruit with suitable soluble solids, balanced acidity, low firmness, good flesh-to-seed ratio, and attractive size are more competitive in fresh markets. Cultivar evaluations under Mediterranean conditions further show that fruit size, soluble solids, seed traits, and ripening time vary substantially among genotypes, indicating that improving loquat production requires not only varietal selection but also crop-load regulation adapted to local production systems. This need is becoming more urgent because recent reviews note that loquat productivity is also being affected by climatic change and environmental stress, while the fruit's short shelf life and sensitivity to physiological disorders reduce the margin for error in orchard management and harvest quality.

Fruit thinning has long been used in horticultural production to regulate crop load by removing part of the developing reproductive structures so that the remaining fruits receive a greater share of assimilates and mineral

nutrients (Wei et al., 2021). Across fruit crops, thinning is regarded as a core management practice because natural fruit drop alone rarely achieves the balance between yield quantity and market quality required in commercial orchards. Broad reviews of thinning research show that its principal effects arise through crop-load adjustment, with fruit size generally increasing as thinning intensity increases, although the response is modified by factors such as wood age, flower quality, within-cluster competition, canopy position, and the timing and method of thinning. Thinning can improve a first group of commercially decisive quality traits-including size, colour, firmness, and sugar-acid characteristics-but excessive reduction in crop load can create trade-offs with total yield and must therefore be optimized for local market goals rather than maximized indiscriminately. Experimental evidence from other fruit trees supports this general pattern. In peach, repeated fruit thinning during early development improved individual fruit weight, yield, internal and external quality, and leaf resource-use efficiency, while late thinning was less effective (Zhang et al., 2024). In pear, hand thinning increased fruit weight, diameter, height, and soluble solids, and although immediate yield could decline, thinning helped stabilize production over years and increased the proportion of marketable fruit. In loquat specifically, thinning has been studied at both flower and fruit stages. Earlier work showed that fruit thinning increased fruit growth and sugar accumulation, but also raised the incidence of purple spot, indicating that quality improvement can be accompanied by physiological risks. More recent studies confirm that loquat thinning is an essential management practice because the species tends toward heavy fruiting, and reducing competition among reproductive sinks can produce larger, sweeter, and more uniform fruit with better consumer appeal (Nordi et al., 2025). Flower-bud thinning at full bloom in the cultivar ‘Precoce de Itaquera’ improved overall fruit quality when four buds per cluster were retained, whereas keeping more buds increased cluster weight and total yield, clearly demonstrating the central agronomic trade-off between fruit quality and crop quantity in loquat production.

Against this background, studying the effects of fruit thinning on loquat yield and quality is important both scientifically and practically. From a physiological perspective, thinning provides a tractable way to modify source-sink relations, fruit set, and subsequent fruit enlargement, and loquat research increasingly links these orchard-level responses to developmental processes such as early cell division and shoot vigor. From a production perspective, growers urgently need management protocols that improve the performance of existing cultivars, because breeding alone has not solved the combined problems of small fruit, low yield, and inconsistent quality. Thinning is also relevant to orchard profitability because larger, higher-value fruit generally obtain better prices, even when hand thinning increases labor costs, and because proper crop-load regulation can support more regular cropping and better return bloom in subsequent seasons. Nevertheless, the benefits of thinning in loquat cannot be separated from important constraints. Responses vary with cultivar, site, climate, and thinning timing or intensity, and improvements in sugar accumulation or rapid fruit growth may increase susceptibility to disorders such as purple spot, while postharvest perishability remains a major bottleneck for market expansion. Future research should therefore move beyond asking whether thinning works and focus instead on how to optimize stage, intensity, and method for specific cultivars and environments; how thinning interacts with pruning, nutrition, and preharvest sprays; and how quality gains in the orchard translate into storability, disorder resistance, and supply-chain performance. Additional opportunities lie in improving the utilization of removed unripe fruit, since thinned fruits contain recoverable bioactive compounds and their revalorization could offset management costs while reducing orchard waste. Overall, fruit thinning appears to be a key tool for reconciling yield regulation with market-oriented quality improvement in loquat, and systematic evaluation of its effects is essential for developing more efficient, sustainable, and profitable loquat cultivation systems.

2 Fruit Development Characteristics of Loquat and Theoretical Basis of Fruit Thinning Regulation

2.1 Flowering, fruit set characteristics and yield components of loquat

Loquat has a distinctive reproductive calendar among rosaceous fruit trees, with flower bud formation beginning in summer, blooming occurring in autumn to early winter, and fruit ripening taking place in spring or early summer. This phenology exposes flowering and early fruit set to low temperature, rain, wind, and reduced pollinator activity, which makes the fruit-setting process especially sensitive to orchard environment and

pollination conditions. Fruit set in loquat depends on the normal sequence of pollen deposition, pollen germination, pollen tube growth, and ovary viability, so any climatic disturbance during bloom can reduce the conversion of flowers into retained fruit. Field studies under Mediterranean conditions further show that minimum temperature significantly affects initial and final fruit set, while humidity and precipitation during bloom can suppress blossoming and reduce fruit retention.

Yield formation in loquat therefore depends not simply on flower abundance, but on the interaction among genotype, flowering traits, fruit set efficiency, and the proportion of fruit that remain to harvest. Considerable cultivar variation has been reported: in one multi-year trial, 'Gold Nugget' showed the highest mean initial fruit set, final fruit set, and productivity among four cultivars grown in the same environment. Rootstock effects also contribute to yield components, because the number of flower buds per cluster, flower number, and final fruit set differed significantly among quince rootstocks, with Quince-C producing higher values for these reproductive traits (Akkuş and Polat, 2021). At the developmental level, loquat fruit growth is not uniform across stages; pulp thickens steadily, whereas rapid early fruit enlargement before the Z02 stage is closely associated with strong seed expansion, indicating that final yield and fruit size are shaped early in fruit development (Lin et al., 2025).

2.2 Fruit load and nutrient allocation

In loquat, fruit load directly alters the internal distribution of assimilates because fruit acts as a dominant sink during development (Assefa and Debella, 2020). Experimental work with field-grown loquat trees showed that as fruit develops, photosynthate translocation to the roots declines markedly, especially from the period when fruit reaches about 50% of final size until the onset of color change. During this same period, carbohydrate concentrations in roots are reduced and root development is strongly inhibited, indicating that actively growing fruit competes effectively with belowground organs for available carbon. This pattern is especially important in loquat because fruit growth occurs in winter, when non-shoot growth is also active, so competition between reproductive and vegetative sinks becomes unusually direct (Reig et al., 2013).

The broader source-sink literature supports this interpretation and helps explain why excessive crop load often reduces both fruit quality and tree vigor. When sink demand is too low, leaves accumulate non-structural carbohydrates and photosynthesis becomes feedback-limited, as shown in low-crop-load apple trees (Yang et al., 2021). When sink demand is high, however, carbon export to fruit is favored at the expense of vegetative growth, and fruit-bearing citrus trees show reduced shoot growth because developing fruits accumulate carbon that would otherwise support new flushes. Loquat appears to follow the same general rule, but with an added hormonal component: heavy fruit load is associated with increased ABA, reduced IAA in roots, and depressed root respiration, showing that crop load regulates not only carbon partitioning but also growth through coordinated metabolic and hormonal signals (Figure 1).

2.3 Theoretical basis and technical principles

The theoretical basis of fruit thinning in loquat is the regulation of the source-sink balance so that the remaining fruits receive more assimilates, mineral nutrients, and growth-promoting capacity per fruit (Assefa and Debella, 2020). This principle is especially relevant in loquat because fruit size is a major production constraint, and both domestication studies and functional analyses indicate that sugar metabolism, hormone signaling, and fruit size-related genes are central to fruit development. At the cellular level, fruit weight in loquat is more strongly associated with cell size than with cell number, which means that reducing competition among fruit can theoretically favor enlargement through enhanced cell expansion rather than only through increased cell division. This framework is consistent with molecular evidence that brassinosteroid-related regulation, including EjbZR1-mediated repression of cell enlargement pathways, contributes to final fruit size formation.

Technically, fruit thinning is an exercise in crop-load optimization rather than simple fruit removal, because excessive retention depresses fruit size and quality while excessive thinning can sacrifice yield or destabilize postharvest performance (Sidhu et al., 2022). Studies across fruit crops show that earlier thinning generally produces better outcomes for fruit size, soluble solids, and return bloom than later thinning, supporting the principle that competition should be reduced before the most critical stages of sink establishment and fruit

enlargement (Bound, 2023). Modeling work in apple likewise shows that fruit weight is jointly determined by thinning time, crop load, flower-bud formation, and shoot growth, reinforcing that thinning intensity must be matched to canopy vigor and production targets rather than applied uniformly. In loquat cultivation, this means that thinning should focus on adjusting panicle or fruit number early enough to improve assimilate availability to retained fruit while preserving a crop load that sustains total yield, return flowering, and stable orchard productivity over successive seasons (Su et al., 2021). In sum, loquat fruit thinning rests on a clear physiological logic: the crop's unusual flowering season, variable fruit set, and strong fruit sink demand make crop-load regulation central to both yield formation and fruit quality. Across the available evidence, the most defensible conclusion is that thinning works best when it is treated as targeted source-sink management rather than as a purely mechanical reduction in fruit number.

Effects of Fruit Load on Source–Sink Relationships and Carbon Allocation in Loquat (*Eriobotrya japonica*)

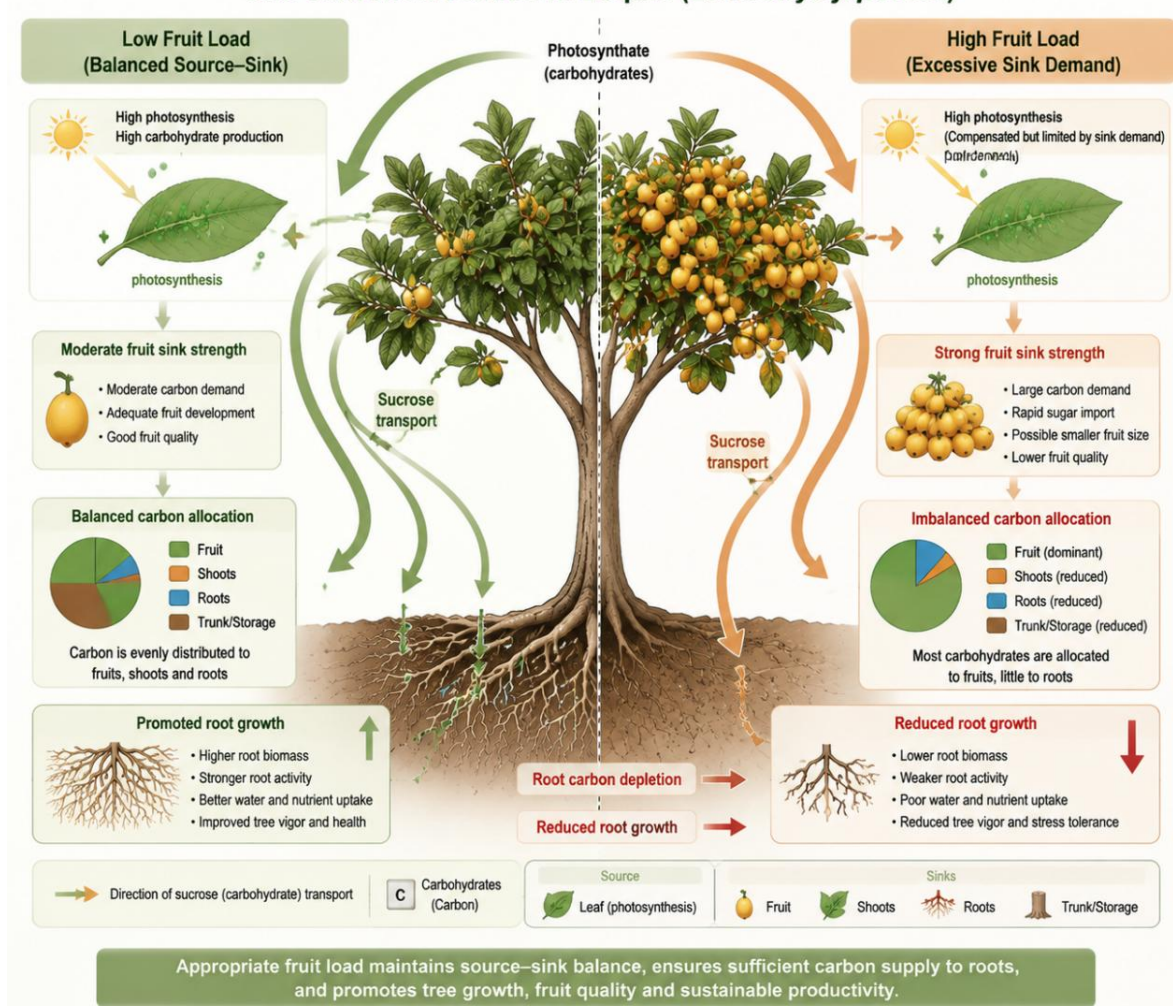


Figure 1 Source-sink regulation of carbon allocation under different fruit loads in loquat

3 Effects of Fruit Thinning on Yield Formation in Loquat

3.1 Effects of fruit thinning on individual fruit weight and fruit size

Fruit thinning clearly increases individual fruit weight and fruit size in loquat, because reducing the number of competing sinks allows more assimilates to be directed to the retained fruit. Early loquat studies directly showed that thinning increased fruit size, and later work confirmed that fruit size is a central determinant of commodity value and profitability in this crop. Recent field evidence in ‘Precoce de Itaquera’ further indicates that stronger flower-bud thinning can produce larger and sweeter fruit, with the best overall fruit-quality response obtained when only four buds per cluster were retained (Nordi et al., 2025).

The size response is also reflected in chemical thinning studies, which show that loquat fruit enlargement depends on both treatment efficacy and developmental timing. Application of naphthaleneacetic acid at 20 mg L⁻¹ about 10-15 days after anthesis was reported as the most effective treatment for thinning and increasing average fruit size, while NAAm applied at the end of bloom increased fruit diameter by an average of 11% to 18% depending on dose. This response is biologically plausible because loquat fruit weight is tightly associated with fruit dimensions across genotypes, and larger fruits are consistently favored by the market (Kodad et al., 2022).

3.2 Effects of fruit thinning on yield per unit area and yield components

The effect of fruit thinning on yield per unit area is more complex than its effect on fruit size, because thinning usually reduces fruit number while improving the marketable proportion of the crop. In loquat, the highest cluster weight and total yield were obtained under the lightest thinning treatment, with 12 buds retained per cluster, even though fruit quality was better at lower bud numbers. Similarly, chemical thinning with high NAA doses produced the largest fruit but also the lowest yield per tree, showing that excessive crop reduction can shift the balance too far from yield formation toward fruit enlargement.

From the perspective of yield components, fruit thinning mainly acts by changing fruit set, fruit number per panicle or tree, and average fruit mass. In ‘Precoce de Itaquera’, fruit set was significantly influenced by thinning intensity, while in ‘Algerie’ loquat heavier thinning slightly improved packout but did not compensate for the substantial yield loss caused by reducing fruit number per panicle. More broadly, yield per unit area in fruit crops is the product of yield per plant and plant number, so in loquat orchards the contribution of thinning to area-based productivity depends on whether gains in fruit mass and market grade can offset the decline in fruit number per tree (Haque and Sakimin, 2022).

3.3 Effects of thinning timing and intensity on yield regulation

The regulatory effects of thinning depend strongly on when thinning is performed and how severe it is. Loquat is usually hand-thinned relatively late, but this has been described as expensive and of limited usefulness because late execution reduces the opportunity to redirect resources during early fruit development. By contrast, chemical thinning at the end of bloom or shortly after anthesis appears more effective for regulating crop load early enough to improve fruit growth, and treatment date was explicitly identified as a determinant of thinning efficacy in loquat. In practice, this means that timing is not a minor technical detail but a central variable controlling the final balance between fruit number and fruit size.

Thinning intensity also has to be optimized rather than maximized. In loquat under deficit irrigation, reducing crop load to one, two, or three fruits per panicle did not generate enough value to compensate for the associated yield loss, and four fruits per panicle gave the highest revenue. Comparable evidence from other fruit crops points in the same direction: low crop loads generally produce heavier fruit, but very high or very low thinning intensity can destabilize yield, whereas medium crop loads often provide the best compromise between size and production consistency (Sidhu et al., 2022). Overall, yield regulation in loquat should therefore target an optimal crop load, not the strongest possible thinning, with timing and severity adjusted to cultivar, orchard conditions, and market objectives. In summary, fruit thinning in loquat consistently improves individual fruit weight and fruit size, but its effect on total yield depends on the trade-off between reduced fruit number and improved fruit mass and grade. The most defensible conclusion is that early, moderate thinning is usually more effective for regulating yield formation than either late thinning or excessively severe fruit removal.

4 Effects of Fruit Thinning on Fruit Quality Formation in Loquat

4.1 Effects of fruit thinning on external fruit quality traits

Fruit thinning improves the external commercial quality of loquat mainly by increasing fruit size and fruit mass. In the recent ‘Precoce de Itaquera’ study, the strongest flower-bud thinning treatment produced an overall improvement in fruit quality, with four buds per cluster giving larger fruit (Nordi et al., 2025). Earlier work on loquat also showed that thinning was necessary because natural crop load produces many low-caliber fruits, and thinning to four fruits per panicle resulted in greater fruit length, width, and weight.

Chemical thinning studies support the same pattern and add information on appearance and maturity. Application of naphthaleneacetic acid 10-15 days after anthesis increased average fruit size and also improved coloration while advancing harvest time (Agustí et al., 2000). NAAM treatments likewise increased fruit diameter by 11% to 18%, improved grading, and promoted earlier harvest, showing that thinning affects not only size but also market presentation and earliness.

4.2 Sugar-acid composition and flavor quality

Fruit thinning generally improves sweetness-related traits in loquat, although the response is not uniform across studies. In ‘Precoce de Itaquerá’, maintaining four buds per cluster produced larger and sweeter fruit, and a higher number of flower buds reduced soluble solids content. A separate thinning study also found that fruit thinning increased sugar contents, indicating that reduced sink competition favors sugar accumulation in the retained fruit.

The balance between sugars and acids, which is central to eating quality, also tends to improve after thinning or thinning-like crop regulation. In the same Brazilian study, pH and ripeness ratio were negatively associated with higher bud number, indicating that stronger thinning improved the sugar-acid balance important for consumer acceptance. Chemical thinning with naphthaleneacetic acid improved total soluble solids concentration (Agustí et al., 2000), although one cultivar trial reported that thinning intensity did not significantly affect pH, titratable acidity, or total soluble solids, so the compositional response appears cultivar- and condition-dependent rather than universal.

4.3 Nutritional quality and bioactive compounds

Evidence on nutritional quality shows that thinning changes fruit composition beyond sugars and acids, particularly through effects on mineral distribution. Fruit thinning significantly altered the mineral composition of loquat fruit (Gariglio and Agustí, 2005), and the most intense treatments increased potassium but reduced iron in flesh tissue at colour break. Thinning also reduced several mineral concentrations in the rind, especially K and Fe, which increased the concentration gradient between flesh and rind tissues.

These compositional changes are relevant because quality improvement can be accompanied by physiological costs. Fruit thinning has been linked to higher purple spot incidence, and the association appears to involve both increased sugar accumulation and altered solute gradients during rapid fruit development. Broader loquat quality studies also indicate that crop-regulating treatments can enhance bioactive substances such as phenolics, flavonoids, and carotenoids while improving the sugar-to-acid ratio and aroma compounds, which supports the view that sink regulation can reshape secondary metabolism as well as external and sensory quality (Zhang et al., 2025). Overall, fruit thinning improves external fruit quality most consistently, especially fruit size, mass, grading, and earliness. Its effects on flavor and nutritional composition are generally positive but less uniform, and excessive thinning can increase purple spot risk even as it enhances sweetness and some compositional traits.

5 Physiological and Metabolic Mechanisms Underlying Fruit Thinning-Mediated Improvement of Loquat Quality

5.1 Regulation of leaf photosynthetic characteristics by fruit thinning

Fruit thinning changes leaf photosynthetic behavior primarily by altering the source-sink ratio between leaves and developing fruits. Source-sink balance is a major determinant of carbon partitioning in fruit trees, and thinning directly modifies this balance by reducing sink demand. In orchard systems, this shift can improve canopy light distribution and gas exchange, and a meta-analysis in apple showed that thinning significantly increased leaf net photosynthetic rate, stomatal conductance, and transpiration while also improving fruit quality traits (Junna et al., 2021). For loquat, this framework is physiologically relevant because sugar translocation from leaves is essential for fruit development, and impaired translocation can compromise sink growth (Sotiras et al., 2019).

The photosynthetic response to thinning is not uniformly stimulatory, because excessive sink reduction can cause feedback inhibition in leaves. In nectarine, thinned trees showed lower net photosynthesis associated with stomatal limitation and transient sugar accumulation in leaves, indicating that an increased source-sink ratio can temporarily exceed drain capacity (Andrade et al., 2019). Peach experiments after fruit removal similarly found

that low sink demand reduced net photosynthetic rate, closely linked to lower stomatal conductance and accompanied by damage to PSII-related components. Comparable work in olive showed that high leaf-to-fruit ratios increased leaf saccharide content and depressed photosynthesis through feedback inhibition, especially when assimilate export was constrained. These results suggest that in loquat, the quality benefit of thinning is more likely to come from optimizing, rather than maximizing, leaf carbon supply to fruit.

5.2 Effects of fruit thinning on hormonal regulation networks

Fruit thinning also acts through hormonal regulation networks because fruit set, early fruit growth, and later maturation are all under strong phytohormone control. Across fleshy fruits, auxin and gibberellin are the core signals promoting fruit set and early growth, while cytokinin supports early cell proliferation and final fruit size (Zhang et al., 2026). More broadly, fruit development proceeds through coordinated crosstalk among auxin, gibberellin, cytokinin, ABA, and ethylene, rather than through any single hormone acting alone. Since thinning changes sink number and developmental competition among fruit, it likely shifts this hormonal balance by altering which fruits maintain growth-promoting signals and which enter arrest or abscission.

The mechanistic basis for this view is supported by studies showing that hormone pathways directly regulate fruit enlargement through cell division and expansion. Auxin and GA act together to promote these processes after fertilization, and their interaction is mediated by ARF/IAA and DELLA signaling modules. Cytokinin is also mechanistically linked to fruit size, because lowering endogenous CK reduced pericarp thickness, cell division, and single-fruit weight while repressing auxin- and GA-related genes. In a broader fruit-size framework, thinning is recognized as a cultivation practice that interacts with hormonal and environmental regulation of final fruit phenotype. For loquat, this implies that thinning improves quality not only by reallocating assimilates, but also by favoring hormonal states that sustain retained fruit growth and maturation.

5.3 Effects of fruit thinning on carbon and nitrogen metabolism and resource allocation

The clearest metabolic effect of thinning is on carbon allocation. Fruit biomass accumulation and metabolite formation depend on photosynthesis and carbon export from source leaves, and thinning increases carbon supply per retained fruit by reducing competition among sinks (Paz Covarrubias et al., 2021). Early developmental stages appear especially sensitive: in nectarine, thinning mainly altered fruit metabolic composition early in development, and early sugar, organic acid, and phenylpropanoid intermediates could distinguish fruits exposed to different source-sink conditions. Peach studies reached a similar conclusion, showing that adequate thinning created early metabolic shifts that later translated into superior fruit quality, consistent with a metabolic priming effect.

Nitrogen metabolism and whole-tree resource allocation also respond to crop-load manipulation, but the response is more complex than for carbon alone. Source-sink manipulation can trigger redistribution of both photosynthate and nitrogen in perennial crops, and stored C and N reserves help buffer temporary imbalances between assimilate supply and sink demand. In pistachio, late-season declines in photosynthesis under high sink demand were associated with lower leaf N, suggesting N remobilization toward kernels (Marino et al., 2023), whereas in kiwifruit a low-crop-load “feast” treatment increased fruit nitrogen concentration relative to a high-crop-load “famine” treatment. However, carbon sufficiency does not automatically improve every metabolic trait: severe sink reduction in grape caused large plant-level losses of sugars, organic acids, and aroma precursors without improving their balance in ripe fruit. In loquat, the most plausible interpretation is therefore that thinning improves quality when it creates a balanced redistribution of carbon and nitrogen to retained fruit, rather than an extreme reduction in sink demand. Overall, the physiological basis of fruit thinning in loquat is a coordinated adjustment of photosynthetic supply, hormonal signaling, and carbon-nitrogen partitioning. The evidence supports moderate, developmentally timed thinning as a way to improve fruit quality by strengthening retained fruit without inducing the metabolic inefficiencies that can follow excessive sink removal.

6 Different Fruit Thinning Strategies and Their Integrated Effects on Loquat Cultivation

6.1 Characteristics and applications of manual fruit thinning techniques

Manual fruit thinning remains the most direct and controllable crop-load regulation method in loquat. Commercial loquat trees often set excessively, so thinning is required to obtain marketable fruit size rather than relying on

natural adjustment alone. In practice, hand thinning is usually done during early fruit development or after fruit set, and traditional operations retain only a limited number of fruit per panicle to reduce sink competition and improve fruit growth. This method is valued because it allows precise selection of fruit number and position within each cluster, which is difficult to achieve with less selective approaches. The main constraint is labor demand, since hand thinning is slow, costly, and dependent on trained workers, which limits its efficiency at larger production scales (Figure 2).

Loquat experiments consistently show that manual thinning improves external fruit quality, but the optimal intensity depends on the balance between fruit size and retained yield. In ‘Precoco de Itaquera’, maintaining four flower buds per cluster produced the best overall fruit-quality response, whereas retaining more buds increased cluster weight and yield. Across multiple loquat cultivars, thinning to four fruit per panicle also resulted in superior fruit length, width, and weight, confirming that stronger hand thinning generally favors fruit enlargement. Even so, the practical target is not the most severe thinning possible, because loquat performance also varies with cultivar, climate, and timing of intervention. Evidence from other fruit crops points to the same compromise, with moderate hand thinning at an early stage often giving high fruit quality without the disproportionate yield loss caused by very severe crop reduction.



Figure 2 Manual fruit thinning process and crop-load adjustment in loquat production

6.2 Research progress in chemical and mechanical-assisted thinning

Chemical thinning in loquat has been studied mainly as an alternative to expensive hand thinning, with naphthaleneacetic acid-related compounds giving the most consistent results. NAAm applied at the end of bloom increased fruit diameter by about 11% to 18%, improved grading, and advanced harvest, while total yield declined only slightly. A separate study found that naphthaleneacetic acid at 20 mg L⁻¹ applied 10-15 days after anthesis was the most effective treatment for thinning and increasing average fruit size (Agustí et al., 2000). Chemical thinning therefore appears useful when growers need earlier crop-load adjustment than hand thinning can provide, especially because late manual thinning has been described as both expensive and of limited usefulness in loquat.

Its main limitation is that chemical thinning is highly sensitive to dose, timing, and environmental conditions. In ‘Golden Nugget’, higher NAA doses caused stronger thinning and larger fruit, but they also produced the lowest

yield per tree, whereas lower doses gave size and yield similar to hand-thinned trees. Response variability within the canopy is another concern, since NAA^m treatment showed variable thinning rates within trees. Mechanical-assisted thinning has not yet been well developed for loquat, but results from other fruit crops suggest why it remains attractive: in plums, mechanical thinning reduced fruit set by about 20% and increased fruit size, especially when integrated with selected chemical programs (Pavanello et al., 2018). That broader evidence suggests a likely future direction for loquat, in which mechanical pre-thinning could lower labor costs while hand or chemical follow-up restores precision.

6.3 Synergistic effects with other practices

Fruit thinning in loquat is rarely an isolated decision, because its effects interact with pruning, bagging, irrigation, and fertilization. Loquat studies explicitly note that fruit enlargement is influenced not only by crop load but also by tree vigor, temperature, and fertilization. Under traditional systems in Fujian, about half of the panicles are thinned for larger fruit, while pruning after harvest promotes strong summer shoots that later bear flower buds. More intensive shoot management can amplify this effect: double-heading pruning produced more vigorous shoots, deeper green leaves, and larger fruit, indicating that thinning and pruning can work together by improving both sink regulation and source capacity. Mechanistic modeling in fruit trees supports this integrated view, showing that the pruning and thinning combinations already used by growers often provide the best compromise between current fruit production and next season's vegetative renewal (Bevacqua et al., 2021).

Bagging is another important complementary practice in loquat because it protects the fruit after crop load has been adjusted. In one loquat study, clusters were bagged immediately after thinning, reflecting the practical pairing of these two operations in orchard management. Independent bagging experiments show why this combination is attractive: bagging improved appearance and fruit health, prevented insect and bird damage, and reduced skin burn, rotting, and black spot. Broader orchard evidence also indicates that thinning responses are modified by water and nutrient supply, with intermediate irrigation and potassium inputs combined with moderate thinning producing better yield and fruit quality than either excessive crop load or excessive input use (Ghazzawy et al., 2023). Similar interaction studies in other perennial systems show that thinning, pruning, and fertilization do not act independently, so the best loquat strategy is likely an integrated program that coordinates crop load with canopy management and resource supply. Overall, manual thinning remains the most precise loquat strategy, chemical thinning offers a labor-saving but less predictable alternative, and mechanical-assisted thinning is a promising but still underexplored option for this crop. The strongest practical conclusion is that fruit thinning works best in loquat when it is integrated with pruning, bagging, and resource management rather than applied as a stand-alone technique.

7 Case Studies: Application Effects of Fruit Thinning Practices in Loquat Production

7.1 Effects of different thinning intensities on loquat yield and fruit quality: case studies

A recent two-season field case study in the Paraíba Valley of southeastern Brazil compared five hand flower-bud thinning intensities in 'Precoce de Itaquera' loquat and showed a clear trade-off between fruit quality and yield. Retaining four buds per cluster gave the best overall improvement in fruit quality, producing greater fruit set per cluster as well as larger and sweeter fruit, whereas retaining 12 buds per cluster produced the highest cluster weight and total yield. This case indicates that stronger thinning benefits market-oriented quality traits, but lighter thinning better preserves output per tree.

Comparable results were reported in another case study covering five loquat cultivars and one selection, in which four fruits per panicle produced superior fruit length, width, and weight. However, that same trial found no clear effect of thinning intensity on pH, titratable acidity, or soluble solids, showing that external size responses are more consistent than internal compositional changes. Work in 'Algerie' loquat under two irrigation regimes reached a similar practical conclusion: heavier thinning slightly improved packout, but the gain did not offset the yield loss caused by removing too many fruits, and four fruits per panicle generated the highest revenue (Stellfeldt et al., 2013).

7.2 Effects of different thinning periods on fruit development and quality formation: case studies

Case studies on thinning period show that timing strongly influences both fruit growth and harvest quality in loquat. A three-year study of chemical thinning with NAAm found that application at the end of bloom increased fruit diameter by 11% to 18%, improved grading, and advanced harvest, while total yield declined only slightly. Another chemical-thinning trial showed that treatment efficacy depended on both date and concentration, and that the most effective schedule for increasing average fruit size was 20 mg L⁻¹ naphthaleneacetic acid applied 10-15 days after anthesis. Together, these cases show that earlier crop-load regulation can improve fruit enlargement more effectively than delayed manual thinning.

Developmental case studies also show why thinning period matters biologically. In ‘Algerie’ loquat, fruit growth followed a sigmoid pattern in both thinned and unthinned trees, but thinning changed the slope of the growth curve, indicating faster fruit growth under reduced crop load (Cuevas et al., 2003). Initial fruitlet size was also highly predictive of final market class, because size differences present at hand thinning did not reverse later, which supports selective thinning based on early fruit size rather than random fruit removal. These findings suggest that the most effective thinning window is the early stage when fruit growth trajectories and competition among fruit are still being established (Figure 3).

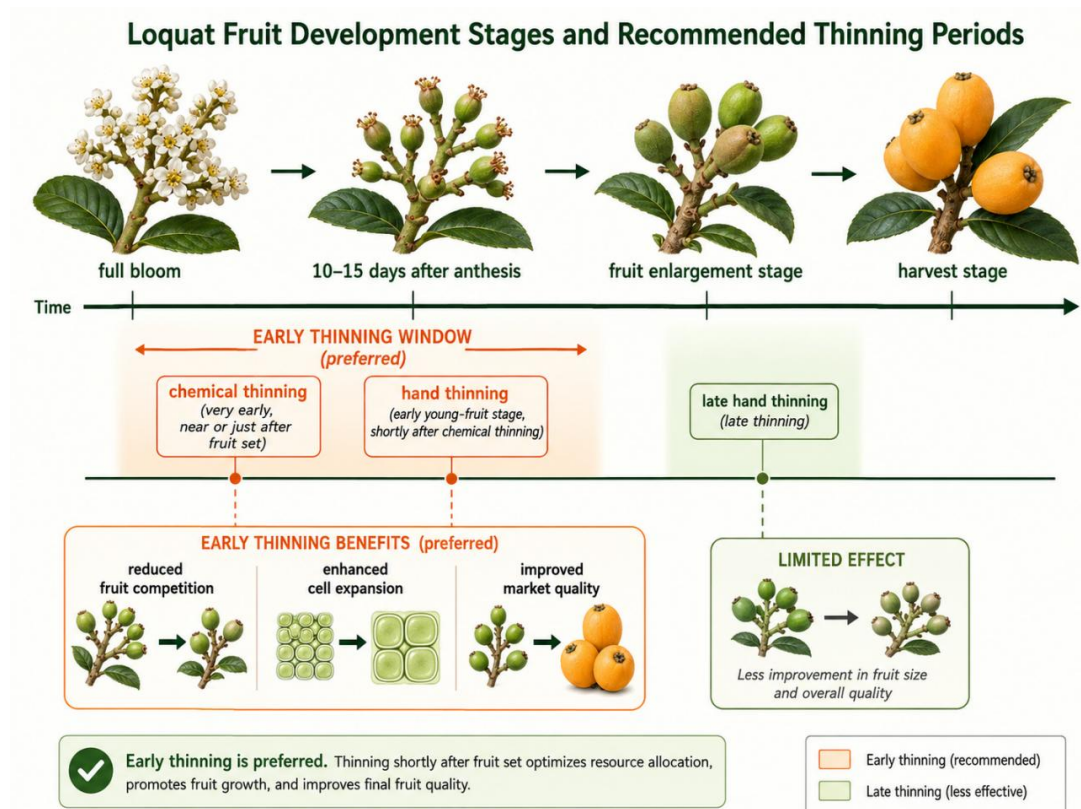


Figure 3 Optimal thinning windows during loquat fruit development and their effects on fruit growth and harvest quality

7.3 Improving loquat production efficiency through fruit thinning combined with modern management practices: case studies

Several case studies show that fruit thinning becomes more effective when combined with other orchard practices rather than used alone. In the Brazilian flower-bud thinning experiment, all clusters were bagged immediately after thinning, and the four-bud treatment produced the best overall fruit-quality response, illustrating a practical thinning-plus-bagging system for fresh-market production. Independent bagging work in Fujian was conducted in orchards that had already been systematically pruned, thinned, and fertilized, and aluminum-polyethylene bags increased fruit weight, length, and width while markedly reducing skin burn, rotting, and black spot (Zhi et al., 2021). This evidence suggests that thinning can be integrated with post-thinning fruit protection to raise the proportion of marketable fruit.

Other production-efficiency case studies combine thinning with pruning or irrigation management. Under the traditional Fujian pruning system, about half of the panicles are thinned, but double-heading pruning was developed to conserve nutrients in the remaining shoots and produced larger fruit together with higher yield. In water-limited orchards, preharvest deficit irrigation interacted with crop-load management in a different way: heavier thinning was not required under the mild stress conditions tested, and four fruits per panicle still provided the highest revenue while saving irrigation water. A related irrigation case study further showed that a short preharvest deficit-irrigation program could produce sweeter, earlier fruit with better handling performance, although excessive water restriction reduced fruit size (Hueso et al., 2021). Overall, the case-study evidence shows that loquat thinning works best as targeted crop-load regulation rather than simple fruit removal. Across different cultivars and management systems, moderate-to-strong thinning improves fruit size and market quality, but the best commercial outcome usually comes from combining appropriately timed thinning with bagging, pruning, or irrigation strategies suited to local production goals.

8 Challenges and Future Research Directions in Loquat Fruit Thinning Technology

8.1 Current limitations in the application of fruit thinning techniques

Manual thinning remains the most precise option in loquat, but its main weakness is that it is slow, labor-intensive, and expensive. In loquat, hand thinning is still valued because it can control the number of retained fruits more effectively than chemical or mechanical alternatives, yet this precision depends on trained labor and raises production costs. Earlier loquat studies reached the same practical conclusion, describing hand thinning as a slow and expensive operation that restricts wider commercial expansion. Manual thinning is also limited by its timing and biological variability. Late hand thinning in loquat has been described as of limited usefulness because it is commonly performed after a substantial part of the competitive phase among fruits has already occurred. Even when thinning is effective, results vary with cultivar, season, and orchard conditions, and recent loquat field work explicitly notes that climate, thinning timing, intensity, and other cultural practices all interfere with final fruit properties (Nordi et al., 2025).

Chemical thinning can reduce labor demand, but its commercial use in loquat is constrained by narrow margins between effective and excessive thinning. NAA responses in ‘Golden Nugget’ were closely dose-dependent, with the highest doses producing the largest fruits but also the lowest yield per tree. NAAM offers a partial alternative, since end-of-bloom applications increased fruit diameter and only slightly reduced total yield, but thinning rates remained variable within trees, which weakens predictability at orchard scale. Beyond efficacy, current thinning methods also create broader operational and biological constraints. Mechanized orchard thinning in other fruit crops still often relies on subjective operator judgment for speed, spindle rotation, and working distance, which results in low precision and uncertain damage to non-target tissues (Lei et al., 2023). In loquat specifically, stronger thinning can improve size and sweetness, but it has also been associated with higher purple spot incidence, showing that quality gains can be accompanied by physiological risk.

8.2 Development trends of precision fruit thinning technologies

A clear development trend is the shift from uniform thinning toward precision crop-load management based on sensing, detection, and tree-specific decisions. In apple systems, rapid and accurate fruitlet detection before thinning is already considered essential for early yield estimation and automatic thinning. The same logic is now extending to decision systems that support thinning timing and fruit-removal choices under natural orchard conditions, with recent models showing real-time detection performance suitable for automated management (Wang et al., 2025). The technical foundation of this trend is machine vision. Deep-learning systems can now segment fruitlets and canopy structures with high precision and low inference time, which is a prerequisite for selective thinning under complex orchard conditions (Sapkota et al., 2023). However, current vision systems still face persistent challenges from occlusion, clustered fruits, variable illumination, and incomplete spatial information, and 2D-only pipelines lose useful depth cues that could improve thinning decisions.

A second trend is the integration of perception with robotic or variable-rate actuation. Field-tested robotic blossom-thinning platforms have already shown targeted thinning of selected clusters, but commercial deployment

is still early and depends on faster, more robust perception-control pipelines. Precision chemical thinning is moving in the same direction: computer-vision-guided variable-rate spraying achieved thinning effects comparable to conventional spraying while using about 18% less thinning agent (Kang et al., 2025). For loquat, these trends suggest that future thinning systems will likely be hybrid, not purely manual or purely automated. Traditional orchard operations already combine pruning, thinning, bagging, and crop-load adjustment, so loquat is well suited to integrated digital management rather than stand-alone hardware substitution. More broadly, PACMAN-type frameworks in apple show that precision crop-load management works best when pruning, chemical thinning, and hand thinning are treated as linked decisions rather than isolated interventions.

8.3 Future research priorities

The first research priority is to generate more loquat-specific thinning evidence across cultivars, environments, and management systems. Existing loquat studies already show that responses differ with cultivar, season, and thinning intensity, but the literature remains thin relative to apple and other major tree fruits. This gap is especially clear for chemical thinning, where additional work has long been identified as necessary before commercial-scale recommendations can be made. A second priority is to build loquat-adapted sensing and decision models rather than transferring tools directly from apple. Automated thinning depends on reliable datasets and detection models, yet even in apple, progress has required dedicated annotated datasets and optimized models to handle small fruit, occlusion, and natural-scene variability. For loquat, this means creating image datasets spanning panicle architectures, fruitlet sizes, lighting conditions, and canopy forms, then linking those inputs to crop-load thresholds that predict marketable yield and quality.

A third priority is to connect precision thinning with whole-orchard economics and sustainability. Variable-rate systems can reduce chemical inputs and potentially improve economic return by matching thinning intensity to local fruit set, but adoption barriers still include calibration demands, equipment compatibility, and grower familiarity with prescription-based systems (Kang et al., 2025). Robotic systems face parallel barriers in platform cost, sensor cost, and operational speed, so progress will depend as much on simplification and affordability as on accuracy alone. A final priority is to widen the concept of thinning from fruit removal alone to resource valorization and integrated orchard design. Loquat flower thinning generates large quantities of discarded biomass, yet recent work shows that these flowers contain recoverable flavonoids and antioxidant activity, creating a plausible by-product pathway for value-added use. In parallel, loquat management studies indicate that thinning interacts with pruning, vigor, and carbohydrate supply, so future work should optimize thinning within integrated canopy and source-sink management rather than treat it as an isolated operation.

9 Conclusions

Fruit thinning should be regarded as a core crop-load regulation practice in loquat because natural fruit set commonly exceeds the tree's carrying capacity, resulting in many undersized fruits and unstable commercial output. Loquat orchards therefore need thinning not simply to reduce fruit number, but to balance marketable yield with fruit size, sweetness, and packout. The main conclusion across loquat studies is that heavier thinning improves individual fruit performance, whereas lighter thinning usually preserves higher total yield. In 'Precoce de Itaquera', maintaining four flower buds per cluster produced the best overall quality response, while twelve buds per cluster gave the highest cluster weight and yield. In 'Algerie', heavier thinning slightly improved packout, but four fruits per panicle generated the highest revenue under both irrigation regimes because severe fruit removal reduced output too strongly. This balance between quality and retained productivity is consistent with broader crop-load evidence from other fruit systems, where low to medium crop loads generally produce higher-quality fruit than overloaded trees. Taken together, the evidence indicates that the practical goal in loquat is optimized crop load, not maximum thinning intensity, and that moderate thinning usually offers the best economic compromise under commercial conditions.

The most consistent quality benefit of fruit thinning in loquat is the improvement of external fruit traits, especially fruit size, fruit weight, and uniformity. Across cultivars, thinning to four fruits per panicle produced superior fruit length, width, and weight. Growth studies also show that thinning increases fruit growth rate, which helps explain

why retained fruits attain larger final size under reduced competition. Fruit thinning also improves important internal quality traits, although these responses are somewhat more variable than size responses. In the recent Brazilian study, a higher number of flower buds reduced soluble solids, whereas stronger thinning produced larger and sweeter fruit. Chemical thinning with NAAm similarly increased fruit diameter, improved grading, and advanced harvest, showing that thinning can enhance commercial quality as well as earliness. At the same time, thinning effects on acidity-related variables are not always uniform across studies or cultivars. One multi-cultivar loquat trial found no significant effect of thinning intensity on pH, titratable acidity, or total soluble solids. This agrees with the broader view that loquat fruit quality is determined not only by crop load, but also by cultivar, climate, mineral nutrition, and orchard management conditions. The overall effect of thinning on fruit quality is therefore best understood as part of a wider management system. Bagging improves fruit health, appearance, and protection from insect, bird, and abiotic damage. Likewise, pruning systems that increase shoot vigor and leaf quality can strengthen carbohydrate supply and support larger fruit, reinforcing the benefits achieved through thinning alone. The future of loquat thinning technology will depend on reducing labor cost while preserving the precision that makes thinning effective. Hand thinning remains highly efficient but is slow and expensive, and this continues to limit wider adoption in commercial orchards. Chemical thinning offers a partial solution, but current loquat studies still show variability in response within trees and a need for further development before routine large-scale use. A second major direction is the integration of thinning with other sustainable orchard practices. In semi-arid production systems, deficit irrigation can save substantial water and, when properly managed, maintain profitability without requiring stronger thinning intensity.

More broadly, sustainable loquat production will likely rely on combining thinning with pruning, bagging, rootstock choice, and mineral management rather than optimizing each practice in isolation. Future research should also move beyond fruit removal itself and consider whole-system efficiency and value creation. Loquat flowers removed during thinning represent a large discarded biomass, yet recent evidence shows they can be upcycled into value-added functional products rich in flavonoids and antioxidant activity. At the same time, predictive tools based on mineral nutrition and fruit quality modeling may help build more precise management frameworks for fruit weight, soluble solids, and acidity in loquat orchards. In conclusion, fruit thinning is not merely a corrective practice for excessive fruit set, but a strategic tool for balancing yield, fruit quality, and orchard profitability in loquat production. Its long-term value will be greatest when it is embedded in precision, resource-efficient, and integrated production systems designed for sustainable loquat cultivation.

Acknowledgments

I extend my sincere gratitude to the anonymous reviewers for their valuable and insightful comments, which have greatly strengthened this paper.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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