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Review Article Open Access

Advances in Production Technology of Marigold and Gomphrena

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Abstract *Tagetes erecta* and *Gomphrena globosa* are important commercial ornamental crops with increasing demand in floriculture, pharmaceutical, and industrial sectors. Recent advances in production technology have significantly improved their yield, flower quality, stress tolerance, and post-harvest performance. In marigold, major advancements include hybrid seed production through genic and cytoplasmic male sterility systems, triploid breeding, marker-assisted selection, mutation breeding, and tissue culture techniques for rapid multiplication of elite genotypes. Improved cultivation practices such as pinching, precision irrigation, artificial lighting systems, integrated nutrient management, biofertilizer application, and the use of plant growth regulators have enhanced productivity and flower quality. Modern post-harvest technologies, including cold chain management and pigment extraction, have further increased commercial value. Similarly, advancements in gomphrena production technology include improved pinching methods, biofertilizer use, high-density planting, and optimized growing substrates for better growth and yield. Advanced drying and dehydration techniques have improved post-harvest quality and color retention of dried flowers. Molecular characterization and variability studies have supported genetic improvement, while plant growth regulators such as GA_3 and NAA have enhanced flowering, vegetative growth, and flower longevity. Overall, the integration of modern breeding, biotechnology, precision cultivation, and post-harvest management has strengthened sustainable and profitable production of marigold and gomphrena.

Keywords Genetic improvement; Hybrid breeding; Micropropagation; Postharvest management; Ornamental horticulture; Sustainable floriculture

1 Introduction

Marigold (*Tagetes erecta* L.) is an important commercial ornamental flower with increasing demand in Nepal due to its cultural, religious, and economic significance. Flower growers are attracted to its cultivation because of its profuse flowering habit, earliness, wide range of attractive flower colours, forms, sizes, and excellent market demand for loose flowers (Datta and Singh, 2008). Marigold (*Tagetes erecta* L.), belonging to the family Asteraceae, accounts for more than half of the global loose flower production (Jyothi et al., 2018). In Nepal, marigold, locally known as *Sayapatri*, remains an integral component of festivals, religious ceremonies, and social events, where flowers are commonly used for garlands and offerings (Gaenszle et al., 2005; Floriculture Association Nepal (FAN), 2023). Beyond its ornamental importance, marigold has gained considerable industrial value owing to its applications in landscaping, pharmaceutical products, cosmetics, poultry feed as a natural source of lutein and xanthophyll pigments, and extraction of bioactive compounds, thereby increasing its commercial significance worldwide.

Globe amaranth (*Gomphrena globosa* L.) is an ornamental species belonging to the family Amaranthaceae, valued for its attractive papery flower heads, long vase life, and excellent suitability as a dried flower crop. The flowers occur in purple, pink, yellow, and white colours and are widely used in landscape gardening, floral arrangements, and ornamental containers. The species thrives under full sunlight and moderately dry soil conditions, making it suitable for cultivation in diverse agroecological environments (Gilman and Howe, 2007). Besides its ornamental value, *G. globosa* has attracted increasing attention as a source of natural pigments and bioactive compounds, including vitamin C, β-carotene, flavonoids, and phenolic compounds with antioxidant, antimicrobial, and

pharmaceutical properties (Dwiyani et al., 2023). The papery colourful bracts surrounding the true flowers enable excellent colour retention after drying, making globe amaranth one of the most important commercial dried flower species.

Despite their considerable commercial importance, the production of both marigold and globe amaranth continues to face several challenges. The availability of superior cultivars with stable flowering behaviour, improved flower quality, and enhanced resistance to biotic and abiotic stresses remains limited. Environmental stresses such as drought, salinity, and temperature fluctuations adversely affect plant growth, flower yield, and pigment accumulation, while post-harvest deterioration during harvesting, transportation, and storage reduces market value (Ma et al., 2020; Babaei et al., 2021; Dalavi et al., 2025). Furthermore, increasing consumer demand for high-quality flowers, natural pigments, and environmentally sustainable production systems necessitates continuous improvement in breeding strategies, biotechnology, precision cultivation, nutrient management, and post-harvest technologies (Saputra et al., 2025; Venkatesan and Ramesh Kumar, 2025).

Marigold and globe amaranth are reviewed together because both are commercially important ornamental crops with expanding applications in floriculture, natural pigment extraction, pharmaceutical products, and landscape horticulture (Udchachon et al., 2021; Dwiyani et al., 2023). Although both crops share common production objectives, including enhanced flower quality, increased productivity, improved stress tolerance, and greater post-harvest longevity, their technological advancement has followed different pathways. Marigold has experienced substantial progress in hybrid breeding, male sterility systems, molecular breeding, mutation breeding, and tissue culture (Sindhuja et al., 2018; Venkatesan and Ramesh Kumar, 2025), whereas production improvement in globe amaranth has relied more heavily on cultivation optimization, plant growth regulation, germplasm evaluation, and post-harvest technologies (Kumar et al., 2023; Akbar and Sahare, 2024; Saputra et al., 2025). Therefore, a comparative review of these two crops provides a comprehensive understanding of their complementary technological developments and identifies future opportunities for sustainable ornamental crop production.

This review summarizes recent advances in the production technologies of marigold and globe amaranth, with emphasis on genetic improvement, breeding strategies, biotechnology, tissue culture, cultivation practices, nutrient management, pest and disease management, and post-harvest technologies. It further discusses the major production constraints, technological limitations, and future research directions for improving productivity, flower quality, resource-use efficiency, and the sustainable commercialization of these economically important ornamental crops.

2 Origin of Marigold and Gomphrena

Marigold (*Tagetes* spp.) is native to South and Central America, particularly Mexico, and belongs to the family Asteraceae (Compositae) (Shafiee et al., 2023). From Mexico, it spread to different parts of the world during the early sixteenth century. The genus *Tagetes* was named after Tages, an Etruscan demigod associated with wisdom and beauty. The genus comprises approximately 33 species, of which *Tagetes erecta* (African marigold), *Tagetes patula* (French marigold), and *Tagetes minuta* are the most widely cultivated (Figure 1). Marigold plants are generally erect, vigorous, and fast-growing, with heights ranging from 30 to 90 cm. Their flowers vary in colour from deep orange and golden yellow to bright yellow and lemon yellow, with flower diameters typically ranging from 4 to 6 cm (Udchachon et al., 2021).

Gomphrena (*Gomphrena globosa* L.) is native to Central America, particularly Guatemala and Panama, and belongs to the family Amaranthaceae (Akbar and Sahare, 2024). The genus *Gomphrena* comprises approximately 120–140 species of annual and perennial herbs distributed across the Americas, Australia, and the Indo-Malayan region, with *G. globosa* being the most widely cultivated ornamental species (Figure 2). In Brazil alone, about 46 species have been documented across diverse ecosystems, including cerrado savannas, open grasslands (*campo limpo*), rocky highland grasslands (*campo rupestre*), and caatinga vegetation, whereas relatively few species occur in forest habitats (Vieira et al., 1994). Most species are herbaceous or shrubby and possess specialized

underground structures, such as woody xylopodia or fleshy tuber-like roots, which facilitate survival under adverse environmental conditions. Owing to its attractive spherical inflorescences, excellent colour retention after drying, and wide environmental adaptability, *G. globosa* has become an important ornamental crop cultivated worldwide.

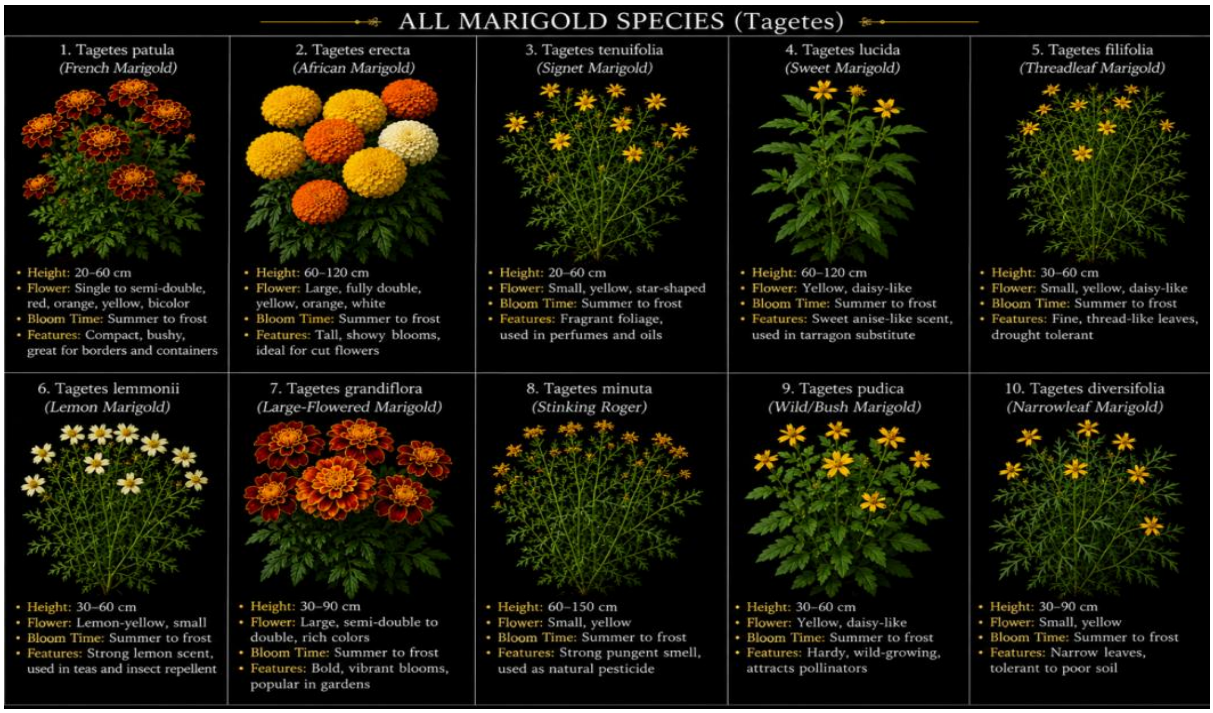


Figure 1 Genetic diversity and breeding resources of *Tagetes* species for marigold improvement



Figure 2 Taxonomic classification, origin, and major morphological characteristics of *Gomphrena globosa* L.

3 Advances in Marigold (*Tagetes* spp.) Production Technology

The increasing commercial demand for marigold flowers in ornamental horticulture, the pharmaceutical industry, poultry feed, and natural pigment extraction has accelerated research on improving production technologies. Advances in breeding, biotechnology, cultivation practices, nutrient management, and post-harvest handling have substantially enhanced flower yield, quality, stress tolerance, and production efficiency. Modern production systems increasingly integrate conventional breeding with molecular approaches, tissue culture, precision cultivation, and sustainable crop management to develop high-performing cultivars capable of meeting industrial demands while improving resource-use efficiency (Hussein et al., 2011; Kumar et al., 2016).

3.1 Advancement in hybrid seed production

The discovery of male sterility has greatly expanded opportunities for efficient hybrid seed production in marigold by eliminating the need for labour-intensive manual emasculation. Both genic male sterility (GMS) and cytoplasmic male sterility (CMS) systems have been successfully utilized in breeding programmes. Apetaloid female lines are controlled primarily by GMS and are widely used in commercial hybrid seed production because they are easily distinguishable during flowering. In contrast, petaloid female lines are governed by CMS, although partial fertility may occasionally occur, resulting in gynodioecious or gynomonoecious reproductive systems (Sindhuja et al., 2018; Sukwiwat et al., 2023). These male sterile systems facilitate efficient cross-pollination, increase hybrid seed purity, and reduce production costs, thereby significantly improving commercial hybrid seed production (Dedhia et al., 2022).

3.2 Conventional breeding advances

Conventional breeding has played a central role in improving marigold cultivars through mass selection, pedigree selection, pure-line selection, hybridization, and mutation breeding. Mass selection has been successfully employed to develop open-pollinated cultivars such as 'Calcutta Orange' and 'Arka Pari', whereas pedigree and pure-line selection have improved flower yield, colour intensity, carotenoid content, plant architecture, and resistance to diseases such as Fusarium wilt (Ayiecho and Nyabundi, 2025; Venkatesan and Ramesh Kumar, 2025). Hybridization has resulted in superior F_1 hybrids, including 'Arka Abhi', 'Arka Shubha', and 'Arka Agni', characterized by larger flowers, improved shelf life, and enhanced transportability. Mutation breeding using gamma rays and ethyl methanesulfonate (EMS) has generated valuable genetic variability, including novel flower colours and improved ornamental traits, thereby providing useful breeding materials for future cultivar development.

Biotechnological approaches, particularly tissue culture, provide opportunities for rapid multiplication and conservation of superior gomphrena germplasm (Figure 3). Successful callus induction has been achieved using hypocotyl explants cultured on Murashige and Skoog (MS) medium supplemented with appropriate concentrations of sucrose, NAA, and BA. These protocols facilitate efficient shoot regeneration and root development, thereby supporting large-scale propagation and conservation of elite genotypes (Ruiz and Valadez, 1985). Nevertheless, commercial application remains constrained by relatively high production costs, specialized laboratory requirements and the need for efficient acclimatization protocols.

3.3 Modern biotechnology

Modern biotechnology has substantially accelerated marigold improvement by complementing conventional breeding approaches. Marker-assisted selection enables the identification of quantitative trait loci associated with economically important traits such as flower size, yield, and male sterility, thereby increasing breeding efficiency. The development of SCAR markers has facilitated the rapid identification of desirable male sterile lines for hybrid seed production (Joshi et al., 2024). Genome editing using CRISPR-Cas9 also offers considerable potential for improving flower colour, pest resistance, and abiotic stress tolerance. Although its application in marigold remains limited, successful modification of ornamental traits in related species demonstrates promising opportunities for future genetic improvement (Verma et al., 2023; Nishihara et al., 2024). Furthermore,

Agrobacterium-mediated transformation has been explored to enhance pyrethrin production, highlighting the potential of genetic engineering for value addition.

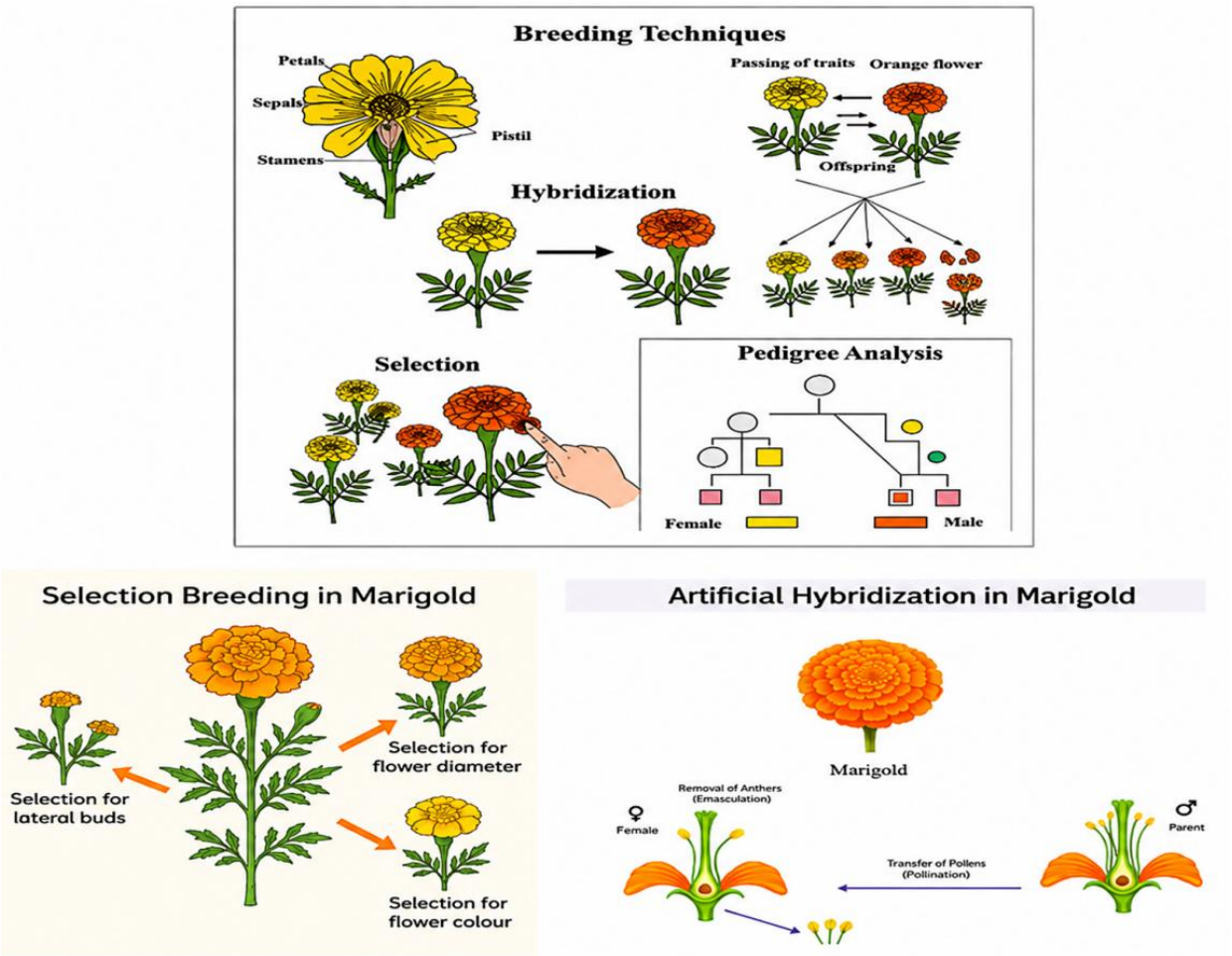


Figure 3 Schematic representation of breeding techniques and improvement strategies in marigold

3.4 Tissue culture and micropropagation in marigold breeding

Tissue culture, particularly in vitro propagation, provides a rapid and efficient method for large-scale multiplication of marigold while ensuring uniform expression of desirable traits (Figure 4). Advanced protocols enable regeneration from various explants such as shoot tips, leaves, and floral tissues. These micropropagation techniques have become valuable tools in modern breeding programs for quick multiplication of elite genotypes, conservation of genetic resources, and improvement of breeding efficiency.

Natural pigments such as carotenoids have important antioxidant, functional, medicinal, and nutraceutical properties, making them more valuable than synthetic colorants. Marigold (*Tagetes erecta*) is an important ornamental plant and a rich source of carotenoids. In vitro callus cultures of marigold can be induced from leaf explants using MS medium supplemented with 2,4-D and BA hormones. Marigold callus cultures can continuously accumulate pigments even after repeated subculturing, indicating stable pigment production potential (Benítez-García et al., 2014). Somaclonal variation has been effectively utilized to develop drought-tolerant marigold lines.exposing marigold tissue cultures to osmotic stress using mannitol led to the selection of drought-tolerant genotypes. These selected clones exhibited higher proline and soluble sugar content, contributing to enhanced drought tolerance. Such drought-resistant lines are particularly valuable in regions facing water scarcity, ensuring sustainable marigold cultivation (Ferreira et al., 2023).



Figure 4 Schematic representation of tissue culture and micropropagation techniques used for marigold improvement

Despite its considerable advantages, commercial application of tissue culture in marigold remains constrained by several factors. Large-scale micropropagation requires specialized laboratory facilities, skilled personnel, and relatively high production costs, limiting its adoption by commercial nurseries. In addition, successful acclimatization of regenerated plantlets under field conditions remains a major challenge, and prolonged in vitro culture may occasionally induce somaclonal variation that affects genetic uniformity. Consequently, further optimization of propagation protocols and cost-effective production systems is required before tissue culture can be widely adopted for commercial-scale marigold production.

3.5 Achievements in marigold breeding

The growing needs of the ornamental, industrial, and religious sectors necessitate the development of highly productive cultivars. To address this, modern research has produced superior hybrids specifically 'Arka Abhi', 'Arka Bhanu', and 'Arka Vibha' which demonstrate remarkably higher flower production. Beyond simple yield increases, these new varieties offer practical advantages like increased durability during transport and a longer shelf life, which ranges from 8 to 9 days. These hybrids have shown potential for commercial cultivation in various agro-climatic zones, enhancing farmer incomes and market availability (Venkatesan and Ramesh Kumar, 2025).

Commercial marigold varieties now have better tolerance to these risks due to breeding operations that have successfully included resistance genes from wild cultivars (Babaei et al., 2021). Abiotic stresses, such as drought, salinity, and heavy metal contamination, also adversely affect marigold growth and essential oil quality. Elevated levels of these stresses can result in the production of reactive oxygen species (ROS), which are harmful to plant cells. Research has shown that drought-responsive genes play a crucial role in regulating important physiological and biochemical processes, supporting the development of drought-tolerant hybrids (Kumar et al., 2023). In a similar way, salinity-tolerant cultivars are being improved by focusing on traits such as osmotic regulation and ion balance, which help maintain productivity under saline conditions (Ma et al., 2020). Advanced biotechnological approaches, including CRISPR-Cas9 and transcriptomic analysis, are increasingly being used to enhance stress tolerance in plants through precise genome editing and in-depth study of stress-response mechanisms. These technologies have enabled the discovery of key genes involved in abiotic stress resistance, accelerating the development of improved resilient varieties (Xu et al., 2020).

Quality traits such as vibrant color, longer vase life, and higher carotenoid content have been prioritized in recent breeding efforts. Varieties like ‘Arka Shubha’, known for its high carotenoid content, have been developed with industrial applications in mind. These varieties offer high yields of carotenoids, which are important for use in the pharmaceutical, food, and cosmetic industries. It is found that ‘Arka Shubha’ produced significantly higher levels of lutein and zeaxanthin, which are valuable carotenoids known for their antioxidant properties. These carotenoids

have widespread applications in supplements, skincare products, and natural food colorants (Udchachon et al., 2021).

3.6 Breeding techniques and marigold released

Breeding programs in marigold have resulted in the development of diverse cultivars with improved flower yield, color intensity, plant architecture, and commercial adaptability. Different breeding approaches, including hybridization, selection, mutation breeding, and male-sterility-based breeding have contributed to the release of improved cultivars in India and other regions (Table 1). Hybrid cultivars generally provide advantages in yield and flower quality, whereas selection and mutation breeding have expanded genetic diversity for specific ornamental traits.

Table 1 Representative marigold cultivars developed through different breeding approaches and their major applications

Breeding approach	Representative cultivars	Main breeding objectives	Major advantages/applications
Hybridization	Arka Agni, Arka Bangara-2, Arka Ambara	Increased flower yield, larger flower size, improved uniformity	Commercial hybrid production
Selection breeding	Pusa Narangi Gainda, Pusa Basanti Gainda	Flower color, yield stability, plant type improvement	Open-pollinated cultivar development
Mutation breeding	Pusa Centenary	Creation of novel variation	Development of unique flower traits
Male sterility-based breeding	IIHR/IARI male sterile lines	Efficient hybrid seed production	Reduced emasculation labor

3.7 Integrated post-harvest technology

Post-harvest management is a critical component of marigold production because flowers are highly perishable and rapidly lose their commercial value after harvest. Recent advances in cold chain management, value addition, and processing technologies have significantly improved flower quality, shelf life, and industrial utilization. Low-temperature storage combined with high relative humidity effectively reduces respiration rate, ethylene production, moisture loss, and microbial deterioration, thereby maintaining flower freshness and extending marketability. Studies have demonstrated that storing marigold flowers at 4 °C with approximately 95% relative humidity can extend shelf life to about 8 days, compared with only 3 days under ambient conditions, while preserving flower colour, firmness, and overall quality (Dalavi et al., 2025). Such cold-chain technologies are particularly beneficial for long-distance transportation and export marketing.

In addition to fresh flower marketing, recent technological advances have enhanced the industrial utilization of marigold through value-added processing. Advanced chromatographic techniques enable the extraction of high-purity lutein (up to 97.1%), which is widely used in pharmaceutical products, nutraceuticals, poultry feed, cosmetics, and natural food colourants. Likewise, solid-state fermentation of fresh flowers with calcium lactate prior to drying has been reported to improve β-carotene retention and increase the recovery of high-quality value-added powders suitable for commercial processing (Hayat, 2024). These post-harvest innovations not only minimize economic losses but also diversify the industrial applications of marigold, thereby increasing its commercial profitability.

3.8 Advancement in cultivation practices

Modern cultivation practices have considerably improved marigold productivity through the optimization of plant architecture, resource utilization, irrigation management, and environmental control. Among these practices, pinching remains one of the most effective cultural operations for regulating plant growth and flowering. Pinching suppresses apical dominance by reducing auxin accumulation at the shoot apex, thereby stimulating lateral bud development, increasing branch formation, and improving assimilate distribution towards reproductive organs. Early pinching at 14 days after transplanting promotes earlier flowering, whereas delayed pinching at approximately 28 days after transplanting generally produces greater plant height, more branches, and a higher number of flowers, ultimately resulting in superior flower yield.

Plant growth regulators (PGRs) further complement cultivation management by regulating physiological and biochemical processes associated with vegetative growth and flowering. Gibberellic acid (GA_3) enhances stem elongation, cell division, and flower initiation, while improving branching and flower size. Research has shown that the application of GA_3 at 200 ppm combined with pinching at 14 days after transplanting provides the most favourable combination for promoting early flowering and improving flower production (Isnawati et al., 2023).

Efficient irrigation scheduling has also become an important component of precision marigold production. Irrigation based on Class A pan evaporation (0.75 Epan) improves water-use efficiency by supplying water according to crop demand while minimizing unnecessary water losses. Such precision irrigation systems enhance nutrient uptake, maintain favourable soil moisture, and improve flower yield and economic returns compared with conventional flood irrigation (Chitra et al., 2025).

Recent advances in artificial lighting have further expanded opportunities for controlled-environment production. Light quality regulates photosynthesis, chlorophyll synthesis, photomorphogenesis, and carotenoid biosynthesis through phytochrome- and cryptochrome-mediated signalling pathways. The combined use of red and blue LED lights has been reported to promote balanced vegetative growth, improve pigment accumulation, and enhance flower quality, whereas red light alone significantly increases lutein concentration. These findings demonstrate that manipulating light spectra offers an effective strategy for improving production efficiency, shortening crop duration, and increasing both ornamental and industrial value under protected cultivation systems.

3.9 Advances in nutrient management

Integrated nutrient management has become an essential component of sustainable marigold production. The combined application of biofertilizers such as *Azotobacter*, phosphate-solubilizing bacteria (PSB), *Azospirillum*, and arbuscular mycorrhizal fungi with reduced rates of chemical fertilizers improves nutrient availability, root growth, flower yield, and nutrient-use efficiency (Abdulsada et al., 2013). Seedling root dipping in biofertilizer slurry before transplanting enhances early root colonization and nutrient uptake, while integration with farmyard manure or vermicompost further improves soil microbial activity, nutrient cycling, and long-term soil fertility.

3.10 Integrated pest and disease management

Integrated Pest and Disease Management (IPDM) has evolved from reliance on frequent chemical pesticide applications to environmentally sustainable management strategies that combine cultural, biological, mechanical, and chemical approaches. Modern IPDM programmes emphasize preventive management, conservation of beneficial organisms, and judicious pesticide use to minimize environmental impacts while maintaining effective pest suppression.

Recent studies comparing different pest management modules have demonstrated that adaptable IPDM systems integrating neem cake, vermicompost, biological control agents, and selective pesticides effectively reduce populations of thrips, mites, and bud borers (*Helicoverpa armigera*) while lowering pesticide dependence (Nikita et al., 2026). Such integrated approaches improve crop health by maintaining ecological balance and reducing the likelihood of pesticide resistance development.

Advances in molecular breeding have further strengthened pest and disease management through the identification of quantitative trait loci (QTLs) and marker-assisted selection (MAS) for resistance against important diseases such as powdery mildew and nematodes. The integration of resistant cultivars with biological control and precision crop management provides a more sustainable approach than reliance on chemical control alone.

In addition to its ornamental value, marigold also functions as an effective trap crop in vegetable production systems. According to Parihar et al. (2025), marigold attracts several insect pests and suppresses nematode populations when intercropped with solanaceous crops such as tomato and potato, thereby reducing pest pressure on the main crop. This multifunctional role enhances biodiversity, supports integrated crop protection strategies, and contributes to environmentally sustainable agricultural production.

4 Advancement in Gomphrena Production technology

Recent advances in the production technology of *Gomphrena globosa* have focused on improving flower yield, quality, post-harvest longevity, and commercial value through the integration of improved cultivation practices, biotechnology, genetic characterization, and value-added processing. Compared with marigold, where breeding technologies are relatively well developed, technological improvements in gomphrena have relied primarily on optimizing agronomic practices, plant growth regulation, substrate management, germplasm evaluation, and post-harvest technologies. These integrated approaches have enhanced production efficiency while supporting the increasing demand for fresh and dried flowers, natural pigments, and pharmaceutical raw materials.

4.1 Cultivation and growth optimization

Cultivation management plays a fundamental role in determining the growth, flowering behaviour, and market quality of *Gomphrena globosa*. Among various cultural practices, pinching is one of the most effective techniques for regulating plant architecture and increasing flower production. Pinching suppresses apical dominance by reducing auxin concentration in the terminal shoot, thereby promoting lateral bud development, increasing branching, and improving assimilate partitioning toward reproductive organs. Consequently, plants produce more flowering shoots and a greater number of marketable flowers. However, the response to pinching varies among cultivars, production objectives, and environmental conditions. For example, cut flower production generally favours longer stems with limited pinching, whereas potted plant production benefits from increased branching and compact growth. Recent studies have shown that double pinching performed at 20 and 35 days after planting significantly increases productive branches, flower number, and overall yield, although some cultivars may exhibit greater plant height and primary branching without pinching (Saputra et al., 2025).

The comparative effects of pinching on branching, flower production, flower diameter, and stalk length are summarized in Table 2, which demonstrates that appropriate pinching improves overall flower productivity while modifying plant architecture according to production requirements.

Table 2 Effects of different pinching treatments on growth and flowering characteristics of *Gomphrena globosa*

Parameter	Pinched (at 15 Days)	Non-Pinched
Branching	High (more side branches)	Low (terminal focus)
Flower Count	~602 per plant	~518 per plant
Flower Diameter	2.85 cm	1.5 cm
Stalk Length	Reduced	Longer

Note: Adopted from Rajasekaran et al. (1983)

Biofertilizer application has also become an important component of sustainable gomphrena cultivation. The combined use of Azotobacter, phosphate-solubilizing bacteria (PSB), and potash-solubilizing bacteria (KSB) enhances nutrient availability through biological nitrogen fixation, phosphorus solubilization, and potassium mobilization. These beneficial microorganisms also improve root development, stimulate phytohormone production, and enhance soil microbial activity, resulting in increased vegetative growth, flower yield, and nutrient-use efficiency (Yaseen et al., 2022). Although biofertilizers reduce dependence on chemical fertilizers and improve soil health, their field performance may vary depending on soil type, environmental conditions, and microbial survival.

Selection of suitable growing substrates further influences flower quality and productivity by improving root aeration, water retention, and nutrient availability. A substrate mixture consisting of garden soil, Baltic peat, and Klasmann-Deilmann TS3 medium has been reported to produce larger flowers, greater fresh and dry flower weight, and higher overall yield than conventional substrates (Zeljković et al., 2021). Nevertheless, the commercial adoption of specialized substrates should also consider production costs, availability of raw materials, environmental sustainability, and feasibility for large-scale cultivation.

4.2 Post-harvest and dehydration techniques

Post-harvest quality is particularly important in gomphrena because the crop is extensively marketed as a dried ornamental flower. Modern dehydration technologies aim to preserve flower colour, shape, texture, and structural integrity while minimizing shrinkage during drying. Among available techniques, hot-air oven drying at 50 °C-55 °C consistently produces superior colour retention and flower quality compared with traditional air drying (Akbar and Sahare, 2024). Embedding flowers in silica gel during drying further improves dehydration efficiency by minimizing moisture loss-induced deformation and preserving flower diameter, colour intensity, and fresh appearance. Although these techniques substantially improve product quality, commercial adoption depends on drying costs, energy requirements, and processing capacity.

4.3 Genetic and morphological improvements

Genetic improvement of gomphrena has increasingly relied on morphological evaluation and molecular characterization to identify superior breeding materials. Variability studies involving diverse genotypes have revealed substantial differences in vegetative growth, flowering behaviour, flower weight, branch number, and flower stalk length. High heritability estimates for these traits indicate that they can be effectively improved through selection, thereby providing opportunities for developing superior cultivars adapted to different production environments.

Molecular marker technologies have further strengthened breeding programmes by enabling accurate characterization of germplasm diversity. Inter-simple sequence repeat (ISSR) markers have detected approximately 67.76% polymorphism among gomphrena genotypes, demonstrating considerable genetic diversity for breeding improved cultivars with enhanced productivity, flower quality, and stress tolerance (Kumar et al., 2023).

4.4 Value addition and extraction

The commercial value of gomphrena extends beyond ornamental use because its flowers contain biologically active compounds with applications in food, pharmaceutical, and cosmetic industries. Recent advances in extraction technologies have focused on improving the recovery of natural pigments, particularly betacyanins, while maintaining their antioxidant activity. Ultrasonic-assisted extraction has proven more efficient than conventional extraction methods by improving pigment recovery, extraction efficiency, and product quality, making the extracts suitable for natural food colourants and functional food products such as cookies (Roriz et al., 2020).

Chemical profiling studies have also demonstrated that gomphrena flowers are rich sources of flavonoids, phenolic compounds, and other antioxidants possessing antimicrobial, anti-inflammatory, and enzyme inhibitory properties (Tang et al., 2022). These findings further expand the industrial potential of gomphrena beyond ornamental horticulture.

4.5 PGR innovation

Plant growth regulators have become valuable tools for improving vegetative growth, flowering, and post-harvest quality in gomphrena. Gibberellic acid (GA_3) promotes cell elongation, stem growth, and flower initiation by stimulating cell division and internode elongation, thereby increasing plant height, flower size, and marketable yield. Application of GA_3 at 150 ppm has been reported to provide optimum improvement in growth, flower yield, and post-harvest longevity (Sahoo, 2021). Likewise, NAA at 200 ppm accelerates flowering and prolongs the flowering period, whereas higher concentrations of maleic hydrazide reduce plant height by suppressing vegetative growth. Appropriate selection of plant growth regulators should therefore consider cultivar characteristics, production objectives, and environmental conditions to maximize productivity and flower quality.

4.6 High density planting

High-density planting (HDP) of *Gomphrena globosa* (globe amaranth) in greenhouses is an intensive production technique used to maximize the yield of cut flowers or potted plants per unit area. It focuses on utilizing vertical

space, optimizing light, and maintaining high plant populations (in some systems) for uniform, high-quality production.

4.7 Biotechnology

4.7.1 Micropropagation

The application of biotechnology in *Gomphrena* production, specifically regarding micropropagation, has historically seen limited documentation; however, established protocols now utilize specific tissue culture techniques to enhance multiplication rates. Research indicates that callus induction is most successful when utilizing hypocotyl tissues as explants (Ruiz and Valadez, 1985). These are typically cultured on a basal Murashige and Skoog (MS) medium enriched with sucrose at concentrations of 3%, 5%, or 7%. To achieve successful morphogenesis, a precise hormonal balance is required: a combination of 10^{-5} M NAA (Naphthaleneacetic acid) and 10^{-8} M BA (Benzyladenine) effectively induces shoot growth, although higher sucrose levels (5% to 7%) are generally necessary to stimulate concurrent root development. Furthermore, aseptic seedlings provide viable leaf and stem segments which, when placed on gelled MS medium supplemented with BA alone or in combination with auxins, serve as efficient starting points for mass propagation.

4.7.2 Molecular markers

Molecular marker technology has become an important tool for characterizing genetic diversity and supporting breeding programmes in gomphrena. Random Amplified Polymorphic DNA (RAPD) markers have revealed approximately 94.38% polymorphism, confirming the existence of substantial genetic variation among cultivated genotypes (Fatinah et al., 2012). Such information facilitates parent selection, germplasm conservation, and the development of improved cultivars with superior ornamental and agronomic characteristics.

5 Conclusion

Recent technological advancements have transformed the cultivation and commercial production of *Tagetes erecta* and *Gomphrena globosa* by improving productivity, quality, and adaptability under diverse growing conditions.In marigold, progress in hybrid seed production, male sterility systems, molecular breeding, tissue culture, and stress-resilient breeding has accelerated the development of superior cultivars suitable for commercial production. Likewise, innovations in gomphrena production, including improved cultivation practices, biofertilizer application, plant growth regulators, high-density planting, and advanced drying technologies, have enhanced flower productivity and value addition.

The integration of biotechnology, precision cultivation, integrated nutrient management, and modern post-harvest handling techniques has contributed to sustainable and profitable flower production systems. Furthermore, the use of environmentally friendly approaches such as biofertilizers, integrated pest management, and efficient irrigation practices supports sustainable floriculture development under changing climatic conditions. Continued research and adoption of these advanced technologies will play a vital role in improving productivity, maintaining flower quality, and strengthening the commercial potential of marigold and gomphrena in both domestic and international markets.

Authors' contributions

SS, AP and AA were involved in conceptualization, methodology, editing, writing the original draft, manuscript revision and providing the final structure to the manuscript. All authors read and approved the final manuscript.

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Feature Review Open Access

Effects of Calcium and Boron Nutrition on Fruit Firmness and Storage Quality of Blueberry

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Abstract Blueberry fruits are prone to softening, water loss, and decay after harvest, and fruit firmness and storage quality have become important factors affecting their commercial value. This study reviews the effects of calcium and boron nutrition on blueberry fruit firmness, storage performance, and quality formation, and analyzes the underlying mechanisms, synergistic effects, and production application strategies of these two nutrients. The results indicate that calcium improves fruit firmness and delays postharvest quality deterioration by promoting pectin cross-linking, enhancing cell wall stability, and reducing the activities of softening-related enzymes. Boron mainly influences fruit development and structural stability through its involvement in RG-II cross-linking, pollen germination, and cell expansion. Combined calcium and boron supply has the potential to synergistically improve fruit quality; however, its effectiveness is influenced by cultivar characteristics, application timing, nutrient transport efficiency, and environmental conditions. Future blueberry nutrient management should integrate nutrient diagnosis, phenological stages, and rhizosphere environment regulation to establish a precision calcium-boron management system, providing a theoretical basis for improving blueberry fruit quality and extending storage life.

Keywords Blueberry; Calcium nutrition; Boron nutrition; Fruit firmness; Storage quality; Precision nutrient management

1 Introduction

Blueberry is an economically and nutritionally important fruit crop worldwide, and its production has expanded rapidly in recent years. Doyle et al. (2021) reported that global blueberry production has increased approximately fourfold over the past two decades. With the growing demand for fresh blueberries, increasing attention has been directed toward postharvest quality maintenance and storage performance (Vance et al., 2017; Lopes et al., 2026). As fresh fruit supply chains continue to extend, blueberries must maintain desirable appearance, texture, and biochemical quality during postharvest transportation and storage (Vance et al., 2017; Manzi and Lado, 2019). Among these quality traits, fruit firmness is a critical indicator of blueberry market value, as it directly affects resistance to mechanical damage, transportation adaptability, and storage life (Olmedo et al., 2021; Hirzel, 2023). However, blueberry fruit is highly susceptible to softening, water loss, and decay after harvest, resulting in quality deterioration and economic losses.

The development of blueberry fruit firmness is closely associated with cell wall structure and mineral composition; therefore, calcium nutrition has become an important target for preharvest quality regulation. Calcium maintains the stability of cell walls and cell membranes, participates in pectin structural maintenance and cellular signaling regulation, and plays a crucial role in preserving fruit texture (Wang et al., 2024; Lopes et al., 2026). Previous studies have shown that higher concentrations of cell wall-bound calcium, together with specific structural characteristics of cell wall polysaccharides, including calcium-associated homogalacturonan domains and xyloglucans, are closely correlated with greater firmness during storage (Olmedo et al., 2021; Lopes et al., 2026). Calcium can also enhance pectin stability, restrict pectin degradation, and reduce the activities of softening-related enzymes, such as polygalacturonase and pectin methylesterase, thereby delaying fruit softening (Jaime-Guerrero et al., 2024; Wang et al., 2024).

Calcium nutritional regulation in blueberry is highly complex. Doyle et al. (2021) systematically summarized the physiological processes involved in calcium nutrition in blueberry and indicated that calcium uptake into fruit mainly depends on xylem transport. However, as fruit development progresses toward maturity, reduced fruit transpiration limits calcium accumulation. Previous studies have shown that calcium concentration in blueberry fruit generally declines from approximately 0.2% during early development to below 0.05% at maturity. Consequently, preharvest calcium application has received considerable attention, although its effectiveness varies substantially depending on cultivar, application timing, and treatment method. Some studies have demonstrated that calcium treatments can increase fruit firmness and reduce weight loss and decay incidence, whereas others have reported limited effects on fruit calcium concentration, firmness, and shelf-life improvement (Lobos et al., 2021b; Hirzel, 2023; Lopes et al., 2026).

Boron is another essential nutrient involved in blueberry growth and quality formation. It contributes to the maintenance of cell wall and membrane functions and plays important roles in pollen germination, pollen tube elongation, cell expansion, and fruit development (Álvarez-Herrera et al., 2025). Blueberry has a relatively short flowering and fertilization period and is therefore highly sensitive to boron availability. Boron deficiency is more likely to occur under conditions of low organic matter content, coarse-textured soils, or drought stress. Studies have shown that foliar or fertigation-based boron applications can increase boron concentrations in blueberry leaves, roots, and fruits; however, improved boron status does not necessarily translate into increased yield, fruit weight, or firmness (Arrington and DeVetter, 2017; Leon-Chang and Bryla, 2024). In addition, because the optimal range of boron availability is relatively narrow, excessive application may cause toxicity, highlighting the need for precise boron management.

Both calcium and boron participate in cell wall stabilization, membrane maintenance, and fruit quality development. In several fruit crops, combined calcium and boron applications have been shown to further improve fruit firmness and storage performance. However, blueberry responses to calcium and boron nutrition remain highly variable, which may be associated with differences in nutrient uptake capacity, transport efficiency, cultivar characteristics, developmental stage, and environmental conditions. This study analyzes the effects of calcium and boron nutrition on blueberry fruit firmness and storage quality, with particular emphasis on firmness maintenance, weight loss regulation, and postharvest quality stability. The aim is to provide a theoretical basis for precision nutrient management and quality improvement in blueberry production.

2 Physiological Basis of Blueberry Fruit Firmness Formation

2.1 Cell wall structure and firmness development

Pectin is one of the major components determining fruit firmness and is primarily distributed in the middle lamella and primary cell wall. In the middle lamella, pectin regulates adhesion between adjacent cells, whereas in the primary cell wall, pectin forms a hydrated matrix structure that influences cell wall strength and porosity characteristics (Posé et al., 2019; Huang et al., 2023). Blueberry fruit texture is closely associated with pectin composition. Pectin maintains intercellular connections, while changes in pectin solubility and side-chain structure are highly consistent with the decline in fruit firmness during ripening. Hemicellulose and cellulose also contribute to fruit firmness by strengthening the structural framework of the cell wall. Chea et al. (2019) found that blueberry fruits with higher firmness or stronger crispness generally contained higher levels of hemicellulose polysaccharides and cellulose. In particular, hemicellulose content showed a positive correlation with fruit firmness during fruit development. Although cellulose content typically changes less markedly than matrix polysaccharides during ripening, its interactions with pectin and hemicellulose remain an important basis for maintaining cell wall mechanical properties (Wang et al., 2018).

Fruit softening is mainly driven by cell wall degradation processes, including pectin solubilization and depolymerization, matrix polysaccharide remodeling, and the loss of neutral sugars from pectin side chains (Wang et al., 2018; Huang et al., 2023). In blueberry, fruit firmness decreases progressively during ripening, with the most pronounced decline occurring between the light-green and red-purple stages. This reduction is generally

accompanied by disruption of parenchyma tissue microstructure, degradation of cell wall materials, increased levels of water-soluble pectin, and decreased contents of hydrochloric acid-soluble pectin and hemicellulose (Chea et al., 2019). During ripening, the activities of enzymes associated with cell wall loosening gradually increase. Changes in the activities of polygalacturonase, α-arabinofuranosidase, β-galactosidase, and xylanase-related enzymes during late ripening collectively contribute to the degradation of pectin and hemicellulose, thereby accelerating fruit softening (Hocking et al., 2016; Chea et al., 2019).

2.2 Calcium-mediated regulation of cell wall stability

Calcium primarily enhances cell wall stability by binding to de-esterified homogalacturonan (HG) regions, forming cross-linked calcium pectate networks that strengthen pectin gel structure and improve intercellular adhesion, thereby increasing fruit tissue stability. This process depends on pectin methylesterase-mediated de-esterification of pectin, as block-wise de-esterified homogalacturonan provides binding sites for Ca^{2+} cross-linking (Huang et al., 2023). Calcium-pectin interactions are particularly important in the middle lamella and tricellular junction regions, which serve as key sites for cell adhesion. Calcium stabilizes these cell connection areas and enhances tissue resistance to cell separation caused by internal turgor pressure (Wang et al., 2018). In blueberry, Doyle et al. (2021) found that higher fruit calcium concentrations were generally associated with increased tightly bound pectin, reduced loosely bound pectin, lower pectin solubilization, and decreased postharvest softening and water loss, indicating the important role of calcium in maintaining cell wall stability.

Studies have further demonstrated that calcium improves fruit firmness retention by maintaining cell membrane integrity and structural stability (Doyle et al., 2021; Lopes et al., 2026). Calcium deficiency often results in increased membrane leakage, abnormal cell wall degradation, and impaired fruit tissue development (Hocking et al., 2016). Although calcium plays important physiological roles in blueberry production, its accumulation in fruit is relatively limited. This is mainly because calcium is transported predominantly through the xylem and has restricted mobility via the phloem, while fruit calcium concentration generally declines during fruit development. These physiological constraints contribute to the variable quality responses observed following calcium fertilization in blueberry production (Manzi and Lado, 2019; Doyle et al., 2021).

2.3 Boron functions in cell wall formation and fruit development

Boron contributes to cell wall stability by promoting covalent cross-linking between two rhamnogalacturonan-II (RG-II) domains, forming borate diester bridges within pectic polysaccharides of the primary cell wall (Sechet et al., 2018). Under sufficient boron supply, most RG-II molecules can form dimer structures. Although RG-II represents only a minor fraction of total pectin, its cross-linking status has a substantial influence on cell wall mechanical properties and porosity. The absence of boron-mediated RG-II cross-links results in abnormal cell wall properties, reduced structural stability, and impaired plant growth. In contrast, the combined action of calcium and boron can partially alleviate defects in cell wall integrity caused by impaired pectin cross-linking (Feng et al., 2018; Sechet et al., 2018). Begum and Fry (2023) further demonstrated that boron-mediated RG-II cross-linking affects not only local cell wall architecture but also broader pectin organization by enhancing homogalacturonan-calcium interactions and reducing cell wall porosity.

The effects of boron on fruit development extend beyond pectin cross-linking and also involve the regulation of cell expansion and normal tissue growth (Funakawa and Miwa, 2015; Begum and Fry, 2023). When RG-II dimerization is disrupted, plants commonly exhibit reduced growth, restricted cell expansion, and abnormal cell wall permeability, indicating that boron-dependent cell wall organization is essential for maintaining normal cellular expansion and development. Begum and Fry (2022) reported that borate cross-linking primarily occurs within the endomembrane system during pectin biosynthesis, while some dimerization processes may continue after pectin secretion into the cell wall. This suggests that boron availability during active growth stages may influence cell wall assembly both before and after pectin deposition. In blueberry production, boron has also received considerable attention due to its close association with reproductive growth and young fruit development

(Figure 1). However, under field conditions, the effects of boron fertilization on fruit firmness and yield remain highly variable.

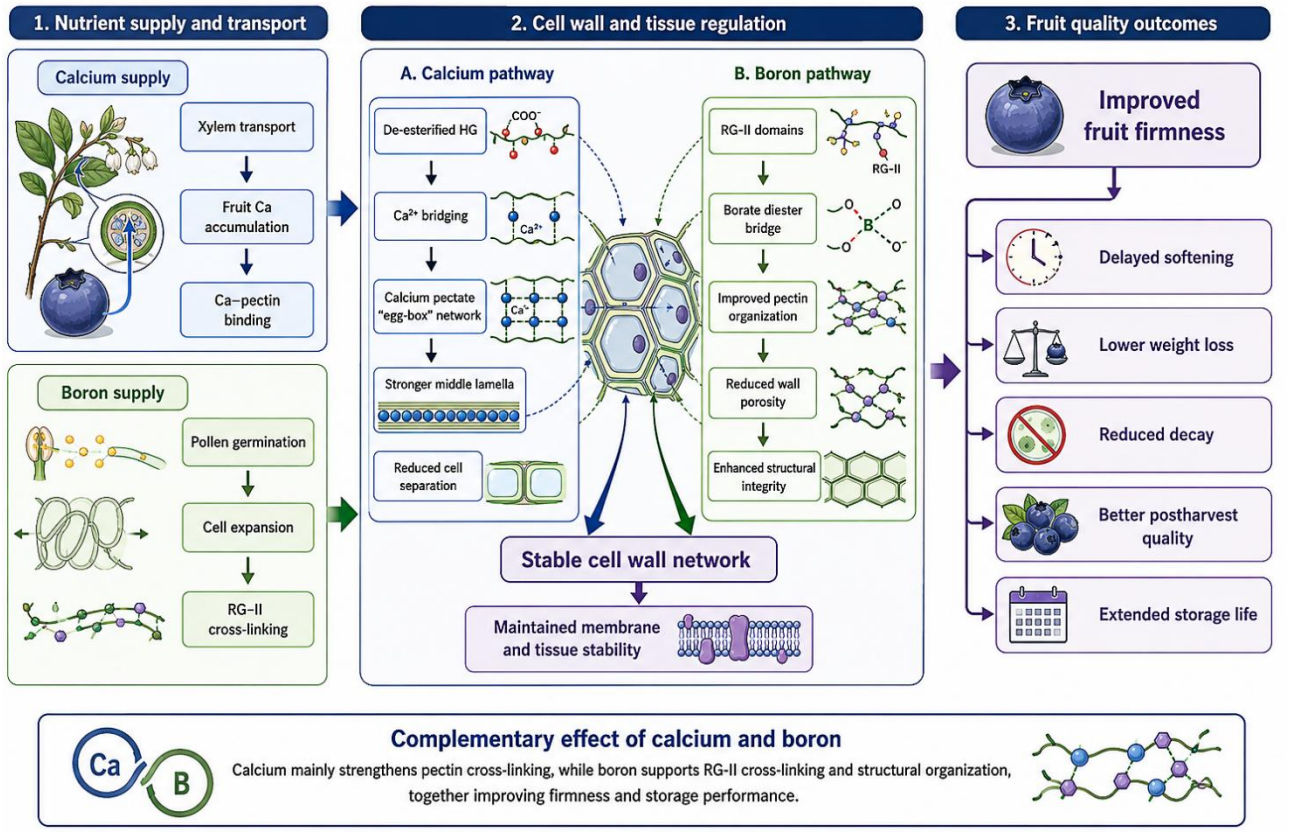


Figure 1 Integrated roles of calcium and boron in blueberry fruit firmness formation and quality regulation

3 Effects of Calcium Nutrition on Blueberry Fruit Firmness and Storage Quality

3.1 Calcium uptake, transport, and distribution in blueberry plants

Calcium uptake begins in the root system, and its continuous absorption depends on maintaining concentration gradients across root cell membranes and a low cytosolic Ca^{2+} level. Calcium is subsequently transported mainly through the xylem into different plant tissues (Hocking et al., 2016; Jaime-Guerrero et al., 2024). In fruit trees and berry crops, the amount of calcium delivered to fruits is jointly determined by xylem water flow, fruit transpiration, and vascular structural characteristics, while membrane-associated transport systems regulate Ca^{2+} allocation among different tissues (Hocking et al., 2016). Although calcium transport mechanisms in blueberry remain insufficiently characterized, existing studies suggest that fruit transpiration intensity, xylem functionality, and calcium transporter activity are key factors influencing Ca^{2+} uptake and distribution in blueberry fruits, which require further investigation (Doyle et al., 2021).

Calcium accumulation in fruits mainly occurs during the early developmental stage, when cell division, rapid fruit expansion, and xylem transport activity are relatively high. During later developmental stages, the contribution of phloem transport to calcium supply remains limited because calcium has relatively low mobility within the phloem, resulting in reduced additional calcium input into fruits (Larocca et al., 2025; Rojas-Barros et al., 2025). In blueberry, fruit calcium concentration generally decreases progressively during fruit development and ripening (Figure 2). For example, Doyle et al. (2021) reported that calcium concentration in blueberry fruits declined from approximately 0.2% at early developmental stages to below 0.05% at maturity. Manzi and Lado (2019) also observed that calcium concentration in the cultivar 'O'Neal' decreased from 0.32% at 25 days after full bloom (25 DAFB) to 0.11% at harvest.

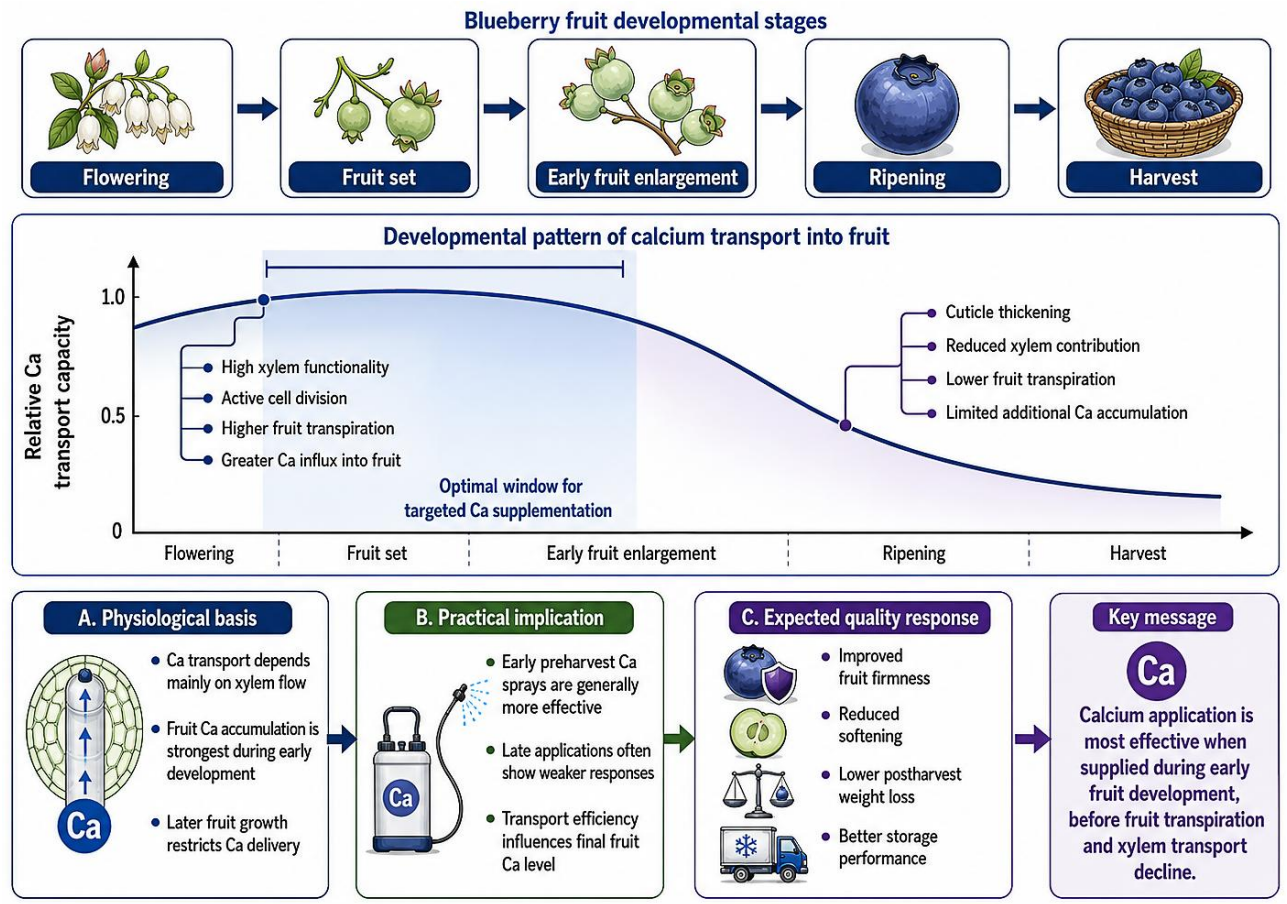


Figure 2 Developmental changes in calcium transport capacity and optimal timing of calcium application in blueberry

Recent hydroponic studies further indicated that calcium uptake in blueberry reaches its peak during periods of rapid vegetative growth, whereas calcium absorption becomes stable or even declines during later fruiting stages. This trend is particularly evident under high-temperature conditions and high vapor pressure deficit environments, which is consistent with the limitation of xylem-mediated calcium transport during late fruit development (Peñuelas-Montoya et al., 2026). Because fruit calcium accumulation is closely associated with transpiration and vascular continuity, calcium transport into fruits is further restricted in related berry crops as fruit development progresses, accompanied by cuticle thickening and reduced xylem functionality. These limitations ultimately affect the maintenance of postharvest quality (Rojas-Barros et al., 2025).

3.2 Effects of calcium application on fruit firmness

The primary mechanism by which calcium enhances fruit firmness is through its binding with de-esterified homogalacturonan in the cell wall, forming calcium pectate cross-linked structures that strengthen middle lamella stability and restrict cell wall degradation processes (Martins et al., 2020; Jaime-Guerrero et al., 2024). In blueberry, higher levels of cell wall-bound calcium are generally associated with greater fruit firmness. For example, Olmedo et al. (2021) compared the cell wall composition of the firm-fleshed cultivar ‘Emerald’ and the soft-fleshed cultivar ‘Jewel’ at harvest and after 30 days of storage at 0 °C. The results showed that ‘Emerald’ had higher concentrations of cell wall-bound calcium and stronger signals detected by the 2F4 antibody targeting calcium-binding HG domains. After 30 days of storage, ‘Emerald’ also exhibited increased glucose content and stronger LM15 antibody signals associated with xyloglucan structures. These findings indicate that firmness differences are not determined solely by total pectin content but are closely related to Ca^{2+}-mediated low-methylesterified HG cross-linking and the stability of xyloglucan networks.

Increasing fruit calcium concentration can also reduce pectin solubilization and degradation. Doyle et al. (2021) found that soil calcium application increased cell wall-bound Ca^{2+} concentration in blueberry fruits by approximately 10% at harvest, while increasing the proportion of tightly bound pectin and decreasing loosely bound pectin fractions. These results suggest that calcium can slow down cell wall disassembly processes. Related studies in blueberry have further shown that lower fruit calcium concentrations are often accompanied by higher polygalacturonase activity during storage (Lobos et al., 2021a). During cold storage, Ca^{2+} signaling can suppress the activities of pectin methylesterase and polygalacturonase, thereby delaying the conversion of protopectin and chelator-soluble pectin into water-soluble pectin (Wang et al., 2024).

Multiple blueberry studies have demonstrated that preharvest calcium supplementation can reduce the rate of fruit softening and maintain tissue structural stability during storage. For instance, in 'Liberty' blueberry, early-season foliar calcium application increased fruit firmness by approximately 10% compared with the control, and the effect was greater than that of later applications, indicating that the early fruit developmental stage may represent a critical period for calcium-mediated firmness regulation (Lobos et al., 2021a). Doyle et al. (2021) reported that soil calcium application during the autumn of the previous year also reduced postharvest softening and improved shelf-life performance in the cultivars 'O'Neal' and 'Bluecrop'. From a physiological perspective, calcium mainly maintains fruit firmness by preserving cell wall adhesion, reducing cell separation, and delaying structural deterioration of fruit tissues.

3.3 Calcium effects on postharvest quality preservation

The role of calcium in maintaining postharvest quality depends on its ability to enhance cell wall structural stability, while also being closely associated with the preservation of cell membrane integrity and regulation of water balance. Lobos et al. (2021a) reported that early preharvest calcium sprays reduced weight loss of blueberry fruits during cold storage. The water loss rate was approximately 1% lower than that of the control, and fruit calcium concentration showed a negative correlation with weight loss during storage. Another study also demonstrated that soil calcium application could reduce fruit weight loss after cold storage (Doyle et al., 2021).

Calcium can also reduce decay risk and maintain overall postharvest fruit condition. In 'Liberty' blueberry, early calcium application increased the proportion of healthy fruits after storage while decreasing the proportions of dehydrated and decayed fruits (Lobos et al., 2021a). This protective effect is consistent with the findings of Hocking et al. (2016), who suggested that calcium deficiency increases fruit susceptibility to pathogen infection and promotes abnormal softening, whereas sufficient calcium supply enhances apoplastic barrier function and reduces the risk of quality deterioration.

Calcium nutrition contributes to improvements in blueberry fruit firmness and storage quality; however, its effectiveness depends largely on whether calcium can reach the fruit during early developmental stages and participate in the establishment of stable cell wall and membrane structures. In addition, the response to calcium fertilization is influenced by application timing, transport efficiency, and the intrinsic calcium accumulation capacity of different cultivars (Doyle et al., 2021; Larocca et al., 2025).

4 Effects of Boron Nutrition on Blueberry Fruit Quality

4.1 Boron regulation of fruit development and structural integrity

Boron is an essential nutrient for normal plant growth and development and participates in multiple physiological processes, including cell wall formation, cell membrane maintenance, cell division, cell elongation, and carbohydrate transport. In blueberry, physiological processes such as pollen germination, fertilization, and cell expansion directly influence subsequent fruit set and fruit enlargement, and boron has been shown to be particularly important during flowering and early fruit development stages (De Silva et al., 2022). Studies in other fruit crops also support the promotive role of boron during early fruit development. Michailidis et al. (2023) reported that pre-bloom boron application in sweet cherry increased early fruit set, fruit fresh weight, and mesocarp cell expansion, indicating that adequate boron supply facilitates sink organ establishment and early fruit growth. Similar effects have been observed in pitaya, where boron application improved pollen germination

capacity, fruit weight, and pulp proportion. These effects were associated with enhanced cell division, improved cell membrane integrity, and more efficient assimilate transport (Sahu et al., 2022). However, responses to boron application in blueberry production are not always consistent. Although foliar or soil boron application can improve plant boron nutritional status, it does not necessarily increase berry weight, suggesting that fruit enlargement responses to boron depend on whether plants are actually limited by boron availability, as well as on cultivar characteristics and environmental conditions (Leon-Chang and Bryla, 2024).

The effects of boron on fruit tissue strength are mainly associated with its regulation of cell wall structure. Most boron within plants is located in the cell wall, where it contributes to tissue formation by maintaining cell wall integrity and mechanical stability. Zhang et al. (2022) found that boron deficiency increased cell wall porosity, disrupted cellulose arrangement, and reduced cell wall mechanical strength, thereby promoting tissue weakening and fruit softening. In fruit crops, boron supplementation generally delays softening by reducing the activities of cell wall-degrading enzymes, such as polygalacturonase and pectin lyase, while maintaining interactions between boron and structural components including pectin, cellulose, and hemicellulose (Zhang et al., 2024; Álvarez-Herrera et al., 2025). Studies in strawberry have shown that foliar boron application can increase fruit firmness and extend shelf life, while appropriate boron supply similarly improves pulp firmness in pitaya (Sahu et al., 2022; Zhang et al., 2024). However, in blueberry, the direct effects of boron on fruit firmness remain highly variable. Leon-Chang and Bryla (2024) reported that boron treatments increased boron concentrations in leaves and fruits but did not significantly improve berry firmness. Thus, although boron has a clear physiological basis for maintaining fruit firmness, whether this function translates into measurable firmness improvement depends on specific cultivation conditions and plant nutritional status.

4.2 Boron effects on carbohydrate metabolism and quality formation

Boron participates in carbohydrate metabolism and sugar transport in plants, and boron deficiency can affect photosynthetic efficiency as well as the translocation and distribution of photosynthetic products within the plant. Overall, sugar accumulation in fruits is regulated by the coordinated effects of multiple factors, including the activities of related metabolic enzymes, sugar transport processes, mineral nutrition status, and environmental conditions (Du et al., 2024; Wu et al., 2025). In sweet cherry, boron application can induce sugar homeostasis pathways and promote the accumulation of fructose, glucose, and organic acids during early fruit development (Michailidis et al., 2023). In pitaya, boron supply increased soluble solids, sugar content, and total carbohydrate levels, while enhancing the activities of invertase and sucrose synthase, indicating that boron participates in assimilate metabolism regulation during fruit maturation (Sahu et al., 2022). Similar trends have been observed in blueberry, although the positive effects appear to be relatively limited. For example, Leon-Chang and Bryla (2024) found that boron fertigation or foliar application did not significantly increase yield or berry size, but soluble solids content increased in some cultivars, suggesting that boron may promote sugar accumulation without necessarily causing concurrent changes in external fruit characteristics.

Because sugars, organic acids, and their balance are key determinants of fruit flavor, boron nutrition can indirectly regulate flavor development by influencing carbon metabolism and fruit biochemical processes. Reviews of various fruit crops have shown that boron application generally increases soluble solids content, regulates titratable acidity and pH, and contributes to the maintenance of ascorbic acid levels, all of which are closely associated with sensory fruit quality (Thakur et al., 2023; Álvarez-Herrera et al., 2025). In citrus, Luo et al. (2024) reported that excessive boron supply reduced soluble solids, sugar content, vitamin C concentration, and sugar-acid ratio, indicating that both boron deficiency and excessive boron availability may negatively affect flavor-related quality formation. In blueberry, direct evidence regarding the effects of boron on flavor quality remains limited. However, increases in soluble solids content observed in some cultivars following foliar or fertigation-based boron application suggest that, under appropriate conditions, boron may contribute to the development of sweeter fruits (Leon-Chang and Bryla, 2024).

4.3 Boron deficiency and its impact on blueberry production

Boron deficiency commonly occurs in acidic and high-rainfall cultivation environments. This issue is particularly important in blueberry production because low soil pH reduces boron availability, while strong leaching processes can further accelerate boron loss from the root zone (Reyes-Díaz et al., 2024; Vera-Maldonado et al., 2024). Symptoms of boron deficiency in blueberry mainly include shoot tip necrosis, leaf mottling and chlorosis, leaf curling, shortened internodes, reduced leaf area, and restricted new shoot growth (Arrington and DeVetter, 2017; Meriño-Gergichevich et al., 2017). De Silva et al. (2022) found that with increasing boron deficiency severity, flower buds may fail to open normally, pollen tube growth can be inhibited, seed development may be impaired, and fruit deformation may occur, highlighting the essential role of boron in reproductive tissue development. In various fruit crops, boron deficiency has also been associated with physiological disorders and reduced commercial fruit quality (Álvarez-Herrera et al., 2025).

Both male and female reproductive tissues have relatively high boron requirements, and boron deficiency can reduce pollen production, pollen viability, pollen tube elongation, and the functionality of transmitting tissues (De Silva et al., 2022). However, studies in blueberry have shown that even when tissue boron concentrations are increased, correcting low boron status does not necessarily improve fruit set or yield, indicating that boron availability represents only one of multiple factors limiting production performance (Arrington and DeVetter, 2017; Leon-Chang and Bryla, 2024). The optimal range between boron deficiency and toxicity is relatively narrow and is influenced by cultivar differences, making excessive boron application more likely to exceed suitable levels under intensive fertilization conditions.

Excessive boron supply can inhibit plant growth, reduce photosynthetic efficiency, and subsequently affect yield and fruit quality. Such effects have been demonstrated in blueberry and other fruit crops (Luo et al., 2024; Reyes-Díaz et al., 2024). Therefore, the objective of boron management in blueberry production should be to maintain an appropriate nutritional level. Proper control of boron application rates and timing is essential for maximizing its beneficial effects on fruit development and quality formation while avoiding potential toxicity risks.

5 Synergistic Effects of Calcium and Boron Nutrition on Blueberry Quality

5.1 Interaction between calcium and boron in cell wall formation

Calcium and boron act on different components of fruit cell walls, and their synergistic effects are mainly reflected in pectin stabilization and the maintenance of cell wall structural integrity. Lopes et al. (2026) reported that blueberry fruit texture is highly dependent on cell wall composition, cell membrane integrity, and pectin structures responsible for connecting adjacent cells. Cell wall-bound Ca^{2+} enhances pectin stability and regulates the activities of cell wall degradation-related enzymes. In various fruit systems, both calcium and boron interact with pectin structures and jointly contribute to the stability of cell wall networks. Calcium mainly enhances pectin network stability through the formation of “egg-box” structures between Ca^{2+} and de-esterified pectin, whereas boron improves cell wall adhesion and rigidity by participating in the formation of borate ester bonds associated with RG-II (Figure 3). Du et al. (2025) reported in citrus that combined Ca+B treatment reduced water-soluble pectin content while increasing the proportions of CDTA-soluble pectin and sodium carbonate-soluble protopectin, indicating that this treatment delayed pectin solubilization and enhanced peel structural stability.

Similar mechanisms have been demonstrated in tomato and strawberry. In tomato, boron was found to promote calcium distribution in the symplast and reduce pectin methylesterase activity (Gholamnejad et al., 2023). In strawberry, boron maintained cell wall-bound boron levels and promoted cross-linking interactions between boron and structural components such as pectin, cellulose, and hemicellulose, thereby improving cell wall stability during storage (Zhang et al., 2024).

Calcium and boron also exhibit complementary effects in maintaining fruit firmness. Calcium mainly increases tissue strength by enhancing middle lamella stability and the structural integrity of cell wall polysaccharide networks, whereas boron contributes to firmness preservation by limiting pectin degradation and softening-related

cell wall disassembly processes (Khalaj et al., 2016; Álvarez-Herrera et al., 2025). In apple, postharvest calcium treatment and combined calcium-boron treatment both delayed fruit softening, primarily through reduced pectin solubilization and decreased activities of pectin lyase, β-galactosidase, and α-L-arabinofuranosidase, although calcium treatment showed a stronger effect than boron application alone (Mohebbi et al., 2020). In tomato, Haleema et al. (2024) found that combined Ca+B treatment improved fruit firmness more effectively than either nutrient applied separately, which was attributed to boron-mediated enhancement of calcium metabolism and reinforcement of cell wall cross-linked polymer networks. Liu et al. (2022) reported that calcium treatment increased apricot fruit firmness by 41.53% while reducing the activities of polygalacturonase, β-galactosidase, and pectin methylesterase. Strawberry studies have also shown that foliar boron application can increase fruit firmness and delay firmness loss during storage (Zhang et al., 2024). For blueberry, this synergistic mechanism has strong physiological relevance. During blueberry ripening and storage, continuous pectin solubilization contributes to fruit softening and firmness loss. However, responses under commercial production conditions remain strongly influenced by cultivar characteristics and application timing, and consistent improvements are not observed under all circumstances.

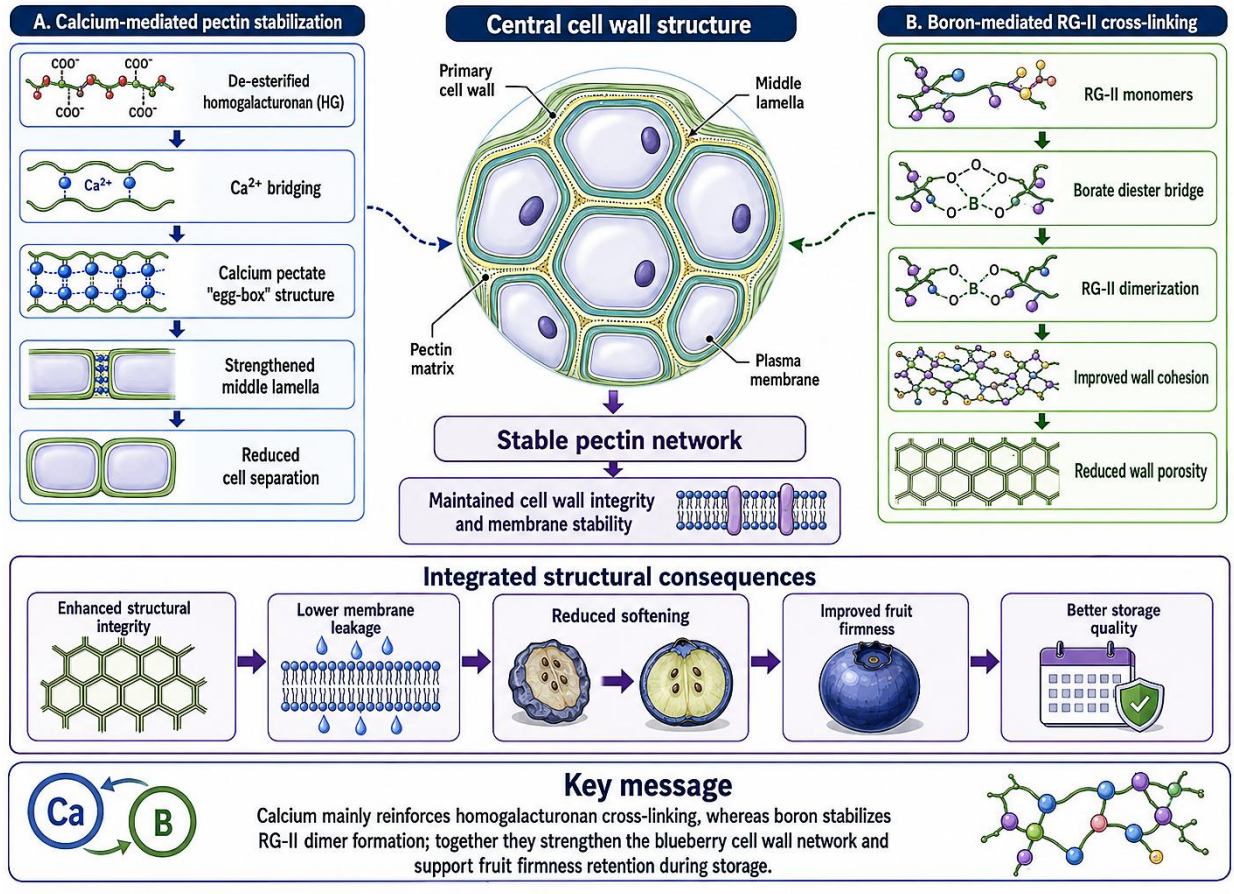


Figure 3 Complementary roles of calcium and boron in maintaining blueberry cell wall integrity

Image caption: Calcium and boron maintain blueberry fruit cell wall stability through complementary functions. Calcium primarily binds to de-esterified homogalacturonan (HG) to form calcium pectate cross-linked structures, thereby enhancing middle lamella stability. Boron promotes RG-II dimerization and borate ester bridge formation, improving pectin network integrity. The synergistic effects of calcium and boron reduce cell wall degradation and membrane damage, thereby delaying fruit softening and improving fruit firmness and storage stability

5.2 Combined effects on fruit development and storage performance

Calcium–boron combined nutrition can improve fruit size and quality components in some fruit crops; however, compared with other fruit trees, blueberry exhibits a more complex response to this combined treatment. El-Motaium et al. (2025) found that combined application of nano-calcium and boron resulted in the highest

mango yield, while also improving fruit firmness, total soluble solids content, and reducing acidity. In strawberry, Ca+B treatment increased fruit firmness, soluble solids, sugar content, vitamin C, anthocyanin content, and marketable fruit yield (Mohamed et al., 2021). However, research results in blueberry are not entirely consistent. In the southern highbush blueberry cultivar 'Sharpblue', preharvest boric acid + $CaCl_2$ foliar application increased yield and extended storage duration, while combined nutrient treatment reduced physiological weight loss and decay rate under cold storage conditions (Negi and Upadhyay, 2024). However, in northern highbush blueberry, repeated foliar applications of calcium and boron did not increase fruit firmness, single fruit weight, fruit set rate, or yield. Although calcium concentrations in plant tissues changed after treatment, fruit calcium concentration did not increase significantly (Arrington and DeVetter, 2017). These differences indicate that the effects of calcium-boron synergism on blueberry fruit size and firmness largely depend on cultivar characteristics, initial nutritional status, and the efficiency of nutrient transport into developing fruits.

Currently, the most convincing evidence for calcium–boron synergistic effects is mainly focused on postharvest quality maintenance. In blueberry, Lobos et al. (2021a) reported that early calcium application increased fruit firmness of 'Liberty' blueberry by approximately 10%, reduced water loss, increased the proportion of healthy fruits, and decreased decay and dehydration after storage, indicating that calcium application timing plays an important role in storage performance. Reviews related to blueberry also indicate that storage losses mainly result from water loss, fungal infection, and continuous weakening of cell wall structures. When preharvest nutrient management effectively enhances fruit structural stability, it has the potential to improve storage performance (Lopes et al., 2026). However, not all calcium-based nutritional programs can extend shelf life. Vance et al. (2017) evaluated $CaCl_2$, $CaCl_2$+B, calcium silicate, chelated calcium, and calcium acetate in strawberry, raspberry, blackberry, and four blueberry cultivars, including Spartan, Liberty, Draper, and Legacy, with calcium concentrations ranging from 0.05% to 0.30%. Treatments were applied three to four times continuously from the immature green fruit stage, and fruit quality was evaluated at 5, 10, 15, and 20 days after harvest. The results showed that none of the treatments significantly altered calcium concentrations in leaves or fruits, nor did they improve fruit firmness, skin toughness, weight loss rate, collapse rate, or shelf life. Electrostatic spraying also did not outperform conventional spraying. These findings indicate that simply increasing spray coverage does not necessarily mean that calcium can effectively enter fruit tissues or cell wall structures.

5.3 Nutrient balance and optimization strategies

Improvement of fruit quality depends more on the balance between calcium and boron supply rather than simply increasing the input of a single element. For example, in tomato, higher calcium levels combined with higher boron supply resulted in better quality and yield performance. Meanwhile, boron was able to modify calcium distribution within plants and fruits, increase symplastic Ca content, and slightly enhance the transfer index from apoplast to symplast (Gholamnejad et al., 2023). Haleema et al. (2024) also found in tomato that Ca+B treatment had a significantly greater effect on improving fruit firmness than calcium or boron application alone. Moreover, boron increased fruit calcium content, indicating that boron may promote calcium binding and utilization within cell wall structures. El-Motaium et al. (2025) reported that in mango, the optimal treatment was not the highest nano-calcium application rate, but rather 250 mg/L boron combined with 50% of the recommended nano-calcium level, further demonstrating that appropriate nutrient ratios and balanced supply are more beneficial for quality formation than simply increasing nutrient inputs. This principle is also applicable to blueberry because fruit firmness is closely associated with pectin structure and cell wall-bound calcium, while boron may participate in cell wall maintenance and reproductive development processes. However, direct studies on the optimal Ca:B ratio in blueberry remain limited.

Optimization of calcium and boron nutrition also requires avoiding nutrient imbalance, inappropriate application timing, and low nutrient utilization efficiency. Calcium is mainly transported through the xylem, while fruit transpiration is relatively low; therefore, calcium delivery to fruits is often restricted. Meanwhile, both calcium and boron have certain limitations in their transport and distribution within plants. Compared with non-targeted fertilization, multiple foliar applications during critical developmental stages are often more effective. Arrington

and DeVetter (2017) demonstrated in blueberry that conventional foliar calcium and boron applications do not necessarily improve fruit quality when plant nutritional status, cultivar differences, and nutrient transport efficiency are not considered, because treatments may only increase leaf boron concentration without improving fruit calcium levels, firmness, shelf life, fruit set, or yield.

6 Integrated Calcium and Boron Management for Blueberry Production

6.1 Optimization of calcium and boron application strategies

During the period from flowering to fruit maturity, plant nutrient requirements and nutrient transport capacity undergo significant changes. Therefore, integrated calcium and boron management in blueberry should be regulated according to phenological stages. During flowering and early fruit set stages, calcium and boron are closely associated with reproductive success. Insufficient nutrient supply during flowering, ovule fertilization, and young fruit development may reduce fruit set, with boron being particularly important for pollen germination and cell elongation (Álvarez-Herrera et al., 2025). During the early fruit expansion stage, before extensive cuticle formation occurs, calcium absorption and transport into fruits are relatively efficient. Therefore, the first few weeks after flowering are generally considered the optimal period for targeted calcium supplementation to fruits (Lopes et al., 2026). As fruits enter the ripening stage, reduced fruit transpiration and increased wax deposition on the cuticle restrict nutrient entry, resulting in gradually reduced calcium uptake capacity. Meanwhile, under high-temperature and high vapor pressure deficit stress conditions, calcium and boron uptake may also become stabilized or even decline (Arrington and DeVetter, 2017; Lopes et al., 2026). This developmental pattern explains why early calcium spraying in ‘Liberty’ blueberry improved fruit firmness and reduced weight loss, whereas later applications showed relatively weaker effects (Lobos et al., 2021a).

Current studies indicate that the focus of calcium and boron management in blueberry should be maintaining appropriate nutrient supply and optimizing application timing rather than simply increasing fertilizer inputs. In ‘Draper’ and ‘Bluecrop’ blueberry, Arrington and DeVetter (2017) found that continuous calcium and boron spraying from the early pink bud stage to the end of flowering increased leaf boron concentration but did not improve fruit calcium concentration, fruit set, yield, single fruit weight, or firmness, indicating that routine annual applications do not necessarily result in quality improvements. Similarly, foliar calcium application at recommended concentrations during the green fruit stage in multiple blueberry cultivars did not increase fruit calcium levels, firmness, or shelf life, suggesting that nutrient delivery efficiency into fruits remains a limiting factor (Vance et al., 2017). In contrast, preharvest application of 400-800 g Ca/ha improved postharvest quality in ‘Liberty’ blueberry, while high-frequency calcium spraying beginning at mid-full bloom in ‘Draper’ blueberry alleviated green fruit drop. These results indicate that cultivar differences, nutrient deficiency status, and application timing are more decisive factors determining final outcomes than simply supplying nutrients.

For boron management, current recommendations suggest supplementing 0.4-2.5 kg/ha boron when summer leaf boron concentrations in blueberry are ≤30 ppm, while foliar spraying concentrations exceeding approximately 500 ppm may increase the risk of phytotoxicity (Arrington and DeVetter, 2017; Leon-Chang and Bryla, 2024). Controlled environment studies further demonstrated that a foliar boron concentration of approximately 400 mg/L was safer and more effective than 800 mg/L, as excessive boron reduced photosynthetic performance and increased lipid peroxidation levels (Hirzel et al., 2025; Lopes et al., 2026). Currently, direct studies on the optimal Ca:B ratio in blueberry remain insufficient. However, studies in tomato, mango, strawberry, and Asian pear have consistently shown that, under appropriate nutrient ratios, combined Ca+B application generally improves fruit firmness, soluble solids content, and yield more effectively than single nutrient treatments, whereas excessive nutrient supply does not further enhance fruit quality (Mohamed et al., 2021; Gholamnejad et al., 2023; El-Motaium et al., 2025).

6.2 Integration of nutrient management with orchard practices

Irrigation strategy is an important component of the blueberry calcium and boron management system, as the uptake and transport of both elements are highly dependent on xylem transport and water movement in the

rhizosphere. Boron mainly enters blueberry roots through mass flow, making boron deficiency more likely in coarse-textured soils with low organic matter content. Under such conditions, drip irrigation combined with fertigation is generally more suitable than large-scale soil fertilization for maintaining a stable boron supply. A field study conducted in Oregon by Leon-Chang and Bryla (2024) showed that weekly boron fertigation from April to July was the only approach that increased soil extractable boron concentrations to recommended levels, whereas foliar boron application was more effective in increasing boron concentrations in leaves, roots, and fruits. Irrigation conditions also influence calcium use efficiency because under low transpiration conditions, calcium accumulation in fruits is usually lower than that in leaves, and high root-zone temperatures during later growth stages can further restrict calcium and boron uptake.

Studies on sweet cherry provide additional mechanistic insights. Under boron-deficient soil conditions, calcium allocation to branches, leaves, and edible tissues was reduced, while more calcium remained in roots and seeds, indicating that boron deficiency may impair effective calcium transport and distribution within plants (Bonomelli et al., 2025). Therefore, in blueberry production, calcium and boron nutritional management should consider the interactions between these two elements to achieve synergistic regulation. Rhizosphere chemical conditions determine whether applied calcium and boron can be effectively absorbed and utilized by plants. Blueberry prefers acidic soil conditions; however, excessively low pH and high rainfall conditions generally reduce boron availability, while excessive concentrations of aluminum, iron, and manganese in acidic substrates may also inhibit calcium uptake (Zydlik et al., 2022; Leon-Chang and Bryla, 2024). In soilless cultivation systems, the proportion of ammonium nitrogen and the type of nitrogen fertilizer can also alter nutrient balance. For example, Anwar et al. (2024) found that an NH_4^+:NO_3^- ratio of 50:50 increased leaf calcium content, promoted flowering and fruiting, and enhanced photosynthetic capacity. However, under potted conditions, increasing ammonium sulfate application increased leaf calcium content in some cultivars but reduced leaf boron levels in most cultivars.

The suitable range of soil calcium availability in blueberry is relatively narrow and shows strong site-specific variation. Under commercial production conditions, low-dose soil calcium application increased exchangeable calcium content but did not improve fruit firmness, size, or weight in ‘Duke’ and ‘Legacy’ blueberry (Hirzel, 2023). Optimization of the root-zone environment requires comprehensive consideration of soil pH, nitrogen forms, water supply, soil physical properties, and the nutrient requirements of specific cultivars.

6.3 Application of calcium and boron regulation in quality-oriented production

For blueberry production targeting high quality and high commercial value, the currently more reliable strategy is to implement early precise calcium supplementation combined with boron nutritional management based on boron deficiency risk assessment. Existing studies have shown that calcium has the most significant effects on fruit firmness and storage performance when it can effectively enter fruits and increase fruit calcium levels. For example, in ‘Liberty’ blueberry, early preharvest calcium application increased fruit firmness, reduced polygalacturonase activity, and decreased decay and dehydration, thereby improving postharvest quality (Lobos et al., 2021a). Some foliar fertilizers containing calcium and micronutrients have also been shown to increase blueberry fruit weight, firmness, soluble solids content, and post-storage quality; however, these effects are usually influenced by the combined action of multiple components in the formulations and cannot be fully attributed to calcium alone (Zydlik et al., 2022).

In contrast, boron management plays a more consistent role in maintaining normal reproductive development and can increase soluble solids content in some cultivars through foliar spraying or fertigation (Leon-Chang and Bryla, 2024). Negi and Upadhyay (2024) found in southern highbush blueberry that preharvest $CaCl_2$, boric acid, and their combined treatments all reduced physiological weight loss and decay rate during cold storage, indicating that appropriate calcium–boron combinations have the potential to extend storage life.

Sustainable high-quality blueberry production requires the establishment of an integrated nutrient management system based on cultivar characteristics, tissue nutrient diagnosis, and orchard stress management. Blueberry responses to calcium are highly variable, the optimal range of boron availability is relatively narrow, and the

transport of both elements into fruits is subject to certain limitations. Future sustainable management strategies should integrate leaf and soil testing results, implement precise fertigation or foliar fertilization according to phenological stages, and strengthen pH regulation and rhizosphere ecological management. Lopes et al. (2026) demonstrated that rhizosphere microbial inoculation and other preharvest regulation measures can promote nutrient uptake in blueberry and improve fruit size, yield, and firmness. Therefore, calcium and boron nutritional management should shift from a single fertilizer input model toward an integrated regulation system based on plant requirements, environmental conditions, and quality objectives, thereby achieving coordinated improvement of fruit quality and efficient resource utilization.

7 Concluding Remarks

Calcium and boron are important mineral nutrients affecting blueberry fruit firmness formation and postharvest quality maintenance. Their functions are mainly associated with cell wall structural stability, membrane system maintenance, and fruit development regulation. Calcium forms stable pectin cross-linked structures by binding with de-esterified pectin, thereby enhancing middle lamella stability, reducing pectin degradation and cell separation, and delaying fruit softening. Boron contributes to fruit structural formation through RG-II cross-linking, maintenance of cell wall integrity, and promotion of pollen germination and young fruit development. Both nutrients participate in the construction of cell wall networks, providing a physiological basis for maintaining blueberry fruit texture and storage stability.

Current studies indicate that preharvest calcium supplementation has relatively clear effects on improving blueberry fruit firmness and delaying postharvest quality deterioration; however, its effectiveness is highly dependent on application timing, cultivar characteristics, and calcium transport efficiency into fruits. For example, early preharvest calcium spraying in ‘Liberty’ blueberry increased fruit firmness and reduced weight loss and decay risk, whereas later applications showed relatively limited effects. This difference is mainly related to the fact that calcium transport into blueberry fruits relies predominantly on xylem movement, while fruit transpiration decreases and calcium accumulation capacity declines during ripening. In comparison, boron plays a more stable role in maintaining normal reproductive development and the formation of certain quality traits. However, increasing boron levels in plants or fruits does not necessarily directly translate into improvements in firmness and yield, as its effects are constrained by nutritional status and environmental conditions.

Combined calcium and boron regulation provides a new management approach for improving blueberry quality. Theoretically, calcium mainly enhances pectin network stability, whereas boron contributes to RG-II cross-linking and improves cell wall structure, indicating complementary functions between these two nutrients. However, the synergistic effects of calcium and boron in blueberry production remain highly variable. Some studies have demonstrated improvements in firmness, weight loss reduction, and storage performance, whereas others have not observed significant quality enhancement. These differences indicate that simply increasing calcium and boron inputs does not guarantee improved fruit quality. Instead, the efficiency of nutrient transport into fruits, the synchronization between application timing and critical developmental stages, and the intrinsic nutrient uptake and utilization capacity of cultivars may be more important than fertilizer input levels alone.

Calcium and boron management in blueberry production should shift from a traditional nutrient supplementation approach toward a precision regulation model based on cultivar characteristics, nutritional diagnosis, and fruit developmental stages. Currently, a more reasonable production strategy is to conduct targeted calcium supplementation during the early post-flowering period, evaluate boron deficiency risks according to soil and leaf nutrient status, and improve nutrient utilization efficiency through integrated measures such as drip irrigation, fertigation, and rhizosphere environment optimization. Future research should further investigate calcium and boron uptake and transport mechanisms in blueberry, optimal Ca:B ratios, and differences in cultivar responses, thereby establishing a more precise and efficient quality-oriented nutrient management system to achieve coordinated improvements in fruit firmness, storage life, and resource utilization efficiency.

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The authors affirm 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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Research Report Open Access

Evaluation of Growth and Yield Parameters of Okra (*Abelmoschus esculentus*) Varieties at Chakarghatta, Sarlahi

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Abstract Farmers continue to struggle with the productivity and production of Okra. One of the main causes of the low productivity of Okra is lack of high yielding varieties. In order to determine the yield of various okra types under open field circumstances, field experiments were conducted from 2025 March 2 to June 14. Seven treatments with three replications in RCBD made up the trial. The treatments included seven different varieties of okra: Arka Anamika, Selection no.07, Bhindi F1, Rohini, Super Anamika, NOL 303 Julie and Swaraj Pan 2155. Among the various variety maximum plant height was obtained in Bhindi F1(9.80 cm) and minimum plant height was obtained in Selection no. 07 (6.93 cm) at 30 DAS. The maximum leaf number was observed in Selection No.07 (47.93) and minimum leaf number was observed in Swaraj Pan 2155 (26.20) at 70 DAS. Moreover, the highest number of primary branches were found in Selection No.07 (3.58). Arka Anamika reached the earliest among the varieties in days to 50% flowering (52.67 DAS). On contrary to this Swaraj Pan (10.46) obtained the maximum number of pods. The pod length was highest in Swaraj Pan 2155 (13.39 cm) and lowest in NOL303 Julie (9.64 cm). Further, the study shows no difference in the girth of pod and individual weight of pod. Maximum yield was obtained by Swaraj Pan 2155 (7.04 t/ha) and minimum in Super Anamika (3.91 t/ha). So, from our study Swaraj Pan 2155 is inferred as high yielding variety and best suited for Chakarghatta, Sarlahi.

Keywords Okra (*Abelmoschus esculentus*); Growth parameter; Replication; Variety

1 Introduction

Okra (*Abelmoschus esculentus* L. Moench) is one of the most widely cultivated and utilized vegetable crops belonging to the family Malvaceae, and it possesses the highest chromosome number (2n=130) among cultivated vegetables. The crop is known by various local names across the world, such as "lady's finger" in England, "gumbo" in the United States, "bhindi" in India, and "bamia" in Ethiopia (Mkhabela et al., 2022). It is an economically important vegetable crop grown widely in the tropical and subtropical regions of the world (Oyelade et al., 2003). India is the world's leading okra-producing country, with Uttar Pradesh, Bihar, and West Bengal as the major producing states (Swamy, 2023).

Despite these shared nutritional and economic benefits, individual okra genotypes differ considerably in their growth habit, flowering behavior, pod characteristics, and yield potential. These differences arise not only from genetic makeup but also from strong genotype-environment interactions, meaning that a variety bred or selected for one agroecological zone does not necessarily perform equally well under different soil, temperature, and photoperiod conditions. Consequently, varietal performance evaluation trials are essential before recommending a cultivar for a new production environment, since a single variety is unlikely to be optimal across all climatic and agroecological conditions.

In Nepal, several studies have evaluated okra varieties across different agroecological regions, and their results consistently demonstrate that varietal performance is location-dependent. In Chitwan, trials on spacing and mulching have shown clear yield and growth responses under local conditions (Jha et al., 2018). More recent

Chitwan-based studies on seed priming have similarly reported significant genotype-linked variation in germination and yield traits. In Morang district, cultivation-method trials have documented distinct growth and yield responses of okra to spacing and mulching practices under the local subtropical climate (Shreevastav et al., 2023).

Although these studies confirm that okra varieties respond differently depending on the growing environment, systematic, comparative information on okra varietal performance specific to the Chakarghatta area of Sarlahi district remains lacking. Sarlahi lies in the Terai agroecological belt, which differs in soil type, temperature regime, and rainfall pattern from Chitwan and Morang where the above trials were conducted. Because varietal response to growth and yield traits is strongly influenced by local agroecological conditions, findings from these other regions cannot be reliably extrapolated to predict variety performance in Sarlahi. This creates a clear need for location-specific varietal evaluation before any variety can be confidently recommended to farmers of this region.

Therefore, the present study was undertaken to evaluate the growth, flowering, and yield performance of different okra varieties under the agroclimatic conditions of Chakarghatta, Sarlahi, with the objective of identifying variety best suited for higher productivity in this region. It is expected that the findings will provide farmers and extension agencies in Sarlahi with reliable, location-specific varietal recommendations and contribute to filling the existing information gap on okra variety performance in this agroecological zone.

2 Materials and Methods

2.1 Experimental site

The research was conducted in the farmer's field in Chakarghatta rural municipality, Khoriya, Sarlahi district, Madhesh province. This region lies in Terai of Nepal covering area of 25.16 Square Kilometer. Sarlahi district is in latitude 26°58'08.04" North and 85°34' 06.24" East longitudes. The research site was located at Chakarghatta rural municipality, Khoriya, Sarlahi. The average highest and lowest temperature is 37.3 °C and 12.03 °C. The soil type of this area is Sandy loam, moderately acidic in soil reaction.

2.2 Research detail

The experiment was conducted in randomized complete block design (RCBD) with seven treatments and three replications (Table 1). All together there were 21 plots, each plot containing 4 rows and 5 plants per row. Each plot contained 20 Plants where inner 5 plants was selected as sample. Net experiment plot was 3.5 meter square, having spacing of 0.5 m between treatment and 1m between replications. Total area for research was 110.5 meter square. The spacing between row to row is 50 centimeter and plant to plant is 30 centimeter. Recommended dose of fertilizer is applied in the field (118:79:39 NPK kg/ha), 0.43 kg of potassium and 0.86 kg phosphorous and 0.65 kg of nitrogen was applied during sowing time and remaining dose of Nitrogen (0.32 kg) was applied at two split doses. Weeding was carried out and irrigation was done at weekly interval.

Table 1 Treatment consists of seven different varieties

S. N	Treatment
1	Arka Anamika
2	Selection no. 07
3	Bhindi F1
4	Rohini
5	Super Anamika
6	NOL 303 Julie
7	Swaraj pan 2155

2.3 Data collection

From each experimental plot randomly 5 inner plants were selected for data collection. Tagging of plants were done using colorful plastics. Plant height and number of leaves were recorded from randomly selected 5 plants at

every 10 days interval. Similarly, number of branches were recorded at 60 DAS. Days to 50% flowering was recorded. The total number of pods from the selected plants was recorded. And it was converted into number of pods per plant. Weight of pod was measured in gram by using digital weighing machine. And it was converted into ton per hectare based on yield per plant.

2.4 Statistical analysis

The collected data was entered into MS Excel (2019) and analyzed using r- studio (4.5.1 version). The mean comparison was done using DMRT.

3 Results and Analysis

3.1 Plant height

The statistical analysis indicates that there is significant difference at 5% level of significance between the plant height of different varieties at observation of 30 DAS (Table 2). Bhindi F1 produce the maximum plant height (9.80 cm). The minimum plant height was produced by Selection no. 07 (6.93 cm). The study shows a significant difference in plant height at 5% level of significance at 40 DAS. The maximum plant height is attained by NOL 303 Julie (18.23 cm) and minimum by Swaraj Pan (14.72). The study shows that the difference in the plant height among the varieties is insignificant after 40 DAS.

Table 2 Plant height of different varieties of okra at Chakarghatta, Sarlahi

Variety	Plant height (cm)				
	30 DAS	40 DAS	50 DAS	60 DAS	70 DAS
Arka Anamika	7.90^{bc}	15.41^{b}	31.00	45.41	63.33
Selection no 07	6.93^{c}	15.87^{b}	27.08	51.48	72.20
Bhindi F1	9.80^{a}	16.26^{ab}	34.16	51.43	71.60
Rohini	8.61^{ab}	15.41^{b}	33.56	53.20	71.40
Super Anamika	8.45^{ab}	15.20^{b}	31.46	49.30	66.06
NOL 303 Julie	8.64^{ab}	18.23^{a}	32.33	49.04	66.60
Swaraj Pan2155	9.09^{ab}	14.72^{b}	33.40	50.64	69.70
Grand mean	8.49	15.84	31.85	50.07	68.70
SEm (±)	0.47	0.66	1.69	2.38	3.28
LSD (0.05)	1.44	2.05	5.21	7.33	10.11
CV (%)	9.59	7.29	9.20	8.23	8.27
F test	*	*	ns	ns	ns

Note: LSD: Least Significant Difference, SEm: Standard Error of Mean; CV: Coefficient of Variation, letters “a”, “b”, “c” represent the ranking of treatments according to DMRT at 0.05 level of significance, DAS: Days After Sowing, ns: Non-Significant, * significant at 5% level of significance, ** significant at 1% level of significance, *** significant at 0.1% level of significance

3.2 Number of leaves

The data recorded at 30 DAS shows significant result in the leaf number at 1% level of significance where maximum leaf number is observed in Bhindi F1(5.23) which is at par with variety Rohini (Table 3). Similarly, minimum number of leaves is observed in Arka Anamika (3.63). Furthermore, at 40 DAS maximum leaf number is observed in Bhindi F1 (8.13) and minimum leaf number is observed in Arka Anamika (6.06). Additionally, Rohini, Super Anamika, NOL 303 Julie and Swaraj Pan 2155 are statistically similar. The observation of leaf number is statistically similar at 50 and 60 DAS. Moreover, Maximum leaf number is observed in Selection no 07 (47.93) at 70 DAS.

3.3 Number of lateral branches

There is a significant difference in the number of lateral branches among the varieties at 5% level of significance. The highest number of lateral branches is observed in Selection no. 07 (3.58). Likewise, Super Anamika (2.86) and NOL 303 Julie are statistically similar and minimum number of lateral branches is observed in Rohini (2.56).

Table 3 Number of leaves of different varieties of okra at Chakarghatta, Sarlahi

Variety	No of leaves				
	30 DAS	40 DAS	50 DAS	60 DAS	70 DAS
Arka Anamika	3.63^{c}	6.06^{c}	13.86	25.26	35.93^{bc}
Selection no. 07	4.70^{b}	7.53^{ab}	14.50	27.91	47.93^{a}
Bhindi F1	5.23^{a}	8.13^{a}	13.06	23.46	37.66^{bc}
Rohini	4.80^{ab}	6.53^{bc}	13.53	23.73	33.06^{bcd}
Super Anamika	4.46^{b}	6.60^{bc}	11.40	20.26	30.33^{cd}
NOL 303 Julie	4.46^{b}	6.23^{bc}	16.53	25.65	40.67^{ab}
Swaraj Pan 2155	4.67^{b}	6.86^{bc}	12.46	20.06	26.20^{d}
Grand mean	4.56	6.85	13.62	23.76	35.97
SEm (±)	0.45	0.33	1.52	2.30	2.51
LSD (0.05)	0.44	1.02	4.71	7.08	7.74
CV (%)	5.42	8.42	19.45	16.76	12.10
F test	**	**	ns	ns	**

Note: LSD: Least Significant Difference, SEm: Standard Error of Mean; CV: Coefficient of Variation, letters “a”, “b”, “c” represent the ranking of treatments according to DMRT at 0.05 level of significance, DAS: Days After Sowing, ns: Non-Significant, * significant at 5% level of significance, ** significant at 1% level of significance, *** significant at 0.1% level of significance

3.4 Days to 50 % flowering

There is a significant result in 50% flowering at 0.1% level of significance where Arka Anamika reached the earliest among the varieties in days to 50% flowering (52.67 DAS). Similarly, Selection no.07 attained 50% flowering at 56.33 DAS which is at par with Bhindi F1, Rohini, NOL 303 Julie and Swaraj Pan 2155 whereas late flowering occurs in Super Anamika (60.67 DAS).

3.5 Length and girth of pod

Length of pod is found statistically significant at 0.1% level of significant (Table 4). The highest fruit length is found in Swaraj Pan 2155 (13.39 cm) followed by Selection no. 07 (11.92 cm) and super Anamika (11.54 cm) which is at par with Rohini (11.07 cm). the lowest pod length is found in NOL 303 Julie (9.64 cm) which is statistically similar with Bhindi F1 (9.79 cm). The average fruit girth is statistically similar ranging from 6.14 cm to 5.03 cm.

Table 4 Number of branches, 50% flowering, length of pod and girth of pod of different varieties of okra at Chakarghatta, Sarlahi

Variety	No of branches	50% flowering	Length of pod (cm)	Girth of pod (cm)
Arka Anamika	3.13^{abc}	52.67^{c}	10.82^{bcd}	5.43
Selection no. 07	3.58^{a}	56.33^{b}	11.92^{b}	6.14
Bhindi F1	3.13^{abc}	56.00^{b}	9.79c^{d}	5.54
Rohini	2.56^{cd}	56.00^{b}	11.07^{bc}	5.03
Super Anamika	2.86^{bcd}	60.67^{a}	11.54^{b}	5.74
NOL 303 Julie	2.86^{bcd}	57.33^{b}	9.64^{d}	5.36
Swaraj Pan 2155	3.26^{ab}	55.33^{b}	13.39^{a}	5.31
Grand mean	3.00	56.33	11.17	5.51
SEm (±)	0.19	0.78	0.42	0.29
LSD (0.05)	0.58	2.41	1.30	0.90
CV (%)	11.01	2.45	6.57	9.27
F test	*	***	***	ns

Note: LSD: Least Significant Difference, SEm: Standard Error of Mean; CV: Coefficient of Variation, letters “a”, “b”, “c” represent the ranking of treatments according to DMRT at 0.05 level of significance, DAS: Days After Sowing, ns: Non-Significant, * significant at 5% level of significance, ** significant at 1% level of significance, *** significant at 0.1% level of significance

3.6 Number of pod and pod weight

The number of pods per plant is statistically significant at 0.1% level of significance (Table 5). The maximum number of pods is found in Swaraj Pan 2155 (10.46) followed by Rohini (8.50) and NOL 303 Julie (7.50). Similarly, minimum number of pods is found in Super Anamika (5.10) which is at par with Arka Anamika, Selection no.07 and Bhindi F1.

The individual pod weight is statistically similar ranging from 14.58 to 13 gram.

3.7 Yield per plant and yield per hectare

Yield per plant is found to be statistically significant at 1% level of significant (Table 5). The maximum yield per plants obtained in Swaraj Pan 2155 (105.33 gram) where Selection no.07, Bhindi F1 and Rohini are statistically at par and minimum yield per plant is found in Super Anamika (58.73) gram.

Similar result is recorded in yield per hectare where maximum yield per hectare is obtained in Swaraj Pan 2155 (7.04 ton per hectare) which is statistically at par with Selection no.07, Bhindi F1 and Rohini. Similarly, minimum yield is recorded in Super Anamika (3.91 ton per hectare).

Table 5 Number of pods, weight per pod, yield per plant and yield per hectare of pod of different varieties of Okra at Chakarghatta, Sarlahi

Variety	No of pod	Weight per pod	Yield per plant	Yield per hectare
Arka Anamika	6.43^{cd}	13.67	79.50^{b}	5.30^{b}
Selection no. 07	6.00^{cd}	14.58	87.33^{ab}	5.82^{ab}
Bhindi F1	6.03^{cd}	14.00	89.33^{ab}	5.95^{ab}
Rohini	8.50^{b}	13.00	96.00^{ab}	6.39^{ab}
Super Anamika	5.10^{d}	14.58	58.73^{c}	3.91^{c}
NOL 303 Julie	7.50^{bc}	14.00	84.33^{b}	5.62^{b}
Swaraj Pan 2155	10.46^{a}	14.13	105.33^{a}	7.04^{a}
Grand mean	7.14	13.80	85.84	5.72
SEm (±)	0.48	1.12	5.68	0.37
LSD (0.05)	1.49	3.46	17.51	1.16
CV (%)	11.75	14.13	11.46	11.46
F test	***	ns	**	**

Note: LSD: Least Significant Difference, SEm: Standard Error of Mean; CV: Coefficient of Variation, letters “a”, “b”, “c” represent the ranking of treatments according to DMRT at 0.05 level of significance, DAS: Days After Sowing, ns: Non-Significant, * significant at 5% level of significance, ** significant at 1% level of significance, *** significant at 0.1% level of significance

4 Discussion

The height variation observed among varieties is more plausibly attributed to inherent genotypic differences than to agronomic factors, a pattern also reported by Magar et al. (2024). Notably, Selection No. 07, despite being the shortest variety, produced the highest number of leaves and primary branches, suggesting a possible compensatory growth pattern in which reduced height was associated with greater lateral branching and foliage production rather than height acting as a limiting factor for leaf development. Magar et al. (2024) similarly proposed that branch number, plant height, and photosynthetic capacity could jointly contribute to differences in leaf number among hybrids. This trend is further supported by Dulal et al. (2024), who reported statistically significant differences in leaf number across most growth stages except at 20 DAS. In the present study, leaf number was statistically similar at 50 and 60 DAS, possibly reflecting reduced nutrient demand for vegetative growth at these later stages.

Delayed flowering, as observed in some varieties, may similarly be linked to prolonged vegetative growth induced by environmental factors such as photoperiod (Aminu et al., 2016). Pod length in the present study was consistent with Khan et al. (2000), though slightly higher value, a difference likely attributable to genotypic variation among varieties. Pod diameter was statistically similar to that reported by Nepali et al. (2025), possibly reflecting the strong adaptability of these cultivars to local environmental conditions (Rahman et al., 2012).

Among the varieties, Swaraj Pan 2155 recorded the highest pod number, longest pods, and highest yield, despite producing fewer leaves and flowering later than Arka Anamika. This combination indicates that, among the traits examined, pod number and pod length contributed more directly to yield than either leaf number or flowering time. The significance of pod number as a yield-determining trait is further supported by Jonah and Kwaga (2019) and Reddy et al. (2012). Pod weight values in the present study, ranging from 13.00 to 14.50 g, fall within the range reported by Nepali et al. (2025) and are broadly consistent with Chaudhary et al. (2023), who observed pod weight ranging from 14.20 to 18.90 g across different mulching treatments. Taken together, the yield differences among varieties appear closely linked to branch number and pod number, both of which showed a direct relationship with final yield in this study.

5 Conclusion

The experimental results show that the different plant parameters help to predict the overall yield and performance of the specific plant. Flowering commences 52 to 60 days after sowing, with early flowering at 52 days for Arka Anamika. Production was varied according to number of pod and weight of pod. Highest yield and maximum number of pods is observed in Swaraj Pan 2155.

Through our experiment, Swaraj Pan 2155 was considered as the high yielding variety among all and best suited to Chakarghatta, Sarlahi. Single field experiment is not suitable for valid result. So similar research trial in the location should be done.

Authors' contributions

APY carried out the conceptualization of research, designed the experiment, collect the data and drafted the manuscript. AP helped in data analysis and helped to draft the manuscript. DK helped to draft the manuscript and supervision of the research. All authors read and approved the final manuscript.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationship that could be contruct as a potential conflict of interest.

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Research Article Open Access

Effect of Date of Pinching on Sex Expression, Growth and Yield of Cucumber (*Cucumis sativus* L. cv. Kamini) at Kawasoti, Nepal

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Abstract Farmers continue to struggle with the productivity and production of cucumbers. One of the main causes of the decreased quantity of female flowers is the low number of lateral branches. A field experiment was conducted at Nawalparasi East, Nepal from March to July 2024 to evaluate the effect of the date of pinching on the sex expression, growth, and yield. The experiment was laid out in a Randomized Complete Block Design with five treatments and four replications. *Cucumis sativus* L. cv. Kamini was used as the test crop with evaluation being the plant height, number of lateral branches, number of male and female flowers, sex ratio, fruit weight, fruit circumference, fruit length, yield per plant, yield per hectare. The treatment group included no pinching, pinching at 15 DAT, pinching at 20 DAT, pinching at 25 DAT, and Pinching at 30 DAT. Pinching can change the flowering pattern of cucurbits, favoring the emergence of female flowers. The data obtained was analyzed using R-studio and Duncan's Multiple Range Test (DMRT) was employed to find out the significant difference between the mean values at a 5% level of significance. Among various treatment control results the highest plant height (138.41 cm) and lowest in 15 DAT (90.86 cm). Pinching at 20 DAT exhibited the highest lateral branches (5.09) and lowest at control (2.06). The maximum number of female flowers was observed in pinching at 20 DAT (33.925) and lowest in control (15.125). Sex ratio was minimum in pinching at 20 DAT (1.64) and maximum in control (7.640). Similarly, Highest yield per plant was found in pinching at 20 DAT (5.77 kg/plant) and lowest in control (3.79 kg/plant). Overall, pinching at 20 DAT gives maximum yield so, farmers are recommended to pinch cucumber plant at 20 DAS for better productivity.

Keywords Cucumber (*Cucumis sativus* L.); Pinching; Lateral branches; Apical dominance

1 Introduction

Cucumber (*Cucumis sativus* L., 2n=14) is a creeping annual vine belonging to the family Cucurbitaceae and represents one of the most economically important vegetable crops worldwide. It is valued for its high water content, refreshing flavor, distinctive texture, and medicinal properties, including bioactive compounds such as cucurbitacins (Cts), which are characteristic bitter principles of this species (Mukherjee et al., 2013). Cucumber is largely consumed as a fresh product and is highly perishable, with a narrow tolerance to frost; optimum vegetative growth occurs between 20 °C and 30 °C. In Nepal, cucumber cultivation covers approximately 9,643 ha, yielding a total production of 150,213 Mt at an average productivity of 15.58 Mt/ha (MoALD, 2024/25). Given this considerable area under cultivation, even modest improvements in yield through low-cost agronomic interventions could substantially benefit smallholder farmers.

Yield in cucumber is strongly influenced by sex expression, which determines the proportion of female flowers ultimately available for fruiting. In a typical monoecious cucumber plant, male flowers predominate at the lower nodes, a mixture of male and female flowers occurs at the middle nodes, and female flowers alone appear at the upper nodes (Li et al., 2019). Fruits produced at the base of the plant tend to be smaller than those borne on lateral branches or higher nodes. Although sex expression is primarily under genetic control, it can be modified by environmental conditions, cultural management, and chemical treatments. Notably, long photoperiods and higher temperatures tend to favor male flower production, and the female-to-male flower ratio in cucumber can range widely, from 1:13 to 1:15 (Bhowmick and Jha, 2015). Therefore, agronomic techniques capable of shifting this

ratio toward a higher proportion of female flowers hold considerable practical value. Pinching, or tipping, is one such technique, in which the apical meristem is removed to break apical dominance and stimulate the emergence of two or more lateral branches from the nodes below the pinch (Rajput et al., 2020). While first- and second-generation branches tend to produce a higher proportion of male flowers often creating a misleading impression of low productivity for farmers the third-generation branches induced by pinching typically bear a greater share of female flowers. Consequently, pinching offers a simple, low-cost method of enhancing female flower production without requiring chemical inputs.

Despite this physiological basis, farmers frequently lack clear guidance on the appropriate timing of pinching to maximize its benefits, and much of the existing literature emphasizes chemical growth regulators over accessible mechanical practices. This represents a notable research gap, particularly for resource-limited farmers who require low-input, easily adoptable techniques. Pinching, being simpler to execute than hormonal spraying, is well suited to farmers with limited technical knowledge. Therefore, the present study was undertaken to determine the optimal timing of pinching in cucumber and to evaluate its effect on sex expression and yield. It is hypothesized that timely pinching improves the proportion of female flowers and enhances yield compared to unpinched plants. Furthermore, this study aims to provide practical, evidence-based recommendations that farmers can readily adopt to improve cucumber productivity.

2 Materials and Methods

2.1 Selection of site

The experiment was conducted at Kawasoti municipality ward number 17 Nawalparasi East district. It lies in the vegetable zone under PMAMP-PIU Nawalparasi East. The study site lies 4.7 km south from Mahendra Highway of Danda. It lies at an elevation of 195 m above sea level, the latitude and longitude are 27.50 °N and 84.08 °E respectively. The research site lies in the Nepal Churia range. 56% of the area lies under the lower tropical zone. The maximum and minimum temperature of the site is 31.45 °C and 20.03 °C respectively.

2.2 Experimental materials and treatment applications

The used variety in the experiment was Kamini and seeds of cucumber were bought from nearby agro vet. The used fertilizers were also brought from nearby fertilizer distributor of Kawasoti municipality. Well-decomposed farmyard manure (FYM) was applied at 1,500 kg/ropani in the experimental plot. Similarly, chemical fertilizers were applied at 7-2-5 kg/ropani (Urea, DAP and Potash). Full doses of FYM, P_2O_5, and K_2O_5 and half doses of nitrogen were placed equally in the whole plots at the time of land preparation. The remaining dose of nitrogen was applied in two equal split doses, first at 20 DAT and second at the time of flowering.

2.3 Experimental design and data collection

The experiment was conducted in a Randomized complete block design (RCBD). There were a total of five treatments and each treatment was replicated four times. Therefore, the number of plots was twenty, and each plot contained sixteen plants in two rows, and eight plants were taken randomly as sample plants. The treatments applied were different levels of Pinching as Treatment 1: Control (No pinching), Treatment 2: Pinching at 15 DAT, Treatment 3: Pinching at 20 DAT, Treatment 4: Pinching at 25 DAT, Treatment 5: Pinching at 30 DAT. The experimental field consists of twenty plots with an individual plot size of 9 m^2. A spacing of 0.75 m×0.75 m was maintained between plant to plant and between rows. 50 cm spacing was maintained between plots in the same block and 50 cm between the blocks.

2.4 Data record and analysis

Eight plants per plot, excluding border plants, were taken as sample plants for study. Plant growth and yield characters were recorded. All the recorded data were arranged systematically in Microsoft Excel version 16.89.1. To determine the significance difference between treatments, analysis of variance was carried out using R studio version 4.4.1. Duncan's Multiple Range Test (DMRT) was used for mean separation at 5% level of significance. recorded and analyzed statistically by least significant difference test.

3 Results and Analysis

3.1 Vegetative parameter

Various observations were made during the experiment on growth and yield attributes. The statistical analysis indicates that plant height was significantly affected by different dates of pinching at 45 days of observation. Control produced the plant with maximum height (138.41 cm) compared to other treatments at par with pinching at 30 DAT (124.72 cm). The minimum plant height was observed in pinching at 20 days (90.86 cm) being at par with pinching at 30 days. The mean plant height of cucumber observed at 60 DAT was statistically similar ranging from 132.125 cm to 196.675 cm (Table 1).

Similarly, the maximum number of lateral branches was observed to pinch at 20 days (5.09) followed by pinching at 25 days (3.75) (Table 1). The minimum number of lateral branches was observed at control (2.06) which was at par with pinching at 15 days (2.37) and pinching at 30 days (2.32).

Table 1 Effect of date of pinching on plant height (cm) and Number of lateral branches of cucumber (*Cucumis sativus* L. cv. Kamini) at Kawasoti, Nepal (2024)

Treatment	Plant height (cm)		Number of lateral branches
	45 DAT	60 DAT	
Pinching at 15 days	90.86^{d}	150.30	2.37^{c}
Pinching at 20 days	102.04^{cd}	132.13	5.09^{a}
Pinching at 25 days	109.72^{bc}	177.00	3.75^{b}
Pinching at 30 days	124.72^{ab}	180.00	2.32^{c}
Control	138.41^{a}	196.68	2.06^{c}
Grand mean	113.15	167.22	3.11
SEM (±)	6.37	17.25	0.30
LSD (0.05)	17.02	46.04	0.778
CV (%)	9.764	17.87	16.20
F- test	***	NS	***

Note: Means followed by common letter(s) within column are non-significantly different based on DMRT at p=0.05; LSD: Least Significant Difference; SEM: Standard Error of Mean; CV: Coefficient of Variation; DAT: Days After Transplanting; NS: Non-Significant, *** significant at 0.1% level of significance

Furthermore, the data achieved by pinching in total male flower, female flower, and sex ratio is shown in Table 2. The total number of male flowers was also found significant statistically. The highest number of male flowers was obtained on the control (114.75), which was statistically similar to pinching at 30 days. The lowest number of male flowers was obtained on pinching at 15 days (51.65), which was similar to pinching at 20 days and 25 days.

Table 2 Effect of date of pinching on male, female flower and sex ratio of Cucumber (*Cucumis sativus* L. cv. Kamini) at Kawasoti, Nepal (2024)

Treatment	Male flower	Female flower	Sex ratio
Pinching at 15 days	51.65^{b}	27.25^{ab}	2.01^{c}
Pinching at 20 days	54.00^{b}	33.92^{a}	1.64^{c}
Pinching at 25 days	58.35^{b}	29.32^{ab}	1.98^{c}
Pinching at 30 days	98.87^{a}	21.25^{bc}	4.67^{b}
Control	114.75^{a}	15.12^{c}	7.64^{a}
Grand mean	3.05	25.37	3.59
SEM (±)	12.10	3.14	0.75
LSD (0.05)	32.29	8.39	2.01
CV (%)	27.75	21.48	36.27
F- test	**	**	***

Note: Means followed by common letter(s) within column are non-significantly different based on DMRT at P=0.05; LSD: Least Significant Difference; SEM: Standard Error of Mean; CV: Coefficient of Variation; DAT: Days After Transplanting; ** significant at 1% level of significance, *** significant at 0.1% level of significance

3.2 Floral and sex expression parameters

The total number of female flowers was also found significant statistically different. Plant pinched at 20 days produced the highest number of female flowers (33.92) which was statistically at par with pinching at 15 days (27.25) and 25 days (29.32) (Table 2). The lowest number of female flowers was produced in control (15.12) which was statistically at par with pinching at 30 days (21.25). The sex ratio was also found significant statistically. The highest sex ratio was found in control (7.64) followed by pinching at 30 days (4.67). The lowest sex ratio was found in pinching at 20 days (1.64) which was statistically at par with pinching at 25 days (1.98) and pinching at 15 days (2.01).

Likewise, Table 3 displays the circumference and length of various fruits. Fruit circumference was found statistically significant. The highest fruit circumference was found in pinching at 25 days (26.43 cm) which was statistically at par with control (25.61 cm) and pinching at 30 days (23.26 cm). The lowest fruit circumference was found at pinching at 20 days (19.23 cm) which was statistically at par with pinching at 15 days (20.72 cm). The mean fruit length of cucumber was statistically similar ranging from 18.55 cm to 23.22 cm.

It also displays the number of fruits and fruit weight (Table 3). The number of fruits per plant was found statistically significant. The maximum number of fruits was found in pinching at 20 days (13.69) followed by pinching at 15 days (9.44) which was statistically at par with pinching at 25 days (9.50) and pinching at 30 days (9.13).

Table 3 Effect of date of pinching on fruit circumference (cm), fruit length (cm), number of fruits, fruit weight (gm) of cucumber (*Cucumis sativus* L. cv. Kamini) at Kawasoti, Nepal (2024)

Treatment	Fruit circumference (cm)	Fruit length (cm)	Number of fruits	Fruit weight (gm)
Pinching at 15 days	20.73^{bc}	22.33	9.44^{b}	570.75^{ab}
Pinching at 20 days	19.23^{c}	21.48	13.69^{a}	633.23^{a}
Pinching at 25 days	26.44^{a}	18.56	9.50^{b}	502.14^{bc}
Pinching at 30 days	23.26^{abc}	23.22	9.13^{b}	466.98^{cd}
Control	25.61^{ab}	23.00	6.12^{c}	415.50^{d}
Grand mean	23.052	21.716	9.575	517.78
SEM (±)	1.917	1.416	0.7067	29.12
LSD (0.05)	5.11	5.445	1.885	77.72
CV (%)	14.40	11.29	12.78	9.743
F- test	*	NS	***	***

Note: Means followed by common letter(s) within column are non-significantly different based on DMRT at P=0.05; LSD, Least Significant Difference; SEM, Standard Error of Mean; CV, Coefficient of Variation; DAT, Days After Transplanting; NS, Non-Significant, * significant at 5% level of significance, *** significant at 0.1% level of significance

Fruit weight was also found to be statistically significant. Maximum fruit weight was obtained in pinching at 20 days which was statistically at par with pinching at 15 days (570.75 gm). Minimum fruit weight was obtained in pinching at control (415.50 gm) which was statistically at par with pinching at 30 days (466.9 gm).

3.3 Yield and yield attributing parameters

Yield per plant and yield per hectare is shown in Table 4. Yield per plant was found to be statistically significant. Maximum yield was obtained in pinching at 20 days (5.7650) which was significantly at par with pinching at 15 days (5.1975). Minimum yield per plant was obtained in control (3.79), which was statistically at par with pinching at 30 days (4.25). Yields per hectare was also found to be statistically significant. Maximum yield was obtained in pinching at 20 days (46.14) which was statistically at par with pinching at 15 days. Minimum yield was obtained in control (30.54) which was statistically at par with pinching at 30 days (34.76) and pinching at 25 days (36.58).

Table 4 Effect of date of pinching on yield per plant (kg) and yield per hectare (mt/ha) of cucumber (*Cucumis sativus* L. cv. Kamini) at Kawasoti, Nepal (2024)

Treatment	Yield per plant (kg)	Yield per hectare (mt/ha)
Pinching at 15 days	5.20^{ab}	42.82^{a}
Pinching at 20 days	5.77^{a}	46.14^{a}
Pinching at 25 days	4.58^{bc}	36.58^{b}
Pinching at 30 days	4.25^{cd}	34.76^{b}
Control	3.79^{d}	30.54^{b}
Grand mean	4.71	38.16
SEM (±)	0.26	2.20
LSD (0.05)	0.71	5.89
CV (%)	9.71	9.64
F- test	***	***

Note: Means followed by common letter(s) within column are non-significantly different based on DMRT at P=0.05; LSD, Least Significant Difference; SEM, Standard Error of Mean; CV, Coefficient of Variation; DAT, Days After Transplanting; *** significant at 0.1% level of significance

4 Discussion

The present study demonstrated that pinching significantly altered vegetative growth, floral sex expression, and yield components of cucumber relative to unpinched controls. Control plants attained the greatest plant height and produced the highest number of male flowers and the highest overall sex ratio, whereas pinching at 20 days after transplanting (DAT) maximized lateral branch number, female flower production, fruit weight, fruit circumference, and marketable yield per hectare. These findings collectively indicate that the timing of apical bud removal is a critical determinant of the balance between vegetative vigor and reproductive (female-biased) output in cucumber.

The reduction in plant height following pinching is consistent with the disruption of apical dominance, the process by which the growing shoot tip suppresses outgrowth of axillary buds. This regulation allows the plant flexibility to respond to environmental factors while optimizing its resources, and removal of the shoot apex alleviates the inhibition of lateral bud outgrowth. Classically, this phenomenon was attributed almost exclusively to auxin (IAA) synthesized in the apical meristem and young leaves, which is transported basipetally to suppress lateral bud activity (Vanneste and Friml, 2009). However, more recent physiological work has substantially revised this view. While apical dominance was originally thought to be mediated by auxin, recent studies highlight the importance of shoot-tip sink strength and the role of sugars in promoting branching, raising questions about the relative contributions of auxin and carbohydrate supply. Cao et al. (2023) further showed that auxin depletion after decapitation is not always the initial trigger of the rapid cytokinin increases observed in axillary buds, which instead correlate more closely with enhanced sugar availability. This suggests that the increase in lateral branching observed in the present study following pinching may reflect not only reduced apical auxin flux but also an improved carbohydrate supply to axillary buds once the assimilate-demanding apex is removed consistent with the higher fruit weight recorded in 20-DAT pinched plants, which was attributed to greater photoassimilate diversion toward lateral branches (Anand et al., 2014; Naafe, 2022).

The hormonal basis for the shift toward female flower dominance under pinching can be further explained by ethylene and gibberellin dynamics. Ethylene evolved in greater quantities from female floral buds than from male ones, and its endogenous production is understood to promote femaleness in cucumber. In cucumber, ethylene and auxin mediate feminization, whereas gibberellins induce masculinization, a pattern also confirmed in later transcriptomic work. Genes associated with hormone transduction and synthesis including ethylene, which promotes femaleness, and gibberellin, which promotes maleness have been identified as differentially expressed between male and female cucumber tissues, and exogenous gibberellin has been shown to inhibit ethylene biosynthesis by suppressing expression of the ethylene-synthesis gene *CsACS1G*. This antagonism helps explain why control (unpinched) plants, which retained an intact, actively growing apex and higher endogenous

gibberellin-associated activity in the main stem, produced disproportionately more male flowers, while pinching-induced lateral branches likely characterized by a more favorable ethylene-to-gibberellin balance produced a higher proportion of female flowers. This is mechanistically consistent with earlier transcriptomic evidence that gibberellin regulates cucumber sex expression via both ethylene-dependent and ethylene-independent pathways, with GA-induced ethylene synthesis genes and ethylene receptors implicated in male flower formation. Cytokinin also appears relevant to this process: in species such as maize and melon, ethylene, auxins, and cytokinins jointly promote female flower formation, aligning with the observation that pinching-related increases in cytokinin activity in released axillary buds may simultaneously stimulate branch outgrowth and reinforce a feminizing hormonal environment. Because fruit length was statistically unaffected by pinching treatment, this parameter appears to be under stronger genetic than hormonal-environmental control, whereas fruit circumference and fruit-per-hectare yield both influenced by carbohydrate allocation and cell division rate responded more directly to the source–sink changes induced by pinching.

The present results are broadly consistent with earlier reports on cucurbit pinching. The suppression of apical dominance and consequent increase in plant bushiness align with the findings of Ghosh et al. (2011), while the reduction in main-stem height following early apical removal corroborates Chaurasiya et al. (2020). The increase in lateral branch number under pinching supports the branching-control framework described by Rafeekhar et al. (2001) and the broader physiological model of apical dominance release described in recent reviews. As synthesized in a century of apical dominance research, auxin was long considered the master regulator acting through secondary messengers such as cytokinin, though this view has since been refined through genetic and multidisciplinary approaches. The reduction in male flower number under pinching corresponds with Kandel and Sah (2023), who reported that removal of lower primary branches reduced overall male flower output, while the increase in female flowers and reduction in sex ratio under pinching mirror the findings of Chapagain et al. (2022) regarding pinching-induced promotion of third-generation, female-biased branches. Similarly, the increase in fruit weight and yield under early pinching is consistent with Nayak et al. (2018), who found that earlier pinching stimulated greater branch number, fruit set, and photosynthate accumulation. The lack of effect on fruit length agrees with Thakur et al. (2018). Notably, a recent comprehensive review of pinching across cucurbitaceous crops reinforces the mechanistic interpretation offered here: by modulating auxin distribution, cytokinin levels, and carbohydrate partitioning, pinching influences apical dominance, lateral shoot growth, and reproductive organ development, supporting the integrated hormonal–physiological explanation proposed in this study rather than a single-hormone account.

Maximum plant height was found in control. It might be due to the free growing of shoots in control conditions. Plant height was affected by pinching as it suppresses apical dominance and makes the plant bushy. It might be related to the flow of auxin in the plants, the synthesis of auxin on the shoot of the main stem is stopped due to the shoot pinching, while the synthesis of cytokinin increases and further affect plant growth. Ghosh et al. (2011) reported that pinching suppresses apical dominance. Earlier pinching of the plant might be the reason for an increase in height of lateral stems and the earlier growth of the primary stem might be the reason for increasing height in case of pinching at 25 DAT and 30 DAT. Growth of lateral stem could be the possible reason for the increase in plant height at 65 DAT. The possible reason behind the reduced height of plants might be removal of the apical portion which promotes the growth of the secondary branch, observed (Chaurasiya et al., 2020). The apical meristem and the young leaves are the centers of TAA and IAA (Indole Acetic Acid) synthesis which are then transported to the stems thus inhibiting the development of lateral shoots. IAA is one type of auxin that causes apical dominance. IAA is a trigger for change in plant development (Vanneste and Friml, 2009).

5 Conclusion and Recommendation for Future Research

Pinching of plants influenced the growth, flowering pattern, and yield of cucumber. In general plant height increases with an increase in the time of pinching initially but has no effect on the later stage of observation. Pinching influenced the growth of stems, branches, and female flowers significantly. Generally, yield character was high in plants treated with pinching compared to those plants that were not pinched. The number of fruits per

plant corresponds to a number of branches on the plant and the fruit weight gained. The total yield per plant and yield per hectare increased with pinching treatment. Results from this study suggest that small landholder farmer can pinch their plants to encourage a lower pinch sex ratio and higher yield. Indeed, the farmer can their plants at 20 DAT to attain maximum female flowers and hence more fruits.

Farmers are suggested and recommended to follow an appropriate time of pinching for increasing yield. Further studies with other pinching methods can be conducted to see their effect on plants. The varietal parameter should be considered for another research. This research was carried out in only one season and at only one location. So, this experiment should be further verified by conducting similar research at different locations.

Authors' contributions

AP carried out the conceptualization of research, designed the experiment and drafted the manuscript. AP participated in the design of the study and helped in data collection. AP helped in data analysis and helped to draft the manuscript. BS helped to draft the manuscript and supervision of the research. All authors read and approved the final manuscript.

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Conflict of Interest Disclosure

The authors affirm 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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Feature Review Open Access

Effects of Irrigation Strategies on Growth, Yield, and Fruit Quality of Greenhouse Tomato

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Abstract Greenhouse tomato production relies heavily on effective water management, and irrigation strategies and water supply levels directly influence plant growth, yield formation, and fruit quality. This study reviewed the effects of different irrigation strategies on physiological responses, root development, yield components, and quality formation in greenhouse tomatoes, and further discussed the development trends of precision irrigation technologies and sustainable management practices. The results indicate that appropriate water supply promotes root growth, photosynthesis, and dry matter accumulation, thereby improving plant growth and yield performance. Excessive irrigation enhances vegetative growth but reduces water-use efficiency and may negatively affect fruit quality. Moderate deficit irrigation improves resource-use efficiency while maintaining relatively high yield by regulating root-shoot balance and promoting the accumulation of quality-related compounds, including sugars, vitamin C, and lycopene. Tomato water requirements vary among growth stages, and precise regulation based on evapotranspiration (ET), growth stage, and root-zone moisture status is more effective for balancing yield and quality. Future greenhouse tomato production should strengthen the integration of irrigation, fertilization, environmental regulation, and smart monitoring technologies to establish efficient, water-saving, and sustainable production systems.

Keywords Greenhouse tomato; Irrigation strategy; Water-use efficiency; Deficit irrigation; Fruit quality; Precision irrigation

1 Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most important economic vegetable crops worldwide, with high nutritional value and extensive applications in fresh consumption and food processing (Sagar and Singh, 2023). Tomato fruits are rich in various functional compounds, including vitamin C, lycopene, phenolics, organic acids, and carbohydrates, which collectively determine fruit quality and market value (Lu et al., 2021; Zhang et al., 2025). With increasing consumer demand, tomato production has continued to expand, and protected cultivation has become an important production system for improving yield stability and supply capacity. According to He et al. (2024), global tomato production reached 2.54×10^{12} kg in 2022, with China contributing 1.37×10^{12} kg, accounting for 53.72% of the global production. Greenhouse and other protected cultivation systems can improve land-use efficiency, support year-round production, and reduce the impacts of climatic fluctuations on yield and quality (Amankwaa-Yeboah et al., 2023). However, protected production relies heavily on water and nutrient management, and resource-use efficiency remains a key factor limiting its sustainable development.

Greenhouse environments receive limited natural rainfall, making irrigation the primary source of water supply. Improper irrigation management can result in resource waste and reduced production efficiency. Previous studies have shown that excessive irrigation decreases water and nitrogen use efficiency and may negatively affect fruit quality and economic returns, whereas insufficient water supply restricts cell expansion, plant growth, and yield formation (Wu et al., 2022; Zhang et al., 2025). In arid and semi-arid regions, water scarcity further increases the uncertainty of greenhouse tomato production (Amankwaa-Yeboah et al., 2023; Liu et al., 2024). Therefore, precise irrigation management based on crop growth stages and environmental conditions is essential for improving resource-use efficiency.

Irrigation strategies directly regulate tomato growth, photosynthetic performance, and yield formation. Appropriate water supply promotes root development, nutrient uptake, photosynthesis, and dry matter accumulation, thereby improving plant growth and productivity (Lyu et al., 2025; Song et al., 2025). Studies under protected cultivation have demonstrated that suitable increases in irrigation amount can enhance plant height, stem diameter, leaf area, chlorophyll content, and fruit yield, while promoting nitrogen uptake and coordinated water-nitrogen utilization (Singh et al., 2024). However, excessive irrigation may reduce water productivity, whereas regulated deficit irrigation can maintain yield while reducing water inputs, making it an important management strategy in water-limited regions.

Water status also plays a critical role in tomato fruit development and quality formation. Severe water stress reduces fruit size, fresh weight, and water content, with particularly strong effects during cell division and fruit expansion stages (Medyouni et al., 2021). Moderate water regulation can promote the accumulation of quality-related compounds, such as soluble solids, sugars, and lycopene, thereby improving fruit flavor and nutritional quality (Lu et al., 2021; Bai et al., 2022). However, the effects of irrigation on fruit quality are jointly influenced by multiple factors, including genotype, growth stage, irrigation level, and cultivation conditions. Understanding how different irrigation strategies affect greenhouse tomato growth, yield, and quality is important for optimizing water management practices. An effective irrigation strategy should consider multiple objectives, including yield formation, quality improvement, water-use efficiency, and economic benefits.

This study analyzed the effects of different irrigation strategies on greenhouse tomato growth, photosynthetic characteristics, yield formation, and fruit quality, with the aim of exploring how water supply levels regulate plant physiological responses and production performance. The changes in growth, yield, and quality indicators under different irrigation regimes were compared to determine suitable water management ranges. The results are expected to provide theoretical support and practical guidance for water-saving, efficient, and high-quality tomato production, as well as contribute to irrigation optimization under water-limited conditions.

2 Water Requirement Characteristics and Physiological Basis of Greenhouse Tomato

2.1 Water demand patterns during tomato growth stages

Research has shown that tomato water requirements vary considerably among different growth stages (Figure 1). Chen et al. (2025) reported that sufficient water supply during the seedling and early vegetative growth stages is essential for maintaining plant height, stem diameter, chlorophyll accumulation, biomass production, and nutrient uptake, whereas insufficient water availability during the seedling and early flowering stages may restrict subsequent yield formation. Measurements of water consumption under greenhouse conditions showed that tomato plants have relatively low water demand during the seedling stage, followed by increased demand during flowering and fruit setting, with the highest water consumption occurring during fruit expansion (Lyu et al., 2025). Long-term water stress studies by Yuan et al. (2016) further demonstrated that tomato responses to drought depend not only on the severity of water deficit but also on the developmental stage at which stress occurs. Although mild water limitation during the vegetative stage can often be tolerated, water deficiency during the reproductive stage is more likely to reduce fruit set and final marketable yield (Cui et al., 2019; Ghannem et al., 2021).

Water regulation is particularly important during fruit expansion and ripening because these stages determine the balance between fruit size and quality. Zhang et al. (2025) showed that leaf net photosynthetic rate, transpiration rate, and stomatal conductance generally increase from flowering to fruit expansion, reaching their maximum levels during fruit enlargement, and then gradually decline during ripening. These changes indicate a high demand for water supply and assimilate transport during this period. Deficit irrigation applied during fruit development or ripening can improve fruit firmness, coloration, soluble solids, sugars, organic acids, and vitamin C contents, whereas severe water stress still restricts fruit growth and reduces yield (He et al., 2024).

Moderate deficit irrigation may provide a suitable balance between yield maintenance and quality improvement. A greenhouse study by Ghannem et al. (2021) found that reducing irrigation water by 20% during the second growth

stage resulted in only a 3% yield reduction, while maintaining the highest yield among different deficit treatments. Another study based on stage-specific irrigation optimization demonstrated that maintaining soil water content at 70%-90% of field capacity during flowering and fruit development, and 40%-60% during ripening, achieved the highest water-use efficiency (Li et al., 2023).

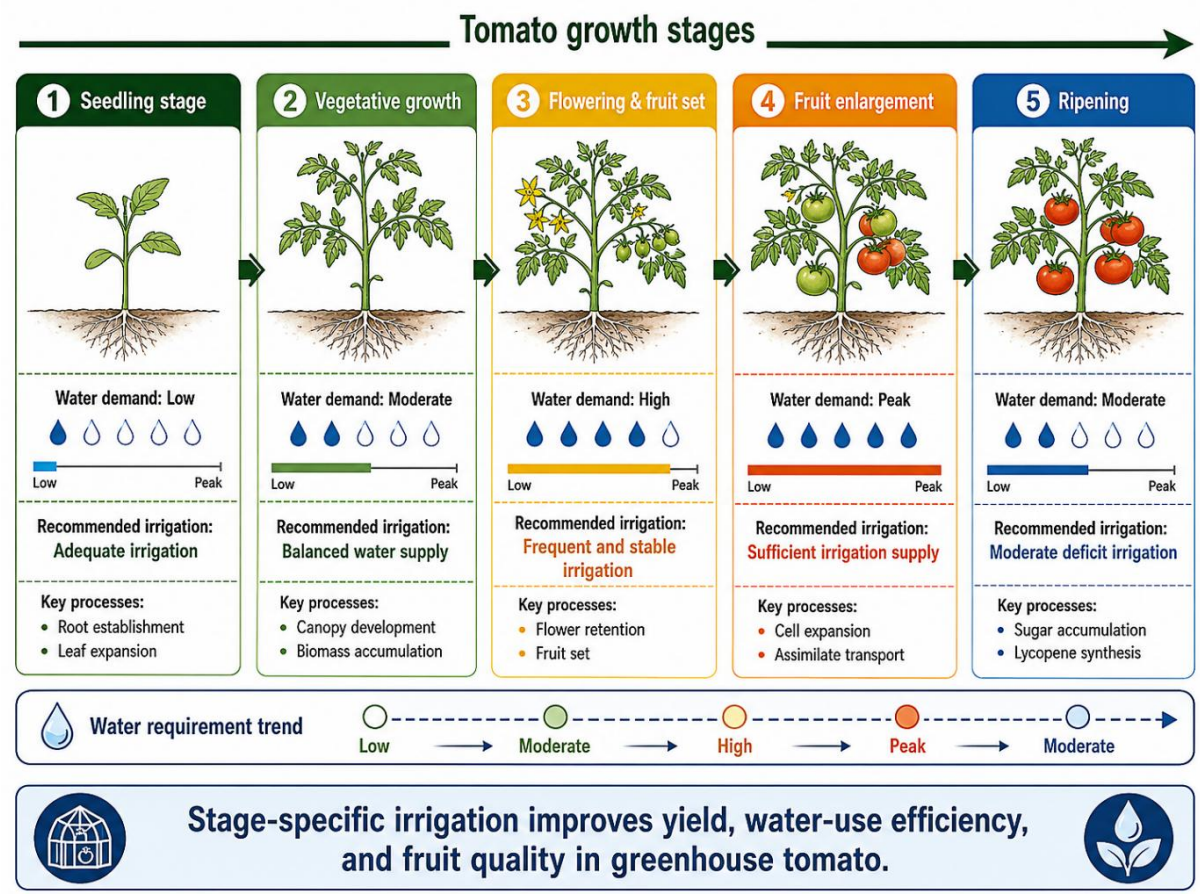


Figure 1 Stage-specific water demand characteristics and irrigation regulation strategies during greenhouse tomato growth

2.2 Effects of water status on tomato root development

Tomato root development is highly sensitive to water availability because root systems directly determine plant capacity for water uptake and nutrient acquisition. Feng et al. (2024) reported that appropriate irrigation combined with sufficient nitrogen supply increased tomato root length, root surface area, and root volume, and these root traits were positively associated with fruit yield and water-use efficiency.

Irrigation level is an important factor affecting root distribution across soil layers. Under greenhouse drip irrigation systems, tomato water uptake mainly occurs within the 0-30 cm soil layer. However, moderate deficit irrigation can increase the relative contribution of deeper roots (30-60 cm) to water absorption across the soil profile while reducing surface evaporation losses (Li et al., 2023). Excessive reduction in irrigation amount, however, inhibits increases in root length density and weakens overall plant growth capacity (Li et al., 2023; Lyu et al., 2025). In contrast, moderate water limitation can increase the root-to-shoot ratio and improve water-use efficiency, reflecting an adaptive strategy in which plants enhance root acquisition capacity under limited water availability.

The rhizosphere water environment also regulates root activity by affecting soil aeration, hydraulic conductivity, enzyme activity, and interactions with microorganisms. Excessive irrigation may cause oxygen deficiency in the root zone, promote reactive oxygen species accumulation, and reduce root absorption capacity, thereby indirectly restricting photosynthesis in aboveground tissues (Ahmad and Li, 2021). Water-saving irrigation systems can

modify root architecture around drip lines and influence rhizosphere enzyme activity, microbial nitrogen cycling genes, and mycorrhizal colonization, indicating that irrigation strategies regulate both the physical environment and biological processes in the rhizosphere (Li et al., 2021). Giovanna et al. (2024) found that under water deficit conditions, rhizosphere microorganisms could partially alleviate plant water stress by improving soil water-holding capacity and increasing root surface area. Other microbial-based approaches can also enhance soil nutrient availability, urease and protease activities, and plant stress tolerance, thereby supporting tomato root function under greenhouse conditions (Zhao et al., 2026).

2.3 Physiological responses to water availability

Water availability directly regulates tomato photosynthetic performance and stomatal behavior. Across different growth stages, water stress generally decreases stomatal conductance, net photosynthetic rate, transpiration rate, chlorophyll content, PSII photochemical efficiency, and electron transport capacity, while increasing non-photochemical quenching and dark respiration (Yuan et al., 2016). A greenhouse irrigation experiment conducted by Zhang et al. (2025) further showed that both insufficient and excessive irrigation reduced gas exchange capacity, whereas appropriate irrigation levels and shorter irrigation intervals improved stomatal conductance and photosynthetic activity. Stomatal closure is a rapid adaptive response to declining plant water status, mainly regulated by reduced leaf turgor and enhanced root-derived abscisic acid (ABA) signaling. This response reduces water loss but simultaneously restricts carbon dioxide uptake and carbon assimilation (Ahmad and Li, 2021; Xue et al., 2021). Under water deficit conditions, changes in stomatal morphology and stomatal conductance are often coordinated with variations in leaf water potential, ABA concentration, and chlorophyll status (Chen et al., 2021).

Tomato plants also respond to water limitation through osmotic adjustment and antioxidant defense systems. Under drought conditions, plants redistribute assimilates toward roots, reduce aboveground growth, and accumulate osmolytes and stress-related metabolites to maintain cellular water balance (He et al., 2024). Potassium plays an important role in this process by regulating stomatal movement, osmotic balance, and the activity of various enzymes involved in stress responses (Sahoo et al., 2025).

At the biochemical level, drought stress increases the activities of antioxidant enzymes, including superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT). However, severe stress can also enhance lipid peroxidation and cause membrane damage (Yuan et al., 2016). Seed priming, salicylic acid application, biostimulants, and beneficial microorganisms can further strengthen these protective mechanisms by improving PSII stability, reducing water loss, enhancing antioxidant enzyme activity, and alleviating drought-induced damage, thereby increasing plant stress tolerance (Fregonezi et al., 2024; Sahoo et al., 2025; Zhao et al., 2026).

3 Effects of Irrigation Strategies on Greenhouse Tomato Growth

3.1 Effects of conventional irrigation on vegetative growth

Under conventional or full irrigation conditions, tomato plant height, stem diameter, and leaf area generally increase with increasing irrigation amount. A greenhouse experiment conducted by Lyu et al. (2025) showed that increasing irrigation levels enhanced plant height, stem diameter, leaf area, SPAD value, and yield, with overall growth performance following the order of I1 > I2 > I3. Similar results were observed under drip fertigation conditions, where Zhang et al. (2025) reported that moderate increases in irrigation promoted plant height, stem diameter, leaf area index, root development, and aboveground biomass accumulation. In a pot-based greenhouse tomato experiment, maintaining soil water content at 100% field capacity resulted in the highest plant height and stem diameter, reaching 186.0 cm and 23.40 mm, respectively (Chand et al., 2020). Alshami et al. (2023) further confirmed a significant positive relationship between irrigation amount and leaf area under saline irrigation conditions. When the irrigation level was reduced to 40% of full irrigation, tomato plant length, stem diameter, stem dry weight, and stem fresh weight decreased by 33.06%, 29.7%, 28%, and 43.1%, respectively, compared with fully irrigated plants. Comparative studies of irrigation methods also showed that drip irrigation combined with suitable soil moisture conditions was more beneficial for tomato growth than furrow irrigation. Under a soil

water potential of -10 kPa, drip-irrigated tomatoes reached a plant height of 99.2 cm and a leaf area of 16,569 cm², whereas furrow-irrigated plants reached only 73.1 cm and 11,763 cm², respectively (Mukherjee et al., 2023).

Biomass accumulation and dry matter allocation exhibited similar patterns. In greenhouse-grown tomatoes, dry matter accumulation increased with increasing irrigation levels, reaching 90.79, 73.42, and 60.27 g/plant under I1, I2, and I3 treatments, respectively (Lyu et al., 2025). Higher water availability increased leaf dry matter, fruit dry matter, and total water consumption, while dry matter accumulation showed a significant positive correlation with yield. Wei et al. (2021) reported that, compared with non-aerated irrigation, aerated irrigation increased plant height, stem diameter, biomass accumulation, and leaf area index by 10.2%, 7.3%, 12.5%, and 6.2%, respectively. These results indicate that sufficient water supply combined with improved root-zone aeration can further promote vegetative growth. Dynamic growth analysis under aerated drip irrigation also demonstrated higher maximum growth rates of plant height and leaf area index, together with an extended effective vegetative growth period, thereby promoting later reproductive growth and yield formation (Xiao et al., 2022).

3.2 Regulation of plant growth under water-saving irrigation

Water-saving irrigation regulates tomato growth mainly by moderately reducing excessive vegetative growth while maintaining basic physiological activity. Under mild water deficit conditions, plants can maintain relatively stable growth through adaptive regulation. Compared with full irrigation, deficit irrigation generally reduces tomato plant height, stem diameter, leaf area, root length, and aboveground biomass. Turan et al. (2023) reported that under 50% field capacity conditions, the shoot fresh weight, root fresh weight, shoot dry weight, root dry weight, plant height, stem diameter, and leaf area of tomato seedlings decreased by 43%, 19%, 39%, 29%, 20%, 18%, and 50%, respectively. A combined salinity and water stress experiment under greenhouse conditions also showed that 40% irrigation significantly reduced leaf area and stem growth, further confirming that severe water limitation suppresses tomato vegetative development (Alshami et al., 2023).

However, mild water deficit generally causes only limited growth reductions while improving resource-use efficiency. In a soilless cultivation system, compared with full irrigation, the W80N100 treatment showed no substantial reductions in photosynthesis or stomatal conductance, and yield decreased by only 2.90%-8.75%, while irrigation water-use efficiency increased by 21.40% and 14.06%, respectively (Ullah et al., 2021). Similarly, Chand et al. (2020) found that maintaining soil water content at 80% field capacity improved irrigation water-use efficiency with only minor yield losses.

Tomato plants exhibit distinct adaptive responses under water stress. Mild deficit irrigation can increase the root-to-shoot ratio and improve water-use efficiency, indicating a shift toward more conservative water-use strategies (Lyu et al., 2025). When water limitation occurs during the reproductive stage, plants tend to allocate more resources to belowground growth. A study on cherry tomato showed that lower irrigation frequency promoted root development and increased the root-to-shoot ratio (Poomkokrak et al., 2024). Water stress also induces a series of biochemical defense responses. Under drought conditions, tomato plants alleviate stress by increasing proline accumulation, enhancing antioxidant enzyme activity, and improving osmotic adjustment capacity. In addition, salicylic acid and potassium can further regulate stress-responsive gene expression, antioxidant defense, stomatal regulation, and osmotic balance (Patané et al., 2022; Sahoo et al., 2025). These adaptive mechanisms explain why moderate deficit irrigation can maintain relatively stable plant growth and improve water productivity in some cases, whereas prolonged or severe water deficiency ultimately reduces biomass accumulation and marketable production performance.

3.3 Effects of irrigation methods on root-shoot coordination

Different irrigation methods alter water and oxygen distribution in the root zone, thereby affecting coordination between tomato roots and aboveground growth (Figure 2). Drip irrigation generally promotes better plant growth than furrow irrigation because it provides more precise water delivery and reduces deep percolation losses. Mukherjee et al. (2023) reported that under -10 kPa conditions, drip irrigation reduced total irrigation water input by approximately 20%-23% compared with furrow irrigation while increasing yield by 22%-28%. In drip

fertigation systems, shorter irrigation intervals can enhance root growth, nitrogen uptake, stem diameter development, and leaf area index, indicating that both irrigation frequency and irrigation amount regulate the balance between belowground water acquisition and canopy expansion (Zhang et al., 2025).

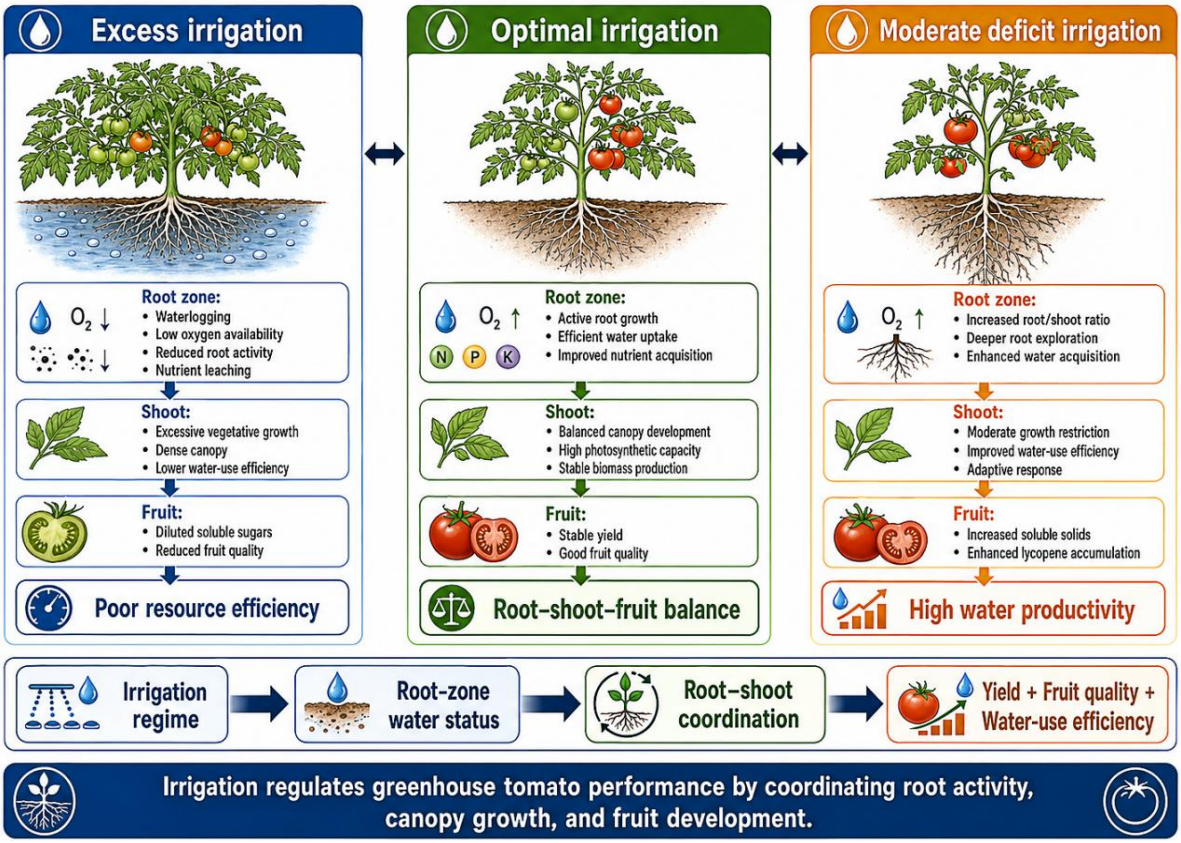


Figure 2 Integrated regulation of root-shoot-fruit coordination under different irrigation regimes in greenhouse tomato

Image caption: Different irrigation regimes regulate greenhouse tomato performance through coordinated effects on root-zone conditions, shoot growth, and fruit development. Excess irrigation may cause waterlogging, reduced oxygen availability, nutrient leaching, and excessive vegetative growth, resulting in lower water-use efficiency and reduced fruit quality. Optimal irrigation maintains active root growth, efficient nutrient uptake, balanced canopy development, and stable fruit production by achieving root-shoot-fruit coordination. Moderate deficit irrigation promotes deeper root exploration, increases the root-to-shoot ratio, improves water-use efficiency, and enhances fruit quality through increased soluble solids and lycopene accumulation

Mulched drip irrigation modifies soil moisture and temperature distribution and influences spatial root development. Under mulching conditions, tomato roots are mainly concentrated in the 0-20 cm soil layer, while low-water mulched treatments exhibit a wider distribution range of root length density compared with high-water mulched treatments (Ge et al., 2025). Model simulations by Sun et al. (2023) showed that 83%-90% of total roots under mulched drip irrigation were distributed within the 0-20 cm soil layer. However, as surface soil water deficit increased, the contribution of deeper roots to water uptake gradually increased.

Studies on substrate cultivation and localized irrigation systems further demonstrate that root-shoot balance depends strongly on water supply patterns. Ullah et al. (2021) found that mild water deficit under soilless cultivation increased average root diameter, total root length, and root surface area, suggesting that moderate water limitation can stimulate root development while maintaining canopy function. In potted cherry tomato production, increasing the number of emitters improved root length, root dry weight, leaf area index, photosynthetic rate, and biomass accumulation. The study recommended using two emitters per plant under deficit irrigation conditions to alleviate root-zone drought stress while simultaneously improving root architecture and canopy growth (Shabbir et al., 2020). Optimization of root-shoot coordination in greenhouse tomatoes depends on irrigation strategies that maintain suitable root-zone moisture and aeration conditions, promoting root expansion

while preventing excessive aboveground vegetative growth. Therefore, moderate deficit irrigation strategies based on drip irrigation or substrate cultivation can generally achieve a better balance between vegetative growth and water-use efficiency.

4 Effects of Irrigation Strategies on Tomato Yield Formation

4.1 Effects of water supply on flowering and fruit set

Water supply is particularly important during flowering and fruit set, which are among the most drought-sensitive stages during tomato yield formation (Zhang et al., 2022; Alomari-Mheidat et al., 2024). Studies across different growth stages have shown that flowering and fruit development are more sensitive to water stress than vegetative growth. Water deficit imposed from the flowering stage can affect both yield formation and subsequent fruit quality (Poomkokrak et al., 2024). During this period, appropriate water management supports reproductive growth by maintaining photosynthesis, promoting nutrient uptake, and ensuring sufficient dry matter supply to flowers and developing fruits. In substrate cultivation systems, Song et al. (2025) found that nutrient supply during the flowering and fruit-setting stages had a particularly strong influence on yield and water-use efficiency (WUE), which was consistent with the high resource demands associated with reproductive organ development.

Water stress during flowering and fruit set affects reproductive success by reducing flower number, fruit set rate, and the survival of young fruits. In a cultivar screening study under 50% reduced irrigation, Grozeva and Ganeva (2024) observed that flower number, fruit number, fruit set rate, and single fruit weight declined as the inflorescence developed from the second to the fifth truss, with large-fruited indeterminate tomato cultivars showing the greatest sensitivity. Other greenhouse studies have also identified flowering and fruit-setting stages as critical periods when tomato plants are highly vulnerable to water stress. However, when plant water status is precisely regulated, moderate stress does not necessarily reduce fruit number. For example, Alomari-Mheidat et al. (2024) reported that irrigation management based on plant water status under moderate water stress conditions generally had limited effects on inflorescence development and fruit number but influenced fruit size. These findings suggest that prolonged or severe water stress is more likely to induce reproductive organ abortion, whereas mild and well-monitored deficit irrigation has relatively limited effects. When severe water stress occurs during fruit truss development, particularly under environments with high evaporative demand, it may delay truss formation, accelerate leaf senescence, and reduce fruit number by approximately 50%. Even after subsequent rewatering, plants can only partially recover from these effects.

4.2 Effects of irrigation levels on fruit enlargement and yield components

In greenhouse tomato production systems using drip irrigation, moderate increases in irrigation amount generally improve fruit weight and fruit size, whereas water stress commonly reduces fruit fresh weight and fruit dimensions. Dirlik et al. (2025) reported that maintaining stable and suitable soil moisture conditions through sensor-based irrigation management increased single fruit weight from 56 g to 85 g, fruit number per plant from 45 to 56, and final yield by 47%. Genotypic differences also influence tomato responses to irrigation levels, with different greenhouse cultivars showing considerable variation in the reduction of single fruit weight under reduced irrigation conditions. Some genotypes exhibited greater sensitivity to water stress than others.

Marketable yield depends not only on total yield but also on the proportion of marketable fruits. Wu et al. (2021) conducted a four-season greenhouse experiment and found that 75% ETc irrigation reduced the proportion of non-marketable fruits and produced larger fruits compared with full irrigation. In contrast, full irrigation during the late growth stage tended to promote the formation of more small fruits, thereby reducing commercial value. Studies on moderate water stress have also shown that fruit size is often the most sensitive yield component, whereas fruit number can remain relatively stable under moderate deficit conditions (Alomari-Mheidat et al., 2023). Under hydroponic conditions, different deficit irrigation strategies significantly affected single fruit weight, fruit number, and water-use efficiency during the fruiting stage, with the PRD85 treatment achieving the highest single fruit weight and water-use efficiency (Hooshmand et al., 2019).

Tomato yield formation under different irrigation regimes generally follows a consistent pattern: full irrigation usually achieves the highest total yield, moderate deficit irrigation can maintain or even improve marketable yield, while severe water deficit reduces both fruit size and fruit number (Lyu et al., 2025; Song et al., 2025). This pattern has been observed under conventional drip irrigation, subsurface irrigation, and salinity stress conditions, where moderate irrigation levels generally outperform both insufficient and excessive water supply treatments (Zhang et al., 2022; Alshami et al., 2023).

4.3 Water use efficiency and yield optimization

The relationship between irrigation amount and tomato yield generally follows an asymptotic response pattern. In a three-year drip irrigation experiment, both tomato yield and water-use efficiency increased gradually with increasing irrigation amount. Yield approached a stable level at approximately 90% pan evaporation replacement, whereas water-use efficiency reached a plateau near 70% irrigation level (Liu et al., 2019). Wu et al. (2021) found that tomato yield increased with increasing irrigation amount in greenhouse production; however, the 100% ETc treatment resulted in the highest total water consumption and the lowest water-use efficiency for both total yield and marketable yield. Similarly, in drip fertigation tomato production, increased irrigation levels enhanced evapotranspiration but reduced water and nitrogen use efficiencies (Zhang et al., 2025). Excessive irrigation may further reduce yield performance by decreasing soil aeration, increasing nitrogen losses, and promoting excessive vegetative growth.

Achieving high yield under water-saving conditions generally depends on moderate deficit irrigation, precise water regulation, and coordinated optimization of irrigation with fertilization or root-zone management practices. Multiple studies have indicated that moderate irrigation targets are more suitable for balancing productivity and resource efficiency. In greenhouse drip irrigation systems, 75% ETc maintained both marketable yield and water-use efficiency at favorable levels (Wu et al., 2021). In greenhouse cherry tomato production, 80% ET_0 combined with appropriate nitrogen supply achieved the highest average fruit yield and economic returns, while maintaining soil moisture at 72%-80% of field capacity improved water-use efficiency and root-to-shoot ratio without substantial yield reduction (Lyu et al., 2025). Irrigation interval also affects yield formation. Liu et al. (2019) reported that, under the same seasonal irrigation amount, increasing irrigation frequency improved yield and water-use efficiency, with the W2D1 treatment increasing yield by 8.0%-26.1% compared with treatments with longer irrigation intervals.

5 Effects of Irrigation Strategies on Tomato Fruit Quality

5.1 Regulation of sugar and organic acid characteristics

Water deficit generally increases soluble solids and soluble sugar contents in tomato fruits, and this response has been widely reported in greenhouse tomatoes, processing tomatoes, and cherry tomato production systems (Wang et al., 2015; Li et al., 2021; He et al., 2024). In greenhouse tomatoes under drip fertigation, Zhang et al. (2025) found that decreasing irrigation levels increased soluble solids, soluble sugars, organic acids, vitamin C content, and sugar-acid ratio, while shorter irrigation intervals further improved most quality parameters. A three-year greenhouse experiment showed that irrigation at 70% pan evaporation, compared with 90% pan evaporation, improved water productivity, vitamin C, soluble solids, soluble sugars, and organic acid contents, while causing only minor yield reductions (Li et al., 2021). Moderate water deficit during fruit ripening can also promote glucose and fructose accumulation, increasing total soluble sugar content by 48.69% and sugar-acid ratio by 43.09% (He et al., 2024). Similar results were observed in processing tomato production under regulated deficit irrigation, where glucose content increased by 17.78%, soluble solids increased by 10.17%, and the soluble solids-to-titratable acidity ratio increased by 15.47% (Burato et al., 2024). Although the magnitude of sugar accumulation varies among studies, water deficit generally enhances sweetness perception by increasing soluble solids, as also demonstrated in low-frequency irrigation treatments of cherry tomato (Poomkokrak et al., 2024).

The physiological basis of water deficit-induced sugar accumulation mainly involves concentration effects and metabolic regulation. Reduced water supply decreases water dilution within fruits while maintaining or enhancing

solute accumulation processes (Zhang et al., 2025). Water stress can activate galactose and sucrose metabolic pathways and increase the activities of sucrose synthase and sucrose phosphate synthase, thereby promoting the conversion of starch into soluble sugars. Organic acid responses generally show similar patterns. He et al. (2024) reported that deficit irrigation increased organic acid accumulation in greenhouse tomato fruits. Moderate water deficit promoted the accumulation of tartaric acid, malic acid, shikimic acid, α-ketoglutaric acid, and succinic acid, while reducing oxalic acid and citric acid contents. The decrease in fruit pH under limited irrigation conditions also indicates enhanced fruit acidity, which may contribute to improved flavor characteristics (Habibi et al., 2025).

However, the response of sugar and organic acid metabolism to water regulation is not always consistent and is influenced by growth stage, harvest maturity, genotype, and irrigation method. For example, Poomkokrak et al. (2024) found that glucose content in cherry tomato fruits did not differ significantly among different irrigation regimes. Therefore, although moderate water deficit generally favors the accumulation of sugars and flavor-related compounds, its effects should be evaluated according to specific production conditions.

5.2 Effects of irrigation on nutritional quality

Vitamin C is one of the most consistent nutritional quality indicators responding to moderate water deficit in tomato fruits. Compared with full irrigation, regulated deficit irrigation generally increases vitamin C content. In a limited irrigation study, Habibi et al. (2025) reported that vitamin C concentration increased from 49 to 64 mg/100 g fresh weight, while electrolyte leakage decreased, indicating that water regulation not only enhanced antioxidant capacity but also improved cell membrane integrity. In greenhouse drip fertigation systems, Zhang et al. (2025) found that both reduced irrigation amount and shorter irrigation intervals increased vitamin C content, which may be associated with improved fruit light exposure due to a smaller canopy structure and enhanced ascorbic acid synthesis.

In addition to vitamin C, deficit irrigation can enhance the overall antioxidant system of tomato fruits, including soluble proteins, proline, total phenolics, total flavonoids, and comprehensive antioxidant activity (Jin et al., 2022). In processing tomatoes, regulated deficit irrigation increased total phenolic content by 20.58% (Burato et al., 2024). Other greenhouse studies have also shown that deficit irrigation improves antioxidant capacity and increases flavonoid and phenolic compound contents, although the magnitude of these responses varies among product types and cultivars (Bogale et al., 2016; Liava et al., 2023).

Lycopene and related carotenoids generally increase under moderate water stress, although their responses show stronger genotype dependence compared with vitamin C. He et al. (2024) reported that moderate deficit irrigation during fruit ripening increased lycopene, lutein, α-carotene, and β-carotene contents by 11.85%, 12.28%, 20.87%, and 63.89%, respectively. In black cherry tomatoes, deficit irrigation increased carotenoid levels while maintaining fruit size and weight (Coyago-Cruz et al., 2022). Salinity-related water stress has also been shown to enhance lycopene, β-carotene, total phenolics, soluble solids, firmness, and vitamin C contents at harvest or during storage. However, tomato cultivars do not always exhibit consistent responses to water regulation. Bogale et al. (2016) found that deficit irrigation increased lycopene and vitamin C contents in the ‘Matina’ cultivar but reduced these quality parameters in ‘Cochoro’. Early-stage water management may also have long-lasting effects on subsequent fruit nutritional quality. Tömösközi-Farkas et al. (2024) demonstrated that plants cultivated under 50% irrigation combined with water-retaining agents produced fruits with the highest lycopene, vitamin C, antioxidant capacity, and total phenolic content during later production stages.

5.3 Effects of water management on fruit appearance quality

Water management has substantial effects on tomato fruit size, firmness, and cracking incidence, although different quality traits do not always respond to water changes in the same manner. Studies have shown that deficit irrigation reduces fruit size and weight, whereas restricted irrigation improves fruit firmness but is often accompanied by smaller fruits (Habibi et al., 2025). However, moderate water regulation can maintain or optimize fruit size. Poomkokrak et al. (2024) reported that in cherry tomato production, irrigation once every three days

resulted in the optimal fruit diameter, fruit length, fruit volume, and fresh weight, while both higher and lower irrigation frequencies reduced fruit size. In black cherry tomatoes, regulated deficit irrigation maintained fruit size and weight while increasing carotenoid content (Coyago-Cruz et al., 2022).

Generally, water deficit or saline irrigation can increase fruit firmness and improve resistance to postharvest handling. However, fruit cracking shows a nonlinear response to irrigation regimes. Both excessively frequent irrigation and severe low-frequency irrigation can significantly increase cracking incidence, with the highest rate reaching 69.53%. In contrast, moderate low-water treatments reduced cracking incidence to 8.75% (Habibi et al., 2025). These changes in fruit physical properties directly affect marketability and storage performance. Restricted irrigation can reduce electrolyte leakage, increase fruit firmness and density, and suppress ethylene production and respiration rates, thereby extending shelf life and improving transport tolerance and postharvest stability.

In processing tomatoes, regulated deficit irrigation increases dry matter content, which reduces the risk of decay during transportation and improves processing efficiency (Burato et al., 2024). Irrigation water quality also influences postharvest performance. Although saline irrigation reduces yield, it can improve fruit sweetness, acidity, overall flavor, and storage-related quality traits under simulated transportation conditions. Under hydroponic conditions, salinity stress may increase the risk of blossom-end rot by reducing calcium uptake; however, this physiological disorder does not necessarily reduce fruit marketability under certain conditions.

6 Precision Irrigation Technologies and Optimization Strategies for Greenhouse Tomato Production

6.1 Irrigation management based on crop water requirements

Irrigation scheduling based on evapotranspiration (ET) remains one of the core approaches for estimating water requirements in greenhouse tomato production. Many optimization studies use crop evapotranspiration (ETc) or a proportion of pan evaporation as irrigation criteria to balance yield, fruit quality, and water-use efficiency. Colimba-Limaico et al. (2022) reported that maintaining 100% ETc with one irrigation event per day achieved a favorable balance among yield, fruit quality, and water-use efficiency, representing a practical irrigation strategy for greenhouse tomato production. ET-based irrigation optimization can be further adjusted by incorporating crop coefficients. A four-season TOPSIS-based comprehensive evaluation study showed that, when yield, quality, and water-fertilizer productivity were considered simultaneously, the optimal pan evaporation coefficient for greenhouse tomato production ranged from 0.74 to 0.78. Under practical production conditions, suitable ranges could be extended to 0.68-0.83 in spring and 0.68-0.82 in autumn (Yu et al., 2023). In substrate cultivation systems, irrigation management based on substrate moisture variation also reflects a crop water demand-oriented approach. Liu et al. (2024) found that initiating nutrient solution supply when coconut coir moisture decreased to 70% improved fruit quality and water-fertilizer use efficiency, while causing only minor yield losses compared with the 80% moisture treatment.

Tomato plants exhibit different sensitivities to water availability during different growth stages; therefore, stage-specific irrigation management is generally more effective than applying a uniform irrigation strategy throughout the entire growth period. Li et al. (2022) demonstrated that maintaining soil moisture at 70%-90% of field capacity during the first stage and 40%-60% during the second stage achieved the highest irrigation water-use efficiency and leaf water-use efficiency, while maintaining stable yield and improving fruit quality. Another greenhouse irrigation experiment based on pan evaporation showed that full irrigation during weeks 1-2 and 21-24, combined with reduced irrigation during intermediate stages, decreased seasonal water consumption and improved water-use efficiency compared with full irrigation throughout the growth period, although full irrigation still produced the highest yield (Singh et al., 2023). A growth-stage-based coupling experiment using yellow sand substrate further indicated that irrigation amount was the primary factor affecting yield and water-use efficiency, whereas fertilizer supply during the flowering and fruit-setting stages was an important secondary factor influencing production performance (Song et al., 2025).

6.2 Application of smart irrigation technologies

Automated irrigation systems based on soil moisture sensors can monitor and regulate root-zone water status in real time, providing a more stable moisture environment compared with fixed-schedule irrigation (Figure 3). Dirlik et al. (2025) developed an Arduino-based smart irrigation system for greenhouse tomatoes and found that maintaining soil moisture within a stable range of 70%-85%, compared with a fluctuating range of 55%-85%, increased fresh weight, dry weight, plant height, and fruit yield of mature plants by 52%, 78%, 121%, and 47%, respectively. Intelligent fertigation control systems also exhibit high operational accuracy. Li et al. (2024) reported that such systems achieved average decision-making and irrigation errors of only 1.1% and 0.8%, respectively, while increasing tomato yield by 7%-12% and reducing water and fertilizer inputs compared with conventional management practices.

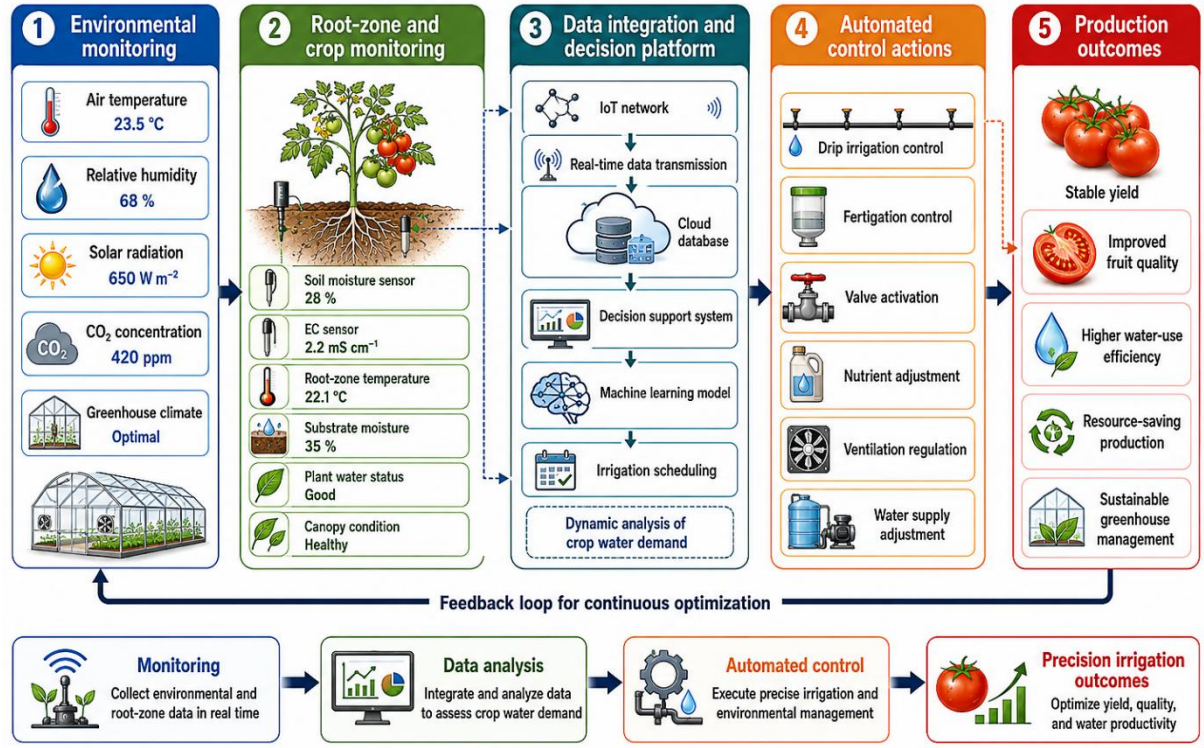


Figure 3 Framework of smart irrigation management for greenhouse tomato production

Image caption: Smart irrigation integrates environmental monitoring, root-zone sensing, data analysis, and automated control to achieve precise water management in greenhouse tomato production. Environmental parameters, including temperature, humidity, solar radiation, and CO_2 concentration, together with root-zone moisture status and crop physiological information, are collected through sensor networks. These data are transmitted to an intelligent decision platform incorporating IoT systems, cloud databases, and machine learning models to dynamically estimate crop water demand. The generated irrigation decisions are implemented through automated control systems, including drip irrigation, fertigation, nutrient adjustment, and environmental regulation. This integrated framework improves yield stability, fruit quality, water-use efficiency, and sustainable greenhouse production

Internet of Things (IoT)-based systems further extend beyond single-sensor control by integrating soil moisture, temperature, humidity, actuator devices, and data analysis modules to establish data-driven intelligent decision platforms. Ariss et al. (2024) indicated that smart greenhouse systems based on zonal management can use real-time monitoring data to adjust irrigation strategies according to crop growth stages and microenvironmental conditions. Experimental results showed that this approach improved tomato quality, yield, and resource-use efficiency. IoT-driven automated irrigation and fertilization systems can also enhance economic returns. In tomato production, threshold-based irrigation combined with 75%-100% of recommended fertilizer application increased yield by 4.8%-13.5%, reduced water consumption by 29%-39%, and achieved higher benefit-cost ratios than conventional management practices.

Machine learning-assisted decision-making systems further improve smart irrigation by integrating sensor data with predictive models to dynamically optimize irrigation strategies. In tomato production, machine learning-guided irrigation systems achieved water productivity comparable to full irrigation under regulated deficit irrigation or moderate deficit conditions, saved approximately 33% of water during high-temperature seasons, and improved fruit quality (Martelli et al., 2025). However, the sensitivity of these models to high-temperature environments and crop stress conditions still requires further improvement.

6.3 Integration of irrigation and fertilization management

Water and nutrient management require coordinated regulation because tomato growth, yield, and quality are jointly determined by water and nutrient availability rather than irrigation level alone. Drip fertigation improves the synchronization of water and nutrient supply in the root zone, reduces nutrient leaching associated with conventional irrigation methods, and is particularly important for indeterminate greenhouse tomatoes, where vegetative and reproductive growth stages overlap for an extended period (Singh et al., 2023). A greenhouse experiment by Lyu et al. (2025) showed that combining suitable or mild deficit irrigation with integrated fertilization management improved yield, water-use efficiency, nitrogen uptake capacity, and root-shoot coordination. For example, maintaining soil moisture at 72%-80% of field capacity combined with soluble organic fertilizer and chemical fertilizer application achieved high yield while improving water-use efficiency and nitrogen uptake compared with higher or lower irrigation treatments. A stage-specific coupling study under substrate cultivation also demonstrated that irrigation amount was the primary factor affecting yield and water-use efficiency, whereas fertilizer supply during flowering and fruit-setting stages played an important role in final production efficiency, highlighting the need to match water and nutrient supply with tomato growth requirements (Song et al., 2025).

Strategies for improving water and fertilizer use efficiency are gradually shifting from fixed management regimes toward integrated optimization models. For example, a decision-making model based on dynamic plant morphological feedback adjusted irrigation and fertilization schemes according to changes in plant height and stem diameter. Compared with fixed management practices, this approach increased fruit yield by 6.9%-14.7% and improved water-use efficiency by 6.93%-43.17%, demonstrating the potential of real-time regulation based on crop growth information (Zuo et al., 2025). The integration of water, fertilizer, and oxygen management provides further opportunities for optimization. Lei et al. (2023) reported that oxygen-enriched subsurface drip irrigation increased yield by 4.25% compared with fixed water management and by 26.13% compared with non-aerated irrigation. The optimized combination included an irrigation amount of 420 mm, dissolved oxygen concentration of approximately 24.55 mg/L, and nitrogen input of 281.43 kg N/ha.

7 Comprehensive Effects and Production Applications of Irrigation Regulation

7.1 Balance between yield and quality under different irrigation regimes

Higher irrigation levels generally promote vegetative growth and increase total tomato yield, but they may also dilute quality-related components, including soluble solids, sugars, vitamin C, and organic acids, thereby reducing fruit quality (Wu et al., 2021). Full irrigation can achieve higher absolute yield; however, it is often accompanied by greater water consumption and lower water-use efficiency. In contrast, severe water deficit generally improves nutritional composition and flavor-related traits but restricts plant growth, reduces fruit size, and may decrease fruit number (Alshami et al., 2023).

Studies have shown that moderate deficit irrigation can achieve a more favorable balance between yield and quality. A four-season greenhouse experiment demonstrated that 75% ETc irrigation reduced the proportion of non-marketable fruits, improved fruit size distribution, and increased marketable yield water-use efficiency, providing better overall benefits than full irrigation. Lyu et al. (2025) also found that mild deficit irrigation maintained relatively high yield while improving root-to-shoot ratio, nitrogen uptake capacity, and water-use efficiency, with stronger effects when combined with appropriate fertilization. Similar results were observed in growth stage-based deficit irrigation studies, where fruit quality showed greater sensitivity to water supply

variation than to nitrogen supply. Moderate deficit irrigation applied during both early and late fruit ripening stages resulted in improved overall performance (Wang et al., 2015).

However, yield and quality responses do not always change simultaneously. Under reduced irrigation conditions, some treatments primarily affect fruit development timing or fruit number distribution rather than total yield across the entire production cycle. This indicates a partial decoupling between quality improvement and production capacity under water regulation (Tringovska et al., 2026). In practical production, irrigation management should be adjusted according to market requirements and production objectives, with a comprehensive balance among yield stability, fruit quality, and resource-use efficiency rather than focusing on a single target.

7.2 Environmental factors affecting irrigation performance

The effectiveness of irrigation is influenced by greenhouse environmental conditions, including temperature, humidity, light intensity, and ventilation. Light intensity and fruit temperature are considered important environmental factors affecting tomato quality formation and shelf life, whereas relative humidity and irrigation regimes mainly regulate fruit firmness, water loss, and the occurrence of physiological disorders (Fanourakis et al., 2025). Ge et al. (2022) reported that greenhouse tomato evapotranspiration is closely associated with microclimatic conditions. Net solar radiation, average temperature, and maximum temperature increase evapotranspiration, while higher relative humidity reduces evapotranspiration. Therefore, irrigation strategies should be dynamically adjusted according to greenhouse environmental changes and actual atmospheric evaporative demand.

Ventilation generally has a stronger regulatory effect on greenhouse temperature and humidity conditions than irrigation management alone, particularly during flowering, fruit development, and harvesting stages. Xue et al. (2023) found that ventilation treatments had limited effects on yield but significantly influenced vitamin C content and sugar-acid ratio. Among different management combinations, the T2W2 treatment provided a favorable balance between yield and fruit quality. During high-temperature periods, irrigation strategies require further optimization. The combination of micro-sprinkler irrigation and drip irrigation can reduce air and leaf temperatures, increase relative humidity, improve photosynthesis and stomatal conductance, and increase tomato yield by 40.4%. This improvement was mainly attributed to reduced flower damage and increased fruit number.

Irrigation methods should also be coordinated with greenhouse production systems. Under mulching conditions, micro-sprinkler irrigation increased tomato yield compared with drip irrigation or non-mulched treatments. However, the response of yield to irrigation amount followed a quadratic relationship, with 1.0 Epan providing a more suitable irrigation target than the highest irrigation level (Zhang et al., 2022). These results indicate that irrigation optimization depends not only on water supply amount but also requires integrated consideration of greenhouse structure, mulching practices, and environmental regulation measures.

7.3 Application prospects in sustainable greenhouse tomato production

An important future direction for sustainable greenhouse tomato production is the development of efficient water-saving systems integrating moderate deficit irrigation, drip irrigation, fertigation, and real-time monitoring and control technologies. Sensor-based smart irrigation can maintain stable root-zone moisture conditions and significantly improve plant growth and yield performance compared with management strategies involving prolonged water fluctuations (Dirlik et al., 2025). Meanwhile, advances in modeling approaches and machine learning technologies further enhance precision irrigation capacity by predicting greenhouse evapotranspiration and crop yield responses, enabling dynamic irrigation scheduling under complex climatic conditions (Ge et al., 2022; Locatelli et al., 2024).

Sustainable protected agriculture requires not only optimization of field-scale irrigation management but also improved water recycling and resource utilization. For example, a recycled water and nutrient system in rooftop greenhouses maintained tomato yield while reducing water consumption per unit tomato mass from 75.2 L to 48.7

L and significantly lowering eutrophication risks through reduced nutrient leaching (Parada et al., 2021). Water-retaining materials, such as superabsorbent hydrogels, can enhance water and nutrient retention in the root zone and improve plant resilience under drought conditions (Idrissi et al., 2023).

Integrated water-nitrogen management is another important strategy for sustainable production. Ma et al. (2024) reported that excessive irrigation and fertilization not only increase resource losses but also elevate environmental risks, whereas optimized water-nitrogen combinations can simultaneously improve yield, water-use efficiency, fruit quality, and nitrogen-use efficiency while reducing greenhouse gas emission intensity. Therefore, future greenhouse tomato production will benefit from climate-smart management systems that dynamically adjust irrigation strategies according to crop growth stages, greenhouse microclimate, and nutrient status. Such approaches can support high yield and stable quality while improving resource-use efficiency and promoting long-term sustainable production.

8 Concluding Remarks

Irrigation management is a key factor regulating growth, yield formation, and fruit quality in greenhouse tomato production. Its effects are achieved through coordinated regulation of root activity, nutrient uptake, photosynthetic capacity, dry matter accumulation, and fruit development. Existing studies have shown that full irrigation promotes vegetative growth, increasing plant height, stem diameter, leaf area, and biomass accumulation, and contributes to higher yield production. However, excessive water supply over long periods can reduce water-use efficiency, increase the risk of nutrient leaching, and potentially impair fruit quality due to excessive vegetative growth. Therefore, irrigation management in greenhouse tomato production should focus on balancing water input and production benefits according to crop requirements and production objectives.

Moderate deficit irrigation provides an effective approach for balancing yield, water-use efficiency, and fruit quality improvement. Studies have demonstrated that mild water limitation can induce adaptive responses, including increased root-to-shoot ratio, enhanced water acquisition capacity, and promoted accumulation of quality-related compounds, thereby improving water productivity while maintaining relatively high yield levels. Particularly during fruit ripening, moderate reductions in irrigation commonly promote the accumulation of soluble sugars, soluble solids, vitamin C, lycopene, and phenolic compounds, improving fruit flavor and nutritional value. However, responses to water regulation are strongly dependent on growth stage and genotype, and excessive water deficit can restrict cell expansion, reduce fruit size, and decrease marketable yield.

Current irrigation optimization strategies in greenhouse tomato production are gradually shifting from conventional experience-based management toward precision and intelligent approaches. Irrigation systems based on evapotranspiration models, soil moisture monitoring, sensor control, the Internet of Things, and machine learning can provide real-time regulation according to crop status and greenhouse environmental changes, thereby improving water-use efficiency and production stability. Meanwhile, irrigation management should be integrated with fertilization, root-zone regulation, and greenhouse microclimate control to further enhance production efficiency through coordinated water-nutrient management and environmental regulation.

The core objective of greenhouse tomato irrigation strategies is to achieve a dynamic balance among yield, quality, resource-use efficiency, and economic benefits under different production conditions. Future research should further clarify irrigation response patterns across different cultivars, growth stages, and environmental conditions, and develop more precise decision-making systems by integrating multi-source sensor data with intelligent models. In addition, greater attention should be given to water recycling, water-nitrogen coordination, and long-term ecological benefits to promote greenhouse tomato production toward higher efficiency, greater stability, and long-term sustainability.

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Conflict of Interest Disclosure

The authors affirm 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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Research Report Open Access

Effect of Different Spawn Rates on the Growth, Yield, and Economics of Oyster Mushroom (*Pleurotus ostreatus*) Cultivation in Bardiya, Nepal

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Abstract Spawn rate is an important management decision in oyster mushroom (*Pleurotus ostreatus*) cultivation, shaping colonization speed, contamination risk, yield, and profitability. Most Nepalese growers nonetheless follow a traditional 10% rate (one 200 g spawn packet per 2 kg dry paddy straw) that reflects packet sizing and habit rather than local evidence. To test this convention, a pot-bag trial was conducted in Bansgadhi, Bardiya, using a Completely Randomized Design with five spawn rates 4%, 6%, 8%, 10% (farmer practice), and 12% each replicated four times. Increasing spawn rate progressively shortened the spawn run from 24.5 days (4%) to 15.9 days (12%), with pinhead initiation and first harvest following suit. Yield and biological efficiency rose with spawn rate up to 10% (468 g/bag; 23.4%) before plateauing at 12% (472 g/bag; 23.6%), while cap diameter and stipe length declined as fruiting-body density increased; contamination fell sharply above 6%. However, once spawn cost was weighed against returns, the 8% rate gave the highest benefit-cost ratio (1.34), ahead of the 10% standard (1.30). An 8% spawn rate is therefore recommended as the more economical choice for smallholder growers in Bardiya and similar Terai districts, while 10%-12% remains preferable where speed and maximum yield outweigh input cost.

Keywords Oyster mushroom (*Pleurotus ostreatus*); Spawn rate; Biological efficiency; Benefit-cost ratio; Bardiya, Nepal

1 Introduction

Oyster mushroom (*Pleurotus ostreatus*) is among the most widely grown mushroom species in Nepal, owing to its short cropping cycle, modest capital requirement, tolerance of a broad temperature range, and its ability to convert lignocellulosic residues such as paddy straw into a nutritious, marketable food (Pokhrel, 2016). National mushroom production has grown roughly eight-fold over the past decade, from about 1,530 t in 2010/11 to about 12,607 t in 2019/20 (MoALD data cited in Sapkota et al., 2022), and the crop is now recognized as one of the more accessible entry points into commercial horticulture for landless and smallholder households (Raut, 2019). Its cultivation has spread quickly among smallholder and landless farmers across the Terai, including Bardiya district one of Lumbini Province's major rice-producing districts, with roughly 77,500 ha under paddy cultivation and an annual paddy output of about 310,600 t (MoALD, 2023) where the resulting paddy straw is abundant right after the main rice harvest and mushroom growing offers a short-duration source of household income through the winter months (Poudel and Bajracharya, 2017).

Spawn is the vegetative seed material through which mycelium is introduced into the substrate, and the spawn rate the proportion of spawn to substrate on a weight basis is one of the most influential, and most cost-sensitive, decisions a grower makes. A higher spawn rate generally speeds up mycelial colonization and narrows the window during which competing molds and bacteria can get a foothold, but it also raises the direct cost of production, since spawn is typically the single most expensive input after labour (Bhandari et al., 2022). An insufficient spawn rate, on the other hand, can prolong colonization, increase contamination losses, and delay cropping cutting into both yield and profit at the same time.

In Bardiya and comparable Terai districts, a spawn rate of about 10% mixing one 200 g spawn packet with roughly 2 kg of dry paddy straw is commonly used in local commercial practice. The rationale behind this specific

rate does not appear to have been documented, and it may owe as much to spawn-packet sizing and grower habit as to deliberate optimization, though this has not been formally verified; comparable studies quantifying the growth, yield, and economic trade-offs of spawn rate under Nepalese Terai conditions remain scarce (Sapkota et al., 2022).

Most published spawn-rate work comes out of other South Asian contexts with different substrates, climates, and cost structures, which limits how directly it can be applied to Bardiya's growing conditions. On wheat straw in Pakistan, Bhatti et al. (2007) found that raising the grain-spawn rate progressively shortened the spawn run and that fresh-weight yield peaked at a 70 g/kg substrate rate (equivalent to about 7%, roughly 45% of substrate fresh weight), only marginally ahead of a 60 g/kg rate (about 6%, roughly 44%). Working with the related species Pleurotus pulmonarius on wheat straw in India, Pal et al. (2017) reported that increasing spawn rate from 0.5% to 8% shortened the spawn run to 10.5 days and pinhead formation to 12.3 days at 8%, which also gave the highest yield (168.7 g per 200 g dry substrate) and biological efficiency (84.3%), with only small gains in yield between 4% and 8%. Both studies point to a similar pattern of diminishing returns beyond a moderate spawn rate, broadly consistent with what was anticipated for Bardiya, but neither reported spawn cost or benefit-cost outcomes, and neither used paddy straw, underscoring the need for locally grounded data (Paudel and Dhakal, 2020).

This study was therefore undertaken to: (i) evaluate the effect of five spawn rates on mycelial colonization, pinhead initiation, and time to harvest; (ii) compare yield, yield-related morphological traits, and biological efficiency across spawn rates; and (iii) determine, through a simple benefit-cost analysis, the most economical spawn rate for smallholder oyster mushroom production in Bardiya, Nepal.

2 Materials and Methods

2.1 Experimental site

The experiment was conducted at Shree Janata Secondary School, Bansgadhi Municipality, Bardiya District, Lumbini Province, Nepal (28.26°N, 81.52°E; approximately 150 m above sea level), in a purpose-built mushroom cultivation shed adjoining the school science laboratory, from November 2024 to January 2025. The district has a subtropical monsoon climate with average annual rainfall of approximately 1,600-1,900 mm, most of it falling between June and September; during the trial period, ambient outdoor temperatures ranged from approximately 9 °C in December to 24 °C in November.

Because oyster mushroom production requires close environmental control, cultivation was carried out indoors rather than in the open field: the shed was constructed of brick walls with a corrugated tin roof lined with thatch for insulation, and incubation and fruiting activities were separated into two adjoining rooms. Incubation-room temperature was maintained at 24 °C-28 °C using ambient conditions supplemented by damp jute-sack curtaining on warmer afternoons, while the fruiting room was held at 18 °C-22 °C with 80%-90% relative humidity through regular hand-misting, and both rooms were monitored twice daily with a digital thermometer and hygrometer. The shed had not previously been used for mushroom cultivation, and all racks and surfaces were cleaned and disinfected with a 2% bleach solution before the experiment was established.

2.2 Experimental design and treatments

The experiment was laid out in a Completely Randomized Design (CRD) with five treatments and four replications, resulting in twenty experimental bags. The treatments were as follows: T_1: 4% spawn rate (80 g spawn/2 kg dry substrate); T_2: 6% spawn rate (120 g); T_3: 8% spawn rate (160 g); T_4: 10% spawn rate (200 g, farmer practice); T_5: 12% spawn rate (240 g).

Certified *Pleurotus ostreatus* grain spawn, obtained from a locally available commercial strain, was procured from Mushroom Seed Nepal & Research Center, Madhyapur Thimi-3, Chardobato, Bhaktapur, Nepal, a registered mushroom spawn producer, on November 5, 2025. The spawn was produced on wheat grain and used within one week of collection to preserve viability. Bags were arranged individually, rather than in field plots, on three-tier bamboo incubation racks, with treatments and replications randomized across rack positions to minimize any position-related microclimate effects within the shed.

2.3 Substrate preparation and bag inoculation

Clean, dry paddy straw sourced from local rice fields around Bansgadhi was chopped into 3-5 cm pieces and pasteurized using the hot-water immersion method (approximately 80 °C for one hour) in a drum heated over a wood-fired stove, after which the straw was drained and spread on a raised bamboo platform until it reached 65-70% moisture content, checked by the hand-squeeze test. Two kilograms of dry-weight-equivalent substrate was weighed for each bag on a digital balance and layered alternately with the assigned quantity of spawn inside perforated polypropylene bags (35 × 50 cm, 10 to 12 ventilation holes per bag, punched by hand rather than to a fixed template). Bags were sealed at the neck with cotton plugs and rubber bands, labelled by treatment and replication, and shifted to the incubation room within two hours of inoculation. Because hole number, diameter, and position were not standardized across bags, and additional cropping holes were later cut where colonization was uneven (Section 2.4), some bag-to-bag variation in ventilation and fruiting conditions cannot be ruled out; this is acknowledged as a limitation of the experimental setup (Section 4.4).

2.4 Crop management

Inoculated bags were incubated in the dark until mycelial colonization was visually complete (white mycelium fully covering the substrate), after which they were transferred to the fruiting room, the bag mouths opened, and cropping holes cut where colonization was uneven. Humidity was maintained through misting three to four times daily, and the room was ventilated by opening mesh-covered windows for 30 minutes each morning and evening to allow fresh-air exchange while excluding insects. No chemical fungicides or pesticides were applied at any stage; the only contamination-management measure was prompt removal and disposal of visibly infected bags to prevent spread to adjacent racks.

2.5 Observations and measurements

Days to complete spawn run, days to pinhead initiation, and days to first harvest were recorded from the date of inoculation for each bag. At every flush, the number of fruiting bodies, cap diameter, and stipe length were measured on five randomly tagged fruiting bodies per bag using a digital Vernier caliper (±0.01 mm) and averaged. Mushrooms were harvested at the button-to-early-flat stage across all flushes for 35 days from the date of transfer to the fruiting room, and total fresh yield per bag was recorded cumulatively using a digital balance (±0.1 g) and expressed on a g/bag and biological efficiency basis. Bags showing visible green (Trichoderma) or bacterial contamination before spawn run completion were recorded and excluded from subsequent yield measurement.

2.6 Biological efficiency and benefit-cost ratio

Biological efficiency (BE) was calculated as follows: BE (%) = (Total fresh mushroom yield ÷ Dry substrate weight) × 100. The benefit-cost ratio (BCR) for each treatment was estimated using a Bardiya farm-gate fresh mushroom price of NPR 250/kg and prevailing local input costs spawn at NPR 0.25/g and fixed non-spawn costs of NPR 40/bag (straw, bags, labour, and fuel for pasteurization) following BCR = Gross return ÷ Total cost of production.

2.7 Statistical analysis

Data were subjected to one-way analysis of variance (ANOVA) appropriate for a completely randomized design (CRD), following the procedures described by Gomez and Gomez (1984). Statistical analyses were performed using R software (version 4.3.1; R Core Team) through the RStudio interface. Prior to ANOVA, the assumptions of normality and homogeneity of variance were assessed using the Shapiro-Wilk and Levene's tests, respectively. Treatment means were separated using Duncan's Multiple Range Test (DMRT) at the 5% level of significance, and DMRT was used consistently as the sole method of mean comparison throughout Tables 1-3. Mean separation was performed using the agricolae package in R [AUTHOR TO CONFIRM: package version]. Microsoft Excel was used for data organization and summary calculations. For each parameter, the results are presented as treatment mean ± standard error (SE; n = 4), together with the ANOVA F-value, corresponding p-value, and DMRT letter groupings. The coefficient of variation (CV%) was calculated for each parameter.

3 Results and Analysis

3.1 Spawn run, pinhead initiation, and harvesting time

Spawn rate had a highly significant effect on the duration of mycelial colonization and the developmental stages that followed it (Table 1). Raising the spawn rate from 4% to 12% progressively shortened the spawn run period, though the rate of improvement clearly diminished beyond 10%. T_4 and T_5 were statistically at par across all three timing parameters, pointing to diminishing returns beyond the farmer-practice spawn rate (see Section 4.1 for interpretation).

Table 1 Effect of spawn rate on spawn run, pinhead initiation, and first harvest

Treatment	Spawn run (days)	Pinhead initiation (days)	First harvest (days)
T_1 (4%)	24.5 ± 0.47^{a}	29.2 ± 0.52^{a}	34.6 ± 0.55^{a}
T_2 (6%)	21.8 ± 0.47^{b}	26.4 ± 0.52^{b}	31.7 ± 0.55^{b}
T_3 (8%)	18.3 ± 0.47^{c}	23.1 ± 0.52^{c}	28.2 ± 0.55^{c}
T_4 (10%, farmer practice)	16.6 ± 0.47^{cd}	21.5 ± 0.52^{cd}	26.6 ± 0.55^{cd}
T_5 (12%)	15.9 ± 0.47^{d}	20.8 ± 0.52^{d}	26.0 ± 0.55^{d}
F-value	59.78^{***}	45.41^{***}	43.83^{***}
p-value	<0.001	<0.001	<0.001
CV (%)	4.31	3.86	3.51
Grand mean	19.42	24.20	29.42

Note: Means in a column followed by different lowercase letters differ significantly at $p \leq 0.05$ (DMRT). ** $p \leq 0.01$; *** $p \leq 0.001$. SE: standard error (n = 4); CV: coefficient of variation

3.2 Number of fruiting bodies, cap diameter, and stipe length

Spawn rate significantly influenced all three morphological parameters (Table 2). The number of fruiting bodies per bag rose consistently with spawn rate, while average cap diameter and stipe length moved in the opposite direction, shrinking as fruiting-body density increased. T_4 and T_5 produced statistically similar numbers of fruiting bodies, both well ahead of the lower spawn rates. Even so, both treatments produced smaller, thinner fruiting bodies than T_1 and T_2 a size-number trade-off discussed further in Section 4.2.

Table 2 Effect of spawn rate on fruiting body number, cap diameter, and stipe length

Treatment	Fruiting bodies (No./bag)	Cap diameter (cm)	Stipe length (cm)
T_1 (4%)	24.3 ± 0.95^{d}	5.8 ± 0.21^{a}	4.9 ± 0.18^{a}
T_2 (6%)	29.1 ± 0.95^{c}	5.4 ± 0.21^{ab}	4.5 ± 0.18^{ab}
T_3 (8%)	34.8 ± 0.95^{b}	5.0 ± 0.21^{b}	4.0 ± 0.18^{b}
T_4 (10%, farmer practice)	38.2 ± 0.95^{a}	4.6 ± 0.21^{bc}	3.6 ± 0.18^{bc}
T_5 (12%)	39.0 ± 0.95^{a}	4.1 ± 0.21^{c}	3.2 ± 0.18^{c}
F-value	43.34^{***}	10.45^{***}	14.43^{***}
p-value	<0.001	<0.001	<0.001
CV (%)	6.02	7.44	8.11
Grand mean	33.08	4.98	4.04

Note: Means in a column followed by different lowercase letters differ significantly at $p \leq 0.05$ (DMRT). ** $p \leq 0.01$; *** $p \leq 0.001$. SE: standard error (n = 4); CV: coefficient of variation

3.3 Yield, biological efficiency, and contamination

Total fresh yield and biological efficiency followed the same upward trend as fruiting body number, while contamination incidence fell sharply as spawn rate increased (Table 3). Yield and biological efficiency at T_4 (10%) and T_5 (12%) were statistically indistinguishable, both significantly exceeding T_1, T_2, and T_3. Contamination was observed only at the two lowest spawn rates: one of four bags at T_1 (25%) and one of eight cumulative bag-observations at T_2 (12.5%) showed visible green mold before spawn run completion, whereas no contamination at all was recorded at 8% spawn rate or above (interpreted further in Section 4.2).

Table 3 Effect of spawn rate on total yield, biological efficiency, and contamination incidence

Treatment	Total yield (g/bag)	Biological efficiency (%)	Contamination (%)
T_1 (4%)	310 ± 8.2^{d}	15.5 ± 0.41^{d}	25.0
T_2 (6%)	372 ± 8.2^{c}	18.6 ± 0.41^{c}	12.5
T_3 (8%)	428 ± 8.2^{b}	21.4 ± 0.41^{b}	0.0
T_4 (10%, farmer practice)	468 ± 8.2^{a}	23.4 ± 0.41^{a}	0.0
T_5 (12%)	472 ± 8.2^{a}	23.6 ± 0.41^{a}	0.0
F-value	71.23***	71.23***	-
p-value	<0.001	<0.001	-
CV (%)	5.28	5.28	-
Grand mean	410.0	20.5	7.5

Note: Means in a column followed by different lowercase letters differ significantly at $p \leq 0.05$ (DMRT). *** $p \leq 0.001$. Contamination incidence is reported descriptively as the percentage of bags affected and was not subjected to ANOVA. Values for total yield and biological efficiency are mean ± SE (n = 4). SE: standard error; CV: coefficient of variation

3.4 Benefit-cost analysis

Because spawn cost rises directly with spawn rate while yield gains taper off beyond 8%-10%, the benefit-cost ratio did not increase monotonically with spawn rate (Table 4). The 8% spawn rate (T_3) returned the highest benefit-cost ratio (1.34), narrowly ahead of 6% (1.33) and comfortably above the conventional 10% farmer practice (1.30). The 12% spawn rate, despite giving the numerically highest yield, actually returned the lowest BCR (1.18), because the extra spawn cost was not matched by a proportional yield gain over T_4.

Table 4 Cost, return, and benefit-cost ratio by spawn-rate treatment

Treatment	Total cost (NPR/bag)	Gross return (NPR/bag)	Benefit-cost ratio
T_1 (4%)	60	77.5	1.29
T_2 (6%)	70	93.0	1.33
T_3 (8%)	80	107.0	1.34
T_4 (10%, farmer practice)	90	117.0	1.30
T_5 (12%)	100	118.0	1.18

4 Discussion

4.1 Effect of spawn rate on colonization and cropping duration

The progressive shortening of spawn run, pinhead initiation, and first-harvest time with increasing spawn rate agrees with the general understanding that a higher density of inoculation points speeds up mycelial establishment throughout the substrate (Bhatti et al., 2007; Royse, 2014; Bhandari et al., 2022). The plateau between 10% and 12% suggests that once colonization points are dense enough, further increases in spawn rate buy very little additional time, since colonization speed becomes limited more by substrate quality and environmental conditions than by inoculum density alone a pattern also noted by Paudel and Dhakal (2020) working with different straw-based substrates in Nepal.

4.2 Effect of spawn rate on yield components and biological efficiency

The trade-off between fruiting body number and individual fruiting body size at higher spawn rates reflects a well-documented density-dependent response in *Pleurotus* cultivation: more numerous pinheads draw on a shared, finite pool of substrate nutrients, which constrains the maximum size any single fruiting body can reach (Chang and Miles, 2004). Despite the smaller individual mushrooms, total yield and biological efficiency were still highest at 10%-12% spawn rate, because the increase in fruiting body number outweighed the drop in individual size a pattern consistent with reports from other straw-based *Pleurotus* trials in South Asia (Ahmed et al., 2009).

The marked reduction in contamination incidence above 6% spawn rate lends some support to Nepalese growers' traditional preference for spawn rates at or above 10%: faster colonization leaves less time and fewer spare nutrients for competing molds to establish, which effectively works as a low-cost, non-chemical form of contamination control (Chang and Hayes, 1978).

4.3 Economic implications

The benefit-cost analysis makes a fairly simple but important point: the highest-yielding treatment is not necessarily the most profitable one. Although T_4 (10%) and T_5 (12%) produced the greatest yield and biological efficiency, the additional spawn expenditure needed to move from 8% up to 10% or 12% was not fully recovered through extra revenue, so the 8% spawn rate came out as the most economical option under the price and cost assumptions used here. This lines up with the broader argument that input-use decisions in mushroom cultivation should be guided by marginal cost-benefit analysis rather than yield maximization alone (Bhandari et al., 2022), and it suggests that Nepalese growers who currently follow the 10% convention could trim their spawn expenditure with only a marginal yield penalty and a corresponding gain in profit margin. Given that inadequate technical guidance and thin profit margins are repeatedly flagged as constraints on the wider mushroom sector in Nepal (MOALD, 2023), even a modest, evidence-based adjustment of this kind could matter at the farm level.

4.4 Limitations and future research

This trial was conducted at a single research station over one cropping cycle, and substrate moisture and internal bag temperature during colonization were not logged continuously; as a result, the specific physiological mechanisms behind the observed responses could not be verified directly. The benefit-cost analysis also relied on a single assumed farm-gate price and a simplified fixed-cost structure, which may not capture the price variability seen across markets and seasons in Bardiya — similar sensitivity has been reported for other input variables in *Pleurotus* systems, such as fertigation timing (Naim et al., 2020). Future work should repeat this trial across multiple locations and cropping seasons, incorporate direct monitoring of substrate temperature and moisture, and test a wider range of spawn rates (for example, 7% and 9%) to pin down the economically optimum rate more precisely, alongside a sensitivity analysis of the benefit-cost ratio under varying mushroom prices, along the lines suggested by Oei (2003) and Pal et al. (2017) for other *Pleurotus* species.

5 Conclusion

This study shows that spawn rate has a real, measurable effect on colonization speed, yield, morphology, contamination incidence, and profitability of oyster mushroom cultivation under Nepalese Terai conditions. Raising the spawn rate from 4% to 12% shortened the cropping cycle and increased yield and biological efficiency, with the largest gains occurring up to 10%, beyond which returns clearly diminished. Once spawn cost was weighed against gross returns, however, the 8% spawn rate emerged as the more economical choice, giving a benefit-cost ratio of 1.34 compared with 1.30 for the conventional 10% farmer practice. Smallholder growers in Bardiya and similar Terai districts who are aiming to maximize profitability rather than raw yield may want to consider trimming their spawn rate from the traditional 10% down to around 8%, while growers who priorities the fastest possible cropping cycle and maximum yield should stick with the 10%-12% range. Multi-season, multi-location trials, together with sensitivity analysis under varying market prices, are recommended before this recommendation is generalized to other regions of Nepal.

Author contributions

BK conceived and designed the study, conducted the research, interpreted the results, and prepared the original manuscript. AG performed the data analysis, assisted with data interpretation, and critically reviewed the manuscript. SC and KB managed the experimental facility, supervised laboratory operations, and collected the experimental data. All authors read and approved the final manuscript.

Conflict of Interest Disclosure

The authors affirm 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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Nitrogen Management Regulates Storage Root Development and Starch Accumulation in Sweet Potato

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Abstract Sweet potato storage root yield and starch accumulation directly determine its food, processing, and economic value. This study examines the effects of nitrogen management on storage root development and starch accumulation in sweet potato, with particular emphasis on source-sink relationships, carbon-nitrogen coordination, hormonal changes, nitrogen transport, and the regulation of related genes. The findings indicate that sweet potato responses to nitrogen vary markedly across developmental stages and among cultivars. During the early stage of storage root formation, an appropriate nitrogen supply favors cambial activity and the establishment of effective storage roots, whereas excessive nitrogen tends to promote vine growth, reduce the harvest index, and restrict carbon translocation to storage roots. After storage roots have been established, moderate nitrogen supplementation helps maintain photosynthetic activity and supports storage root bulking. Split application under reduced nitrogen rates can also improve nitrogen use efficiency and promote starch accumulation by regulating pathways associated with AGPase, GBSS, SBE, and related enzymes. These findings suggest that nitrogen management in sweet potato should shift from the use of a fixed application rate toward precise regulation based on developmental stage, cultivar-specific responses, and integrated soil-plant diagnosis. Such strategies can help achieve coordinated improvements in yield, starch productivity, and nitrogen use efficiency, providing a basis for green and efficient cultivation as well as the breeding of nitrogen-efficient sweet potato cultivars.

Keywords Sweet potato (*Ipomoea batatas* L.); Nitrogen management; Storage root development; Starch accumulation; Source-sink relationship; Nitrogen use efficiency

1 Introduction

Sweet potato (*Ipomoea batatas* L.) is not only an important food crop but also a major raw material for starch processing, food manufacturing, and feed production. In practical production, storage roots are the main organs that determine economic yield. Therefore, the performance of a cultivar or a cultivation practice cannot be evaluated solely on the basis of vigorous aboveground growth. Luxuriant vine growth does not necessarily result in a high storage-root yield. For starch-type sweet potato, storage-root dry matter and starch accumulation also need to be considered. Fan et al. (2025) showed that sweet potato genotypes differ substantially in their capacity for starch production. Such differences arise not only from variation in fresh storage-root yield, but also from starch content and source-sink transport efficiency. Starch quality itself is associated with amylose proportion, amylopectin structure, granule size, and gelatinization properties, all of which directly affect its suitability for different processing purposes.

This relationship becomes clearer when actual yield data are considered. Jiang et al. (2024) investigated the high-starch-yielding genotype H283 and reported a fresh storage-root yield of 43.20 t/ha and a storage-root starch content of 23.56%, corresponding to a starch yield of approximately 10.18 t/ha. In comparison, the control cultivar Shangshu 19 produced 28.455 t/ha of fresh storage roots with a starch content of 23.42%, giving a starch yield of only about 6.66 t/ha. Although the difference in starch percentage between the two genotypes was small, their starch yield differed by approximately 3.51 t/ha. This comparison shows that storage-root yield remains a major determinant of high starch productivity. How much carbon is fixed by source leaves and how efficiently that carbon is transported to the storage roots often determine the final starch yield.

Nitrogen management is closely linked to this process. When nitrogen supply is insufficient, leaf area development, chlorophyll formation, and photosynthetic capacity can be restricted. Plants may show weak early growth, and less assimilate is consequently available for storage-root development. However, increasing nitrogen supply does not always improve productivity. Sweet potato is harvested for its underground storage organs, and excessive nitrogen can readily shift biomass allocation toward shoots. Vines continue to elongate and leaves maintain relatively high nitrogen levels, whereas storage-root differentiation and carbon translocation to belowground organs may be restricted. Experiments with nitrate nitrogen have also shown that the nitrogen-sensitive cultivar Jishu 26 allocated more nitrogen to leaves and growing points under high nitrate supply, resulting in stronger shoot growth and a greater tendency toward excessive vegetative growth. In contrast, the nitrogen-tolerant cultivar Xushu 32 showed a much more moderate response (Duan et al., 2024).

The key issue in nitrogen management for sweet potato is therefore to achieve an appropriate balance. Nitrogen deficiency should be avoided during storage-root initiation, but the root system should not remain under excessively high nitrogen conditions for an extended period. After storage roots have been established and enter the bulking stage, maintaining sufficient leaf area and sustained photosynthetic activity still requires an adequate nitrogen supply. Dong et al. (2022), for example, found that 100 mg/L nitrogen was more favorable for storage-root initiation, whereas 200 mg/L nitrogen promoted greater biomass accumulation and nitrogen uptake during the subsequent growth stage after storage roots had already formed. Thus, the optimal nitrogen level is not necessarily the same at different developmental stages.

This study mainly examines the effects of nitrogen on storage-root initiation, bulking, biomass allocation, and starch accumulation in sweet potato. It further reviews nitrogen uptake, carbon-nitrogen coordination, hormonal changes, and the regulation of related genes. Particular attention is given to why the same nitrogen level may produce very different responses across growth stages, cultivars, and soil conditions. On this basis, several management approaches with practical relevance are also discussed, including split nitrogen application, combined nitrogen and potassium management, coordination between nitrogen fertilization and irrigation, and plant-based diagnosis of nitrogen status.

2 Physiological Basis of Storage Root Initiation and Development in Sweet Potato

2.1 Formation and differentiation of storage roots

Sweet potato storage roots are not formed simply by the thickening of ordinary fine roots. Among the adventitious roots emerging from the nodes of vine cuttings, only a portion eventually develop into storage roots. The differences are not always obvious during the early stages, but internal tissue differentiation has already begun. Adventitious roots with the potential to form storage roots generally show enhanced cambial activity, followed by the development of active secondary meristematic tissues, an increase in parenchyma cells, and accelerated radial growth. In contrast, some adventitious roots undergo progressively greater lignification, accompanied by pronounced development of vascular bundles and fibrous tissues. These roots are more likely to develop into fibrous roots or pencil roots rather than functional storage roots. In a root-segment comparison experiment, Singh et al. (2021) found that the proximal and distal portions of the same adventitious root had already begun to show different developmental fates within 1-2 weeks after planting. The proximal region exhibited stronger xylem development and lignin deposition, whereas the distal region showed greater starch accumulation at an earlier stage. By the fifth week, these differences had become even more pronounced.

Cambial activity is a key feature of this developmental transition. Transcriptomic analyses of root tissues at different developmental stages have shown that storage-root formation is not controlled by the sudden activation of a single gene. Instead, coordinated changes occur in multiple biological processes, including cell division, cell-wall remodeling, lignin metabolism, and carbohydrate metabolism. An early study covering seven stages of storage-root development detected 5,368 significantly altered genes, including 435 transcription factors. A subsequent transcriptomic study of storage-root bulking identified another 1,312 differentially expressed genes, with genes such as *SBEI*, *ARF6*, *NF-YB3*, and *NF-YB10* showing increasing expression during the bulking process (Wang et al., 2015).

2.2 Source-sink relationships during storage root formation

Whether a storage root continues to enlarge also depends on whether a strong sink has actually been established. Leaves serve as the main carbon source. Carbon fixed through photosynthesis is first converted into transportable compounds such as sucrose and is then translocated through the phloem to belowground organs. Fan et al. (2021) noted that once storage roots develop a strong capacity for assimilate unloading and starch synthesis, they can continuously attract and utilize these assimilates. In other words, high photosynthetic activity in the leaves is only the first step. If carbon remains in the stems and leaves rather than being transferred belowground, storage-root growth will still be limited.

Using isotope tracing to compare high- and low-yielding genotypes, Jiang et al. (2024) found that the high-starch-yielding genotype H283 fixed approximately 8.19%-26.07% more ^{13}C, whereas the amount of ^{13}C transported into the storage roots was approximately 282.73%-1,017.01% greater. The difference in carbon allocation to storage roots was therefore much larger than the difference in carbon fixation itself. This result is particularly informative because it suggests that yield differences are not caused simply by leaves producing more assimilates, but also by how efficiently those assimilates are transported into the storage roots. Regulatory factors such as IbPMA1 and IbbHLH49 are thought to participate in this coordination between source activity and sink strength.

2.3 Hormonal regulation of storage root development

Hormonal regulation cannot be described simply in terms of "promotion" or "inhibition." An appropriate auxin level supports root primordium development and cambial activity, but excessive auxin is not necessarily beneficial. In plants overexpressing IbNF-YA1, storage-root yield decreased by 29.15%-40.22%. When its target gene *IbYUCCA4* was further overexpressed, indole-3-acetic acid (IAA) content increased by 71.77%-98.31%, while storage-root yield decreased by as much as 77.91%-80.52% (Xue et al., 2024). These results indicate that auxin needs to be maintained within an appropriate range for normal storage-root development.

Cytokinins, abscisic acid, and gibberellins are also involved in this process. Exogenous application of GA_3 enhances lignification of root vascular tissues and reduces the capacity for storage-root formation. Singh et al. (2019) reported that exogenous GA_3 markedly altered the developmental fate of sweet potato adventitious roots. Following GA_3 treatment, the number of storage roots decreased by approximately 3.3-fold, mean storage-root diameter decreased by about 2.1-fold, and fresh storage-root weight declined by approximately 2.1-fold. At the same time, xylem development and lignin deposition in the roots increased, whereas starch accumulation decreased. At the molecular level, GA_3 upregulated genes associated with vascular differentiation and lignin biosynthesis, including *IbVND7*, *IbSND2*, *IbPAL*, *IbC4H*, *Ib4CL*, *IbCCoAOMT*, and *IbCAD*, while downregulating the starch-synthesis-related genes *IbAGPase* and *IbGBSS*. These findings suggest that high GA levels tend to direct potential storage roots toward the development of lignified conducting roots rather than starch-rich storage organs.

On the other hand, experiments in which low nitrogen supply promoted storage-root formation showed increased levels of zeatin riboside (ZR) and abscisic acid (ABA), together with reduced lignin biosynthesis and enhanced expression of starch-synthesis-related genes. The effects of nitrogen are therefore often intertwined with changes in hormonal signaling and cannot be explained simply by the amount of nitrogen present in the soil.

3 Effects of Nitrogen Management on Sweet Potato Storage Root Development

3.1 Nitrogen supply and storage root initiation

Storage-root initiation is highly sensitive to nitrogen supply, and this sensitivity appears very early in development. In a sand-culture experiment using the cultivar Orleans, four nitrogen levels of 0, 50, 100, and 200 mg/L were evaluated. The 100 mg/L treatment promoted the development of primary and secondary cambia and maintained a relatively high storage-root formation rate from 21 to 56 days after transplanting. Although the 200 mg/L treatment showed faster growth and greater nitrogen uptake after 35 days, its storage-root formation rate and

number of storage roots per plant remained lower than those under 100 mg/L nitrogen when adventitious-root differentiation was largely complete (Dong et al., 2022). This suggests that once the early opportunity for storage-root initiation is missed, additional nitrogen supplied later cannot fully compensate for the loss.

The form of nitrogen supplied can also influence root differentiation. A field experiment comparing different nitrogen sources at 60 kg/ha showed that ammonium nitrogen altered the expression of IbEXP1, Ibkn1, and Ibkn2, accompanied by changes in GA_3 and zeatin riboside (ZR) levels and in the activities of enzymes associated with lignin biosynthesis. Importantly, these effects shifted with developmental stage. A certain degree of vascular tissue development during the early stage may help establish an effective transport system, whereas persistently high levels of lignification at later stages can restrict the expansion of parenchymatous tissues (Meng et al., 2022). Therefore, it is not accurate to interpret storage-root development simply as requiring the suppression of all lignin formation. Timing remains a key factor.

3.2 Effects of nitrogen on storage root bulking

The situation changes once storage roots have already been initiated. At this stage, new cells must continue to form, existing cells must expand, and large amounts of carbohydrates must be imported into the developing storage roots. An appropriate nitrogen supply helps maintain both leaf and root activity. The main problem arises when nitrogen is excessive. Under high nitrogen conditions, newly accumulated dry matter is more likely to remain in stems and leaves, while the number of storage roots and individual root weight may initially increase and then decline. In a field experiment examining nitrogen-potassium interactions, Shu et al. (2024) also observed that vine length continued to increase with increasing nitrogen application, whereas the number of storage roots per plant, fresh storage-root weight, and dry storage-root weight generally showed an initial increase followed by a decline.

Data from split nitrogen application further illustrate that the timing of nitrogen supply can be as important as the total amount applied. Compared with the conventional practice of applying 100 kg N/ha entirely as basal fertilizer, reducing total nitrogen input by 20% and applying 40% as basal fertilizer and another 40% at 35 days after transplanting increased the two-year average number of storage roots by 12.3%, individual storage-root weight by 10.2%, and final yield by 22.1% (Du et al., 2020). In this case, yield improvement was not achieved by increasing the total nitrogen rate. On the contrary, less nitrogen was applied. The higher yield was mainly associated with better synchronization between nitrogen supply and crop demand.

3.3 Regulation of biomass allocation by nitrogen

One of the most typical responses to excessive nitrogen is not that the plant fails to grow, but that biomass is allocated to the wrong organs. In a two-season field experiment in Brazil with nitrogen rates ranging from 0 to 300 kg N/ha, the harvest index gradually declined from 0.81, 0.80, and 0.78 to 0.75 and 0.72 as nitrogen application increased (Higashikawa et al., 2025). In other words, additional nitrogen may increase total plant biomass, while reducing the proportion ultimately allocated to marketable storage roots. At the same time, agronomic nitrogen-use efficiency decreased sharply from 51.22 kg/kg at 50 kg N/ha to only 1.69 kg/kg at 300 kg N/ha, while nitrogen recovery efficiency declined from 69.78% to 28.30%.

For this reason, the performance of nitrogen management should be evaluated using storage-root yield, aboveground biomass, harvest index, and nitrogen-use efficiency together. Comparing vine fresh weight alone can easily lead to the mistaken conclusion that a high nitrogen rate is more effective (Du et al., 2019). In sweet potato, moderate restriction of excessive shoot expansion during the early growth stage may sometimes be more favorable for the establishment of a strong storage-root sink (Figure 1).

4 Nitrogen Regulation of Starch Accumulation in Sweet Potato

4.1 Carbon assimilation and sucrose transport

Nitrogen is an essential nutrient for chlorophyll synthesis and the normal functioning of photosynthetic enzymes, and it therefore directly affects the photosynthetic capacity of sweet potato leaves (Dong et al., 2025). Yao et al. (2025) reported that an appropriate ammonium supply (1 mM) during the storage-root bulking stage increased

chlorophyll content, net photosynthetic rate, and stomatal conductance in the sweet potato cultivar Sushu 16. RNA-Seq analysis further identified 34 differentially expressed genes in storage roots under the optimal ammonium treatment. These genes were mainly involved in photosynthesis, starch biosynthesis, and hormone signaling pathways. Under low-nitrogen conditions, the contents of soluble sugars, sucrose, and starch increased in vegetative organs, while biomass allocation shifted toward roots rather than shoots, reflecting enhanced carbon utilization by sink organs (Amoah et al., 2025). In contrast, excessive nitrogen application tends to promote excessive vine growth at the expense of storage-root development, thereby reducing carbon allocation to sink tissues (Duan et al., 2019; Pan et al., 2026).

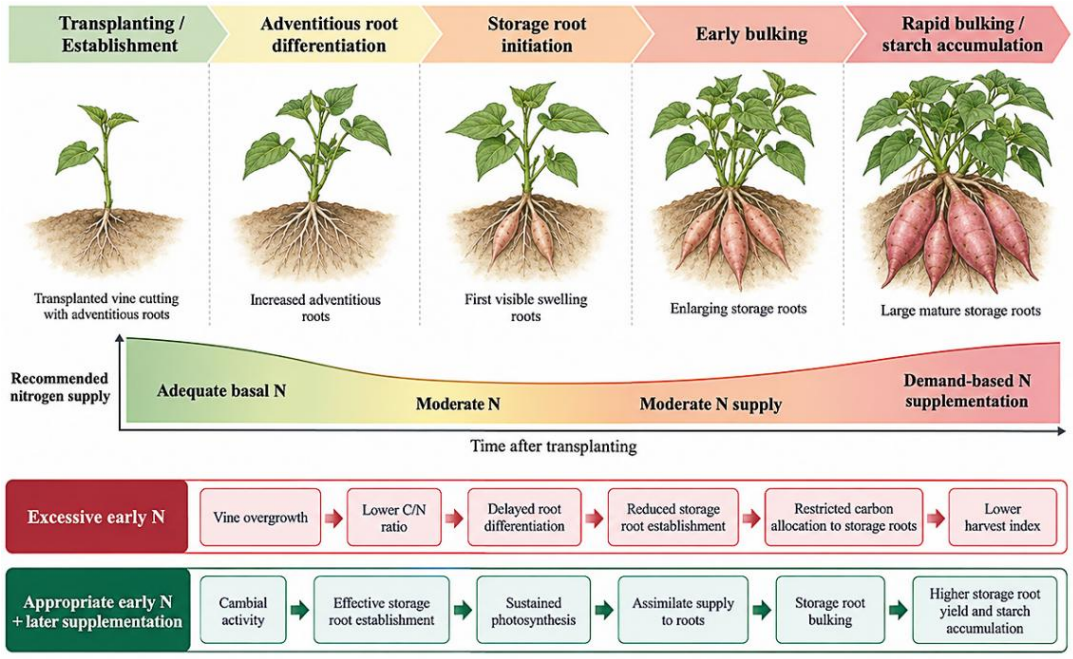


Figure 1 Stage-dependent regulation of sweet potato storage root development by nitrogen supply

Image caption: Moderate nitrogen availability during the early developmental stage favors cambial activity and effective storage root establishment, whereas excessive early nitrogen can promote shoot growth and delay storage root differentiation. After storage roots are established, nitrogen demand increases again, and appropriate supplemental nitrogen helps maintain leaf photosynthesis, assimilate supply, and storage root bulking

Efficient transport of sucrose from source leaves to storage roots through the phloem is an important prerequisite for starch accumulation in sink organs. Fan et al. (2021) found that sucrose transporters (SUTs) participate in sucrose loading into phloem sieve elements, and their overexpression can improve carbohydrate allocation to sink organs. Overexpression of the H^+-pyrophosphatase gene *IbVP1* increased *SUT1* expression, enhanced phloem loading and long-distance sucrose transport, and increased sucrose content in storage roots by 28%-67%. Similar results were reported by Jiang et al. (2024), who showed that the plasma membrane H^+-ATPase gene *IbPMA1*, regulated by the transcription factor *IbbHLH49*, plays an important role in sugar transport and starch biosynthesis in both source and sink tissues. Under relatively high nitrogen supply, nitrogen-tolerant cultivars such as Xushu 32 can reduce carbon flux into secondary metabolic pathways by downregulating genes involved in lignin and flavonoid biosynthesis, thereby redirecting more carbon toward starch metabolism and maintaining a relatively high sugar supply to sink organs (Duan et al., 2021). Source-sink coordination is therefore critical in this process. Even in high-starch genotypes, starch accumulation in storage roots can still be strongly constrained when the production or transport of photosynthates from leaves is limited (Jiang et al., 2024).

4.2 Starch biosynthesis in storage roots

Starch biosynthesis in sweet potato storage roots is coordinated by a series of enzymes (Figure 2). ADP-glucose pyrophosphorylase (AGPase) catalyzes a rate-limiting step in starch synthesis by producing ADP-glucose, which serves as the precursor substrate for the formation of amylose and amylopectin. Granule-bound starch synthase

(GBSS) mainly controls amylose synthesis, whereas soluble starch synthase (SSS) and starch branching enzyme (SBE) are primarily involved in the elongation and branching of amylopectin chains (Sheng et al., 2023). Sucrose synthase (SuSy) and UDP-glucose pyrophosphorylase (UGPase) participate in the upstream conversion of sucrose toward starch and play important roles in starch accumulation in storage-root dry matter (Zhang et al., 2017). As storage roots develop, the expression of AGPase, GBSS, and SBE generally increases. Duan et al. (2023) reported that AGPase expression increased in enlarging storage roots, while GBSSI expression rose markedly during the rapid bulking stage.

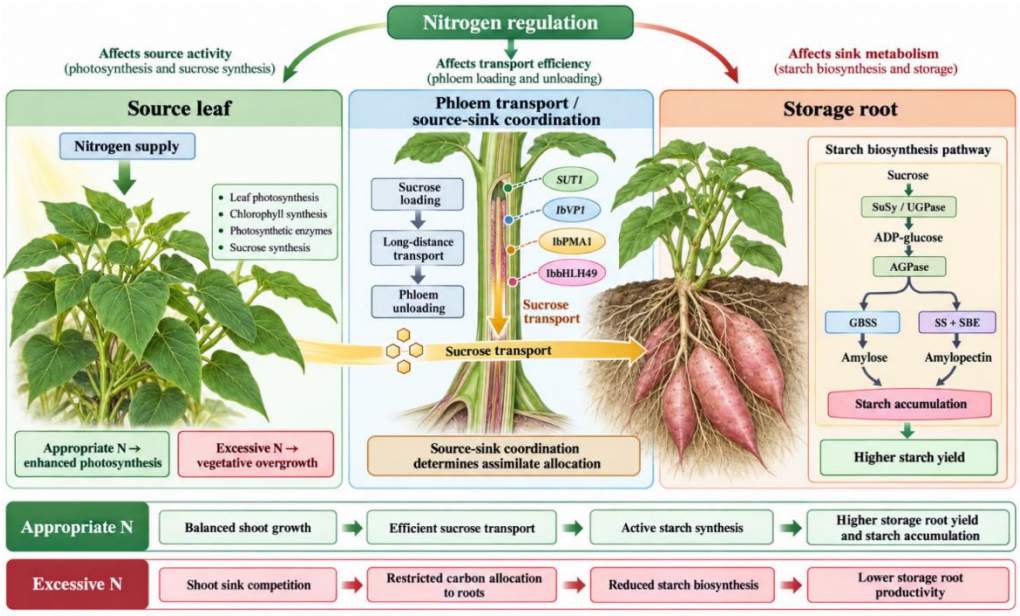


Figure 2 Nitrogen-mediated coordination of source-sink carbon transport and starch biosynthesis in sweet potato
Image caption: Nitrogen availability affects carbon assimilation in source leaves, sucrose loading and long-distance transport through the phloem, and starch biosynthesis in storage roots. Sucrose transported into storage roots is converted through SuSy- and UGPase-associated pathways, followed by AGPase-mediated ADP-glucose formation and subsequent amylose and amylopectin synthesis involving GBSS, SS, and SBE. Appropriate nitrogen supply favors source-sink coordination, whereas excessive nitrogen may divert assimilates toward vegetative organs

Nitrogen management can regulate both the activity of starch-synthesis enzymes and the expression of their related genes. Du et al. (2020) found that reducing nitrogen application to 80% of the conventional rate and applying it in split doses increased starch accumulation by 11.12% through enhanced AGPase and starch synthase activities and upregulation of the corresponding genes. Moderate nitrogen reduction combined with higher planting density increased the expression of *IbSUS2*, *IbSUS5*, *IbAGPS1*, *IbAGPS2*, and *IbAGPL2* from 15 to 45 days after planting, while also enhancing SUS and AGPase activities (Pan et al., 2026). In contrast, excessive nitrogen can restrict starch synthesis by suppressing the expression of *AGPa* and *AGPb* in sweet potato roots. In the nitrogen-sensitive cultivar Jishu 26, high nitrogen under normal water conditions reduced the expression of *AGPa*, *AGPb*, *GBSSI*, and *SBEI*, whereas the nitrogen-tolerant cultivar Xushu 32 was affected to a lesser extent (Duan et al., 2023).

Different nitrogen forms can also produce different responses. Si et al. (2018) reported that amide nitrogen treatment (XN) increased SuSy and AGPase activities as well as starch concentration in potential storage roots, whereas ammonium nitrogen treatment (AN) was more favorable for increasing invertase activity and root number, but had a weaker effect on starch accumulation. Similar patterns have also been observed in potato. In a high-starch potato cultivar, an appropriate nitrogen rate of 150 kg/ha resulted in the highest accumulation of amylose, amylopectin, and total starch. During the early and middle growth stages, the expression of genes such as *AGPP-L*, *GBSSI*, *SBEI*, and *SSIII* generally followed the order N150 > N300 > N0 (Li et al., 2018)..

4.3 Starch composition and physicochemical properties

Nitrogen supply can alter the proportion of amylose and amylopectin in sweet potato storage roots, but the response differs markedly among genotypes. In Jishu 25, for example, the highest amylose content was observed under 150 kg N/ha (N2), whereas the lowest value occurred under the zero-nitrogen treatment (Duan et al., 2019). Guo et al. (2020) evaluated nine sweet potato cultivars with different flesh colors and found that increasing nitrogen application reduced amylose content in the yellow-fleshed cultivar Sushu 16. In contrast, amylose content increased in the white-fleshed cultivar Sushu 29 and in the purple-fleshed cultivars Ningzishu 1 and Ningzishu 4, while no significant changes were observed in the other cultivars. Overexpression of IbVP1 increased total starch content by 20%-32% and amylose content by 27%-32% through the upregulation of AGPase and GBSSI (Fan et al., 2021). In addition, SnRK1 can increase total starch content through coordinated upregulation of genes involved in the starch biosynthetic pathway, while reducing the proportion of amylose and increasing starch granule size (Ren et al., 2019).

Nitrogen treatment can also influence starch granule size, pasting viscosity, and thermal properties, although the responses are not consistent among cultivars. In Jishu 25, nitrogen application had no significant effect on the starch granule size distribution parameters D[v, 0.9], D[4,3], and D[3,2] (Duan et al., 2019). By contrast, starch granule size decreased with increasing nitrogen application in Ningzishu 1, Sushu 28, and Sushu 29 (Guo et al., 2020). In Jishu 25, the 75 kg N/ha treatment produced a relatively high setback viscosity, whereas the 150 kg N/ha treatment increased peak viscosity, final viscosity, and setback viscosity. However, starch gelatinization temperature and pasting properties remain strongly dependent on cultivar and genetic background and cannot be attributed simply to nitrogen application rate. Likewise, starch crystalline structure and gelatinization enthalpy did not change substantially in different cultivars in response to nitrogen treatment. Overexpression of *IbVP1* can further affect starch structure, composition, and physicochemical properties by altering carbon metabolic flux and the expression of genes involved in related pathways (Fan et al., 2021).

5 Molecular and Metabolic Mechanisms Underlying Nitrogen Regulation of Storage Root Development and Starch Formation

5.1 Nitrogen sensing and signal transduction pathways

Roots must first recognize and absorb inorganic nitrogen. Twelve members of the IbAMT family have been identified in sweet potato. In a two-year experiment with nitrogen application rates of 0, 60, 120, and 180 kg N/ha, Meng et al. (2023) found that the 120 kg N/ha treatment generally resulted in relatively high expression levels of *IbAMT1.3* and *IbAMT1.5*, together with greater storage-root nitrogen content, nitrogen uptake efficiency, number of storage roots per plant, storage-root weight, and yield. The expression levels of these two genes were also significantly and positively correlated with nitrogen content in the storage roots. These results suggest that ammonium transport is not simply an uptake process, but is also closely associated with nitrogen utilization and storage-root formation.

Similar evidence has been obtained for nitrate nutrition. Duan et al. (2024) found that Jishu 26 and Xushu 32 responded differently to 0, 4, 8, and 16 mmol/L NO_3^-. High nitrate supply increased the expression of genes such as *NRT1.1*, *NR2*, and *NiR2*. However, the nitrogen-sensitive cultivar Jishu 26 simultaneously allocated more nitrogen to leaves and growing points and showed stronger negative responses of root length and root surface area to high nitrogen. These results illustrate that greater nitrogen uptake does not necessarily lead to better growth or storage-root production.

Within nutrient-signaling networks, relatively direct functional evidence is available for *SnRK1* in sweet potato. Alteration of *IbSnRK1* activity affects sugar metabolism, the starch-synthesizing enzyme system, and ultimately starch-related traits. The role of TOR, however, should be interpreted more cautiously. Based on current studies of nitrogen regulation and storage-root development in sweet potato, direct functional evidence linking TOR to specific nitrogen application levels, storage-root formation, and starch yield remains limited (Ren et al., 2024). TOR is therefore better regarded as a nutrient-signaling node that requires further experimental validation rather than as an established component of nitrogen regulation in sweet potato.

5.2 Regulation of genes associated with storage root development

Storage-root differentiation in sweet potato is governed by a relatively complex transcriptional regulatory network. He et al. (2021) applied dynamic network biomarker (DNB) analysis to continuous transcriptomic data from developing sweet potato roots and found that more than 9% of sweet potato genes displayed clear stage-specific expression patterns. The DNB signal reached a critical state when root diameter was approximately 3.5 mm, and this stage was therefore defined as a "critical transition point" from fibrous-root growth to storage-root swelling. Network analysis further identified the NAC transcription factor IbNAC083 as a central regulatory node. Suppression of IbNAC083 inhibited root swelling and simultaneously disrupted lignin, flavonoid/flavonol, and starch biosynthesis. These results indicate that storage-root formation is not triggered by the activation of a single "starch gene," but instead involves broad reprogramming of the metabolic network.

Genes associated with lignification deserve particular attention. Transcriptomic analyses of two cultivars differing in their rates of storage-root swelling generated 52,137 transcripts, from which 21,148 unigenes and 9,577 differentially expressed genes were identified. *swbp1*, *swpa7*, *IbERF061*, and *IbERF109* were selected as important candidate factors associated with lignin metabolism and storage-root expansion (Meng et al., 2023). Nitrogen supply can also alter the expression of genes such as *IbEXP1*, *Ibkn1*, and *Ibkn2*. Nitrogen management therefore ultimately intersects with the intrinsic developmental programs operating within the root.

5.3 Coordination between nitrogen and carbon metabolism

From a metabolic perspective, storage-root formation is essentially a process of carbon and nitrogen redistribution (Figure 3). During the early stage, a certain amount of nitrogen is required to support cell division and enzyme and protein synthesis. However, excessively high nitrogen concentrations in the roots often correspond to a low carbon-to-nitrogen ratio and continued dominance of vegetative growth.

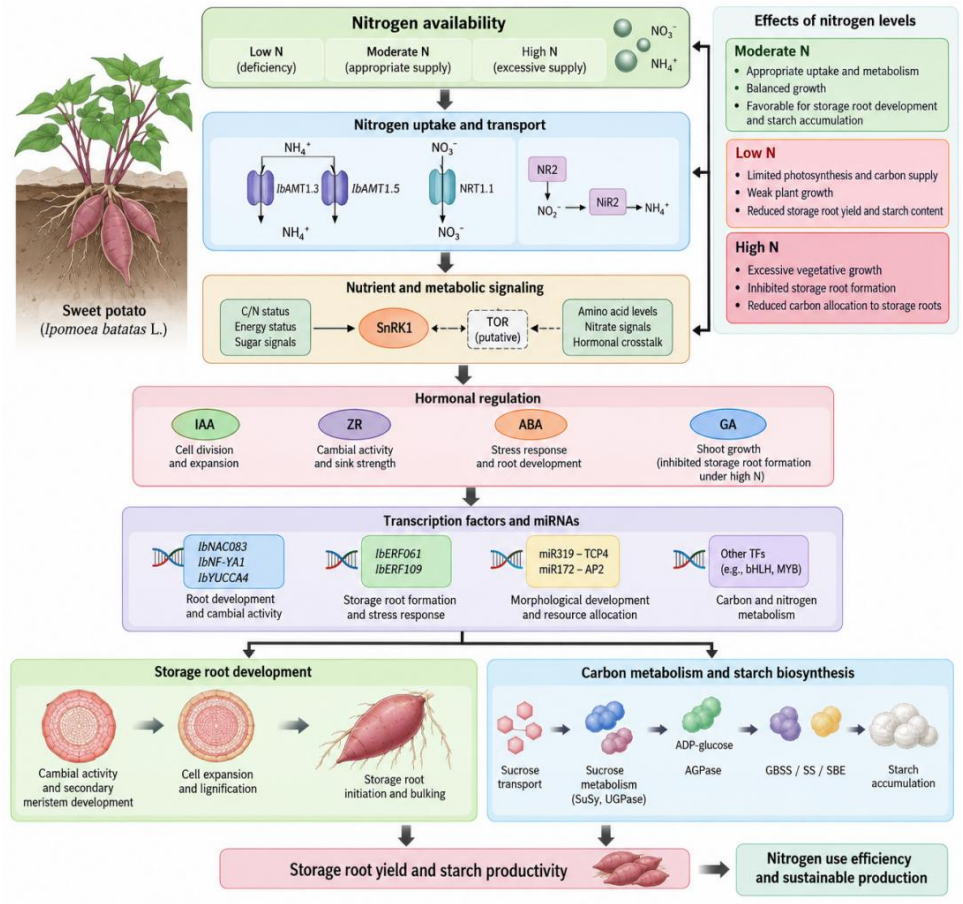


Figure 3 Proposed molecular and metabolic network underlying nitrogen regulation of storage root development and starch formation in sweet potato

Under split and reduced nitrogen application, storage-root nitrogen content decreased at 35 days after transplanting (DAT), while carbon content and the C/N ratio increased. These changes were accompanied by altered hormonal status, including changes in IAA and ZR, and were subsequently associated with the formation of more storage roots. After approximately 80 DAT, however, a more adequate nitrogen supply was again required to maintain leaf function and support storage-root filling (Du et al., 2020). This stage-dependent pattern is more consistent with experimental evidence than the generalized statement that "low nitrogen promotes storage-root formation."

Multi-omics studies also support this stage-specific regulation. Lin et al. (2025) conducted integrated transcriptomic and metabolomic analyses of storage roots from three sweet potato cultivars, SJN, SCZ, and Y25, sampled at 70, 100, and 130 days. A total of 27 RNA-seq samples generated 232.38 Gb of clean data, with at least 7.14 Gb obtained per sample. Q30 values ranged from 93.60% to 95.06%, and 91.02%-95.37% of reads were mapped to the reference genome. In total, 16,303 differentially expressed genes and 1,566 metabolites were identified. Starch and sucrose metabolism were significantly enriched, and starch-related genes generally showed their highest expression at 70 days. Weighted gene co-expression network analysis (WGCNA) ultimately identified 14 candidate genes, among which *IbUGP2* and *IbglgA* were closely associated with D-glucose-6-phosphate and eight starch-related metabolites, suggesting that they may serve as important regulatory nodes during early starch accumulation.

Another integrated study combining miRNA profiling, transcriptomics, and degradome sequencing identified 29,633 differentially expressed genes and 510 differentially expressed miRNAs, and further screened several regulatory modules, including miR319-TCP4 and miR172-AP2 (Wu et al., 2025). Storage-root development therefore cannot be explained by a single "nitrogen-signaling pathway." Rather, it involves coordinated changes in sugar metabolism, hormonal regulation, secondary metabolism, and transcriptional control.

6 Nitrogen Application Strategies for Improving Sweet Potato Yield and Starch Content

6.1 Optimization of nitrogen application rate

One of the most common misconceptions in nitrogen management for sweet potato is to search directly for a fixed "optimal rate." In fact, the optimal nitrogen rates reported in different experiments vary considerably. In a two-year experiment conducted on a Humic Cambisol in Brazil, the maximum technical yield of marketable storage roots was 47.07 t/ha, corresponding to a model-estimated nitrogen rate of approximately 165.5 kg N/ha. However, when fertilizer cost was taken into account, the economically optimal rate was only 74 kg N/ha, at which the marketable storage-root yield was 43.73 t/ha (Higashikawa et al., 2025). In other words, an additional application of approximately 91.5 kg N/ha resulted in only about 3.34 t/ha of additional modeled yield, while nitrogen-use efficiency declined markedly at high nitrogen rates.

Other experiments have reported either lower or higher suitable nitrogen levels. Meng et al. (2023) found that Pushu 32 generally performed best at 120 kg N/ha among treatments of 0, 60, 120, and 180 kg N/ha, whereas in a sand-culture experiment with Orleans, a nutrient-solution nitrogen concentration of 100 mg/L was optimal during the storage-root initiation stage. These values cannot be directly converted or compared as equivalent nitrogen rates. One represents a field-based fertilizer application rate per unit area, whereas the other represents nitrogen concentration in the root-zone nutrient solution. Soil conditions, cultivars, and developmental stages also differed between the experiments. When these data are considered together, the most reliable conclusion is not that "sweet potato should receive 120 kg N/ha," but rather that yield commonly shows a pronounced nonlinear response to increasing nitrogen supply.

6.2 Timing and method of nitrogen application

Research suggests that adjusting the timing of nitrogen application may sometimes be more important than increasing the total amount supplied. Du et al. (2019) replaced the conventional single basal application of 100 kg N/ha with a reduced total rate of 80 kg N/ha, split between transplanting and 35 days after transplanting (DAT). Storage-root yield increased by 16.6%-19.0% over two years, accompanied by greater nitrogen uptake during the

middle and late growth stages and an increased nitrogen harvest index. In contrast, simply reducing the rate from 100 to 80 kg N/ha while maintaining a single basal application decreased yield. The issue, therefore, is not simply to "reduce nitrogen," but to ensure that, after reducing the total amount, nitrogen is supplied at the stages when the crop actually requires it.

From the perspective of storage-root initiation, however, nitrogen cannot be completely withheld during the early growth stage. Studies of carbohydrate dynamics have shown that an appropriate nitrogen supply reaching the root zone before or at planting is more favorable for the subsequent translocation of sugars and starch-related assimilates toward the roots. When nitrogen is supplied too late, a greater proportion of nonstructural carbohydrates may already have accumulated in the vines (Dong et al., 2025). A more reasonable strategy is therefore to use basal nitrogen to support seedling establishment and early root differentiation, while avoiding excessive early application. After storage roots have formed, additional nitrogen can then be supplied according to plant growth, soil nitrogen availability, and leaf nitrogen status rather than applying a large amount at one time during the early stage.

6.3 Coordination with other nutrients and water management

Nitrogen management should not be considered independently of potassium and phosphorus nutrition. Nitrogen-potassium interaction studies have shown that an appropriate potassium supply can improve leaf nitrogen metabolism and photosynthesis and can also promote storage-root formation. In a two-year field experiment, Shu et al. (2024) found that application of 240 kg K_2O/ha increased the average number of storage roots by 19.12%, individual storage-root weight by 16.54%, and total yield by 16.92% compared with the zero-potassium treatment. The coefficients of variation for storage-root length and diameter were also relatively low. This indicates that potassium may not only increase yield but also improve the uniformity and marketability of storage roots.

Phosphorus and water availability are equally important. A field experiment conducted on saline calcareous soil during 2022-2023 showed clear interactions between nitrogen sources and phosphorus fertilizer forms, making it difficult to explain final yield responses on the basis of nitrogen alone. In a late-season irrigation study, irrigation at approximately 75% of crop evapotranspiration favored the allocation of photosynthates to storage roots and resulted in relatively high yield and water-use performance (Kamel et al., 2025). Therefore, practical nitrogen recommendations for sweet potato should be developed in conjunction with soil phosphorus and potassium status as well as irrigation conditions.

7 Integrated Nitrogen Management for High-Yield and High-Starch Sweet Potato Production

7.1 Balancing vegetative growth and storage root formation

Excessive N supply promotes vine overgrowth at the expense of storage root development, reducing yield and harvest index. In high-starch cultivar Jishu 25, raising N from 75 to 150 kg/ha significantly decreased storage root yield despite no change in starch content (Duan et al., 2019). High N increases leaf area index, prolongs the cultivation cycle, and favors vegetative organs over root bulking (Ribeiro et al., 2021; Higashikawa et al., 2025). Conventional basal N management in China (90-200 kg/ha) far exceeds recommended rates and tends to hinder storage root formation (Du et al., 2019; 2020). Split application under reduced N rates mitigates this by lowering early soil-available N, promoting root initiation rather than vine expansion. Nitrogen form also influences vegetative balance: ammonium N (AN) increased adventitious root number and storage root yield, while amide N (XN) promoted starch concentration in potential storage roots (Si et al., 2018). Potassium (K) application counteracts excessive N absorption by reducing the leaf N/K ratio and increasing N transport to roots, improving yield by 15%-39% (Wang et al., 2020). Paclobutrazol (PBZ) application temporarily reduced branch length and increased fresh storage root yield under high N in the rainy season (Ribeiro et al., 2021).

Optimizing root-shoot partitioning requires managing the carbon-to-nitrogen (C/N) ratio and endogenous hormones during storage root formation. Du et al. (2020) found that split N application under reduced N increased storage root yield by 22.1% by elevating IAA and zeatin while reducing ABA during root formation, then

increasing ABA during bulking to promote C allocation into roots. Moderate N with medium planting density (MDMN) increased yield by 15%-25% by accelerating cambial ring formation and shifting gene expression from nitrogen-intensive defense to carbon storage (Zhao et al., 2026). Early N application at or before planting promoted non-structural carbohydrate translocation from vines to roots, increasing storage root number and fresh yield (Dong et al., 2025). Delayed N supply impaired this translocation, accumulating carbohydrates in vines instead of roots. K supply improved N transport rate from 9.8% to 20.1% and root N distribution from 50.3% to 59.3%, enhancing root dry matter allocation (Wang et al., 2020). A rate of 50 kg N/ha produced a better harvest index and higher nitrogen use efficiency (NUE) than elevated rates (Higashikawa et al., 2025).

7.2 Genotype-specific responses to nitrogen

Sweet potato cultivars differ markedly in N tolerance and use efficiency. The N-tolerant cultivar Xushu 32 (X32) absorbed less N and distributed more N to developing storage roots than the N-susceptible Jishu 26 (J26) under increasing N rates (Duan et al., 2021). X32 storage root development was sensitive only to the highest N rate (400 mg/kg), while J26 was sensitive to both 200 and 400 mg/kg. Under high N and normal moisture, J26 exhibited root lignification, reduced starch accumulation, and limited assimilate transport, whereas X32 was largely unaffected (Duan et al., 2023). Among five cultivars evaluated under varying N concentrations, Yao et al. (2020) pointed out that SS19 and GS87 showed greater tolerance to low N and produced higher storage root yield at 30 days (Yao et al., 2020). Split N application increased yield by 16.6-19.0% across two cultivars (Xushu 22 and Shangshu 19), though optimal split ratios may depend on cultivar and rainfall regime (Du et al., 2019). N-tolerant cultivars are recommended for fertile plain areas because they form storage roots earlier under high N conditions (Duan et al., 2021).

Cultivar identity strongly influences starch and root trait responses to N. In Jishu 25, 75 kg N/ha produced the highest storage root yield, starch yield, and dry matter accumulation exceeding one ton per mu, while 150 kg N/ha reduced starch yield through lower root yield despite increased amylose content (Duan et al., 2019). For cultivars Xushu 22 and Xushu 28, N rates of 60-120 kg/ha did not greatly decrease starch content, but 180 kg N/ha significantly reduced storage root yield. In contrast, starch levels in cultivar Rainha Branca decreased with increasing urea, with the lowest starch percentage at 460 kg/ha.

Under high N, X32 downregulated lignin and flavonoid synthesis genes, redirecting carbon flux toward starch metabolism and reducing lignification (Duan et al., 2021). J26, however, showed downregulated AGPa, AGPb, GBSSI, and SBEI expression under high N and normal moisture, inhibiting starch synthesis (Duan et al., 2023). Purple-fleshed sweet potato at northern latitudes showed the highest tuber-to-root mass ratio and leaf C/N ratio at N0, suggesting that N fertilization can constrain productivity in short-season environments (Zekker et al., 2025).

7.3 Precision nitrogen management

Portable chlorophyll meter readings provide a practical tool for in-season N diagnosis. A nitrogen sufficiency index (NSI) threshold of 90% reduced N application rates by 44-66% without negatively impacting storage root yield across three sites in Brazil (Rodrigues et al., 2024). An NSI threshold of 95% increased N application rates without yield benefit, making 90% the recommended diagnostic threshold. Soil nutrient diagnosis underpins rate selection: for Jishu 25, N application of 60-90 kg/ha was based on soil nutrient content, with 75 kg/ha identified as optimal (Duan et al., 2019). Combined NPK fertilization significantly increased storage root yield by 34.8%-53.1% compared with single-nutrient deficiency treatments, and random forest regression identified P accumulation in storage roots as the most important yield predictor (Zhao et al., 2025). Urease and nitrification inhibitors improved NUE and marketable yield, with double-inhibitor treatment producing the highest yield (30,923 kg/ha) and a significant positive correlation between marketable yield and NUE (Kakabouki et al., 2020).

Stage-specific N management models synchronize N supply with developmental transitions from storage root initiation to bulking. Moderate N (100 mg/L) promoted early starch accumulation during the first 35 days, while higher N (200 mg/L) enhanced total non-structural carbohydrate accumulation at 49 days, indicating shifting N

requirements across growth stages (Dong et al., 2025). Split application at basal and 35 days after transplanting prolonged the fast N uptake phase and increased N partitioning to storage roots during middle and late growth stages (Du et al., 2019). The economic optimum N rate (74 kg/ha) was substantially lower than the maximum technical efficiency rate (165.5 kg/ha), providing a basis for site-specific rate calibration (Higashikawa et al., 2025). MDMN treatment accelerated cambial ring formation at 15-30 days after planting and upregulated starch/sucrose metabolism genes, establishing a sink-optimized strategy under high-density, low-input systems (Zhao et al., 2026). Optimal split proportions should be determined according to primary soil fertility, cultivar identity, and rainfall regime, integrating soil diagnosis, plant monitoring, and growth-stage-specific N delivery to achieve high-yield and high-starch production (Du et al., 2019).

8 Concluding Remarks

Current evidence shows that the response of sweet potato to nitrogen is not simply positive or linear. Nitrogen deficiency restricts leaf growth, photosynthetic capacity, and the establishment of the whole-plant carbon source, whereas excessive nitrogen tends to strengthen aboveground growth and causes more nitrogen and dry matter to remain in leaves, vines, and growing points. The storage-root initiation stage is particularly sensitive. Moderate nitrogen supply is generally more favorable for cambial activity and the establishment of effective storage roots, while higher nitrogen levels may delay or reduce early storage-root formation. Once storage roots have been established, however, plant nitrogen demand increases again. Therefore, a moderate nitrogen supply during the early stage followed by demand-based supplementation later is more reasonable than maintaining a high nitrogen level throughout the entire growth period.

For starch production, it is also necessary to distinguish between starch concentration and starch yield. Nitrogen determines not only how much assimilate can be produced by the leaves, but also how efficiently sucrose is transported to storage roots and how metabolic processes involving AGPase, SS, GBSS, SBE, and related enzymes are regulated. Under nitrogen deficiency, starch concentration in storage-root dry matter is not necessarily low, but total starch accumulation at the whole-plant level may still be constrained by limited biomass production. Moderate nitrogen supply is often more favorable for early starch formation and the establishment of storage-root sink strength. Ultimately, starch yield per unit area is jointly determined by fresh storage-root yield, dry matter content, starch proportion, and carbon translocation efficiency.

Several major limitations remain in the current evidence. First, many nitrogen experiments focus only on final yield and do not simultaneously measure cambial activity, lignification, sugar transport, hormonal status, or starch-related enzyme activities. As a result, it is often difficult to determine at which physiological step yield loss actually occurs. Second, nitrogen indices from sand culture, pot experiments, nutrient-solution systems, and field trials cannot be directly converted into one another. For example, a nutrient-solution nitrogen concentration of 100 mg/L cannot be mechanically converted into a field application rate of 100 kg/ha. Genotypic differences are also substantial. Nitrogen-sensitive and nitrogen-tolerant cultivars already show different patterns in NRT expression, root morphology, and nitrogen allocation, meaning that the same fertilization regime may not perform equally well across multiple cultivars.

Similar limitations exist in molecular studies. *IbAMT*, *IbNAC083*, *IbNF-YA1*, *IbNAC22*, *IbSnRK1*, and several other genes have obtained relatively strong candidate or functional evidence, but most studies still focus on individual genes or specific genetic backgrounds. A regulatory network that can fully explain how nitrogen signaling simultaneously alters cambial activity, hormonal regulation, lignification, source-sink transport, and starch granule formation under field fertilization conditions has not yet been established. In particular, nutrient-sensing nodes such as TOR still lack sufficient direct validation in sweet potato storage roots.

Future research should more closely integrate field nitrogen gradients with multi-omics approaches. Rather than simply comparing “high nitrogen” and “low nitrogen”, continuous sampling should be conducted before storage-root initiation, during initiation, during rapid bulking, and during the period of rapid starch accumulation. At each stage, root NO_3^-, NH_4^+, sugars, organic acids, amino acids, hormones, and starch structure should be

measured together with transcriptomic, metabolomic, proteomic, and isotope-tracing analyses. Existing studies have already shown that integrated omics can identify candidate regulatory nodes such as IbUGP2, IbglgA, miR319-TCP4, and miR172-AP2. The next step is to connect these candidate nodes directly with realistic nitrogen fertilizer treatments.

Breeding objectives should also shift from selecting only for "high yield" toward the simultaneous improvement of high yield, high starch productivity, and high nitrogen-use efficiency. Genome-wide association studies (GWAS), expression quantitative trait locus (eQTL) analysis, and natural allelic variation can be used to identify germplasm that maintains strong storage-root sink activity and starch-forming capacity under relatively low nitrogen supply. On the crop-management side, topdressing timing and rate could be adjusted dynamically by combining critical nitrogen concentration, plant nitrogen nutrition index, soil available nitrogen, and weather conditions. Ultimately, the most useful goal in practice is not simply to reduce nitrogen fertilizer input, but to maintain storage-root yield, starch yield, and marketable quality after nitrogen reduction. This is a more practical objective than pursuing a single maximum-yield value.

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The authors affirm 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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Meta-Analysis Open Access

Effects of Exogenous Silicon on Growth, Photosynthesis, Antioxidant Defense, and Yield of Pepper under Salinity Stress: A Meta-Analysis

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Abstract Salinity stress restricts pepper growth, photosynthesis, and yield, and exogenous silicon (Si) has been proposed as a potential means of alleviating salt-induced damage. Based on available experiments involving pepper under salinity stress with Si application, this study conducted an exploratory meta-synthesis using response ratios to evaluate the effects of Si on growth, photosynthesis, water relations, antioxidant defense, ion homeostasis, and yield. The results showed that Si increased shoot dry weight, net photosynthetic rate, and leaf water status by representative median values of approximately 12%, 13%, and 14%, respectively. Malondialdehyde (MDA) content and electrolyte leakage decreased by about 31% and 33%, respectively, while the activities of SOD, CAT, APX, and GR were enhanced. In sweet pepper, tissue Na^+ concentration decreased by an average of approximately 45%, and total yield increased by 44%-56% in some studies. Overall, Si can alleviate salinity damage by improving plant water status, ion balance, and antioxidant capacity, although its effectiveness is influenced by salinity level, genotype, Si source, and application method. Yield-related evidence remains limited, and future studies should emphasize multi-location and full-season experiments and adopt standardized reporting of effect sizes and variance data to improve the reliability of meta-analyses.
Keywords Pepper (*Capsicum annuum* L.); Salinity stress; Silicon; Meta-analysis; Antioxidant defense; Ion homeostasis

1 Introduction

Pepper (*Capsicum annuum* L.) is a horticultural crop that is relatively sensitive to salinity, particularly during the seedling, flowering, and fruiting stages. Salinity problems are not restricted to conventionally salt-affected soils. Under protected cultivation, repeated fertilizer inputs, irrigation with saline water, and strong soil evaporation can progressively increase salt accumulation in the root zone. Giorio et al. (2020) reported a salinity threshold for pepper of approximately 1.5 dS/m, indicating that reductions in growth and yield may occur even at relatively moderate levels of root-zone salinity. Considerable genotypic variation also exists in pepper responses to salinity stress. Under the same salinity level, some genotypes are still able to maintain fruit set, whereas others already exhibit leaf senescence, reduced plant stature, and yield loss (Ntanasi et al., 2024). Long-term evidence further suggests that salt tolerance in pepper cannot be adequately assessed from short-term seedling responses alone, because ion accumulation, reproductive development, and fruit formation over the entire growth cycle are also important components of salinity tolerance (Qiu et al., 2017).

Salinity stress initially imposes an osmotic constraint by lowering the water potential around the root system, thereby reducing the availability of water for root uptake. With prolonged exposure, the continued entry and accumulation of Na^+ and Cl^- further induce ionic toxicity (Xue et al., 2021). Together, osmotic and ionic stress disrupt several physiological processes, including stomatal regulation, chlorophyll maintenance, and CO_2 assimilation, while also promoting the accumulation of reactive oxygen species. Salt-tolerant pepper genotypes generally maintain a more favorable ionic balance, characterized by higher K^+ retention and lower Na^+ accumulation, together with stronger antioxidant capacity and osmotic adjustment. In a transcriptomic study, the salt-tolerant genotype P300 maintained higher K^+ levels, antioxidant enzyme activities, and compatible solute contents under salinity stress, while accumulating less Na^+ than the sensitive genotype 323F3. These physiological responses were consistent with the better growth performance observed in P300 (Zhang et al., 2022).

Silicon (Si) is not considered essential for completion of the life cycle in all higher plants, but its beneficial effects often become more evident under abiotic stress. Previous studies have associated Si application with improved root water relations, enhanced membrane stability, reduced Na^+ transport to shoots, improved K^+ retention, and modulation of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) (Zhu et al., 2019). However, Si should not be regarded as a universally effective treatment for salinity stress. Plant species differ considerably in their capacity to absorb and accumulate Si, and the magnitude of the response may vary with Si source, application rate, and method of application. Direct evidence in pepper has nevertheless increased in recent years. In 'Bugwang' pepper, Manivannan et al. (2016) found that 50 mM NaCl reduced net photosynthetic rate by 41.3%, whereas application of 1.8 mM Si substantially alleviated this decline and also reduced H_2O_2 accumulation, malondialdehyde (MDA) content, and electrolyte leakage. Similar responses were subsequently reported in salt-tolerant and salt-sensitive pepper genotypes by Altuntas et al. (2018). A sweet pepper study published in 2020 further showed that the physiological benefits associated with Si application could also be reflected in fruit yield. More recent studies conducted during 2024-2025, including work on nanosilicon and combined applications of Si with mycorrhizae or potassium, have added further evidence on antioxidant responses and yield-related effects.

This study focuses on direct experiments examining the effects of Si application on pepper under salinity stress and compares treatment responses using response ratios. An exploratory meta-analysis is conducted primarily on within-study comparisons for which original treatment means can be extracted. By quantitatively synthesizing the available evidence, this study aims to estimate the overall effects of Si application on pepper growth, photosynthetic performance, antioxidant defense, and yield, while also examining differences among response categories. The analysis explores major sources of variation in Si effectiveness, including salinity intensity, Si application rate, and genotype, with the aim of providing a more quantitative basis for future experimental design and the use of Si in salt-stressed pepper production.

2 Physiological Basis of Salinity Stress and Silicon-Mediated Tolerance in Pepper

2.1 Growth inhibition induced by salinity stress in pepper

Following NaCl exposure, the earliest response in pepper is not necessarily a marked increase in leaf Na^+ concentration, but rather a decline in the osmotic potential of the rhizosphere. Under these conditions, roots must expend more energy to acquire the same amount of water, leaf turgor decreases, and cell expansion consequently slows. At the whole-plant level, this is reflected in reduced plant height increment and restricted expansion of newly formed leaves. Root systems also reallocate growth resources in response to salinity. This salinity-induced "physiological drought" is not identical to actual water deficit, but both ultimately affect stomatal behavior and photosynthetic performance (Munns et al., 2020).

As the duration of stress exposure increases, the primary constraint gradually shifts from water uptake to ion homeostasis. Excessive Na^+ accumulation can interfere with K^+uptake, while K^+ plays important roles in stomatal regulation, enzyme activity, and osmotic adjustment (Gul et al., 2019). The uptake and homeostasis of other nutrients, including Ca^{2+}, Mg^{2+}, and phosphorus, may also be disrupted. Pepper genotypes differ considerably in their responses to these ionic disturbances. The salt-tolerant genotype P300 maintains higher K^+ and lower Na^+ levels under salinity stress, whereas the sensitive genotype 323F3 shows more pronounced Na^+ accumulation. In a long-term sweet pepper experiment, Zhang et al. (2022) found that the relatively salt-tolerant cultivar 'Quadrato D'Asti' was more effective at restricting Cl^- accumulation in green tissues. Thus, salinity tolerance is not simply a matter of taking up less Na^+; the spatial distribution and compartmentation of ions within the plant are also important.

2.2 Photosynthetic and oxidative damage induced by salinity stress

As salinity increases, chlorophyll loss and stomatal closure often occur simultaneously. In the pepper experiment conducted by Manivannan et al., 50 mM NaCl reduced net photosynthetic rate, stomatal conductance, and transpiration rate by 41.3%, 23.8%, and 19.1%, respectively. Altuntas et al. (2018) likewise observed reductions

in photosynthetic rate under 75 and 150 mM NaCl, with a more pronounced decline at 150 mM. Under such conditions, CO_2 diffusion into the leaf becomes restricted, while photochemical processes within mesophyll cells may also be impaired. Therefore, the decline in photosynthesis cannot be attributed solely to stomatal closure.

Salinity stress also disrupts electron transport in chloroplasts, mitochondria, and peroxisomes. When the production of O_2^- and H_2O_2 exceeds the capacity of antioxidant scavenging systems, lipid peroxidation occurs. Increased malondialdehyde (MDA) content and electrolyte leakage are common consequences. Comparisons among pepper genotypes further indicate that salt-tolerant materials generally maintain stronger activities of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Zhang et al., 2022). However, this process is not entirely detrimental, because moderate levels of reactive oxygen species (ROS) also function as signaling molecules under stress. The major problem arises when ROS remain excessively elevated for prolonged periods.

2.3 Physiological roles of silicon under salinity stress

One of the most direct effects of Si in alleviating salinity damage is an improvement in plant water status. Previous studies suggest that Si may not only reduce nonproductive water loss, but also influence root hydraulic conductance and aquaporin activity. Rios et al. (2017) proposed that Si-mediated regulation of aquaporins can enhance root water uptake under salinity stress. Corresponding responses have also been observed in pepper. Application of 2 mM Si significantly improved leaf water potential in salt-stressed plants, and this improvement occurred together with recovery in stomatal conductance and dry matter accumulation.

Another important role of Si involves the antioxidant system and ion homeostasis. Si does not directly "eliminate" all free radicals, but it can modify enzymatic scavenging capacity and reduce the sustained generation of ROS. At the same time, Abdelaal et al. (2020) observed reduced Na^+ uptake and improved K^+ retention following Si application. In sweet pepper treated with foliar Si, tissue Na content decreased from 0.40% to 0.19% under 1500 ppm NaCl and from 0.48% to 0.30% under 3 000 ppm NaCl, corresponding to reductions of approximately 52.5% and 37.5%, respectively. These changes are physiologically substantial.

In intact plants, these processes do not operate independently (Figure 1). Improved water status can alter stomatal behavior, while enhanced photosynthesis provides additional carbon skeletons and metabolic energy. Reduced ionic toxicity may in turn lower the generation of ROS. More recent studies have further incorporated abscisic acid (ABA), aquaporins, secondary metabolism, and gene expression into this regulatory network. Liu et al. (2024) showed that Si can improve root hydraulic conductance through effects on ABA biosynthesis and aquaporin expression. However, direct molecular evidence in pepper remains limited at present. Mechanistic findings from other plant species can therefore provide useful references, but they should not be directly extrapolated to pepper without further validation.

3 Effects of Exogenous Silicon on Pepper Growth under Salinity Stress

3.1 Shoot growth responses

Under salinity stress, pepper plants generally show reduced plant height, while the formation of new leaves and leaf area expansion are also restricted. However, plant height does not always respond to Si application with a consistent increase. Manivannan et al. (2016) reported that, under 50 mM NaCl, shoot length increased from 6.80 cm in the salt-stressed treatment to 13.40 cm following Si application, representing an increase of approximately 97%. In contrast, Badem and Söylemez (2022) found that under 100 mM NaCl, Si increased stem diameter and dry weight without a corresponding increase in plant height; some treatments even showed reductions in plant height and root length. These findings indicate that taller plants do not necessarily reflect better growth. In some cases, Si may primarily alter plant compactness and dry matter accumulation rather than promoting stem elongation.

Biomass appears to show a more consistent positive response than plant height. In 'Bugwang', Si application under salinity stress increased fresh weight from 0.91 to 2.11 g, corresponding to an increase of approximately

132%, while dry weight increased from 0.09 to 0.13 g, or by about 44%. In the two-genotype experiment of Altuntas et al. (2018), Si application increased shoot dry weight by approximately 5.5%-19.7% under 75 and 150 mM NaCl. When these five directly comparable treatments were considered as exploratory effect units, the median increase was approximately 12.4%. This estimate is considerably more conservative than the near-doubling effects reported in some individual experiments and better reflects the variation among studies.

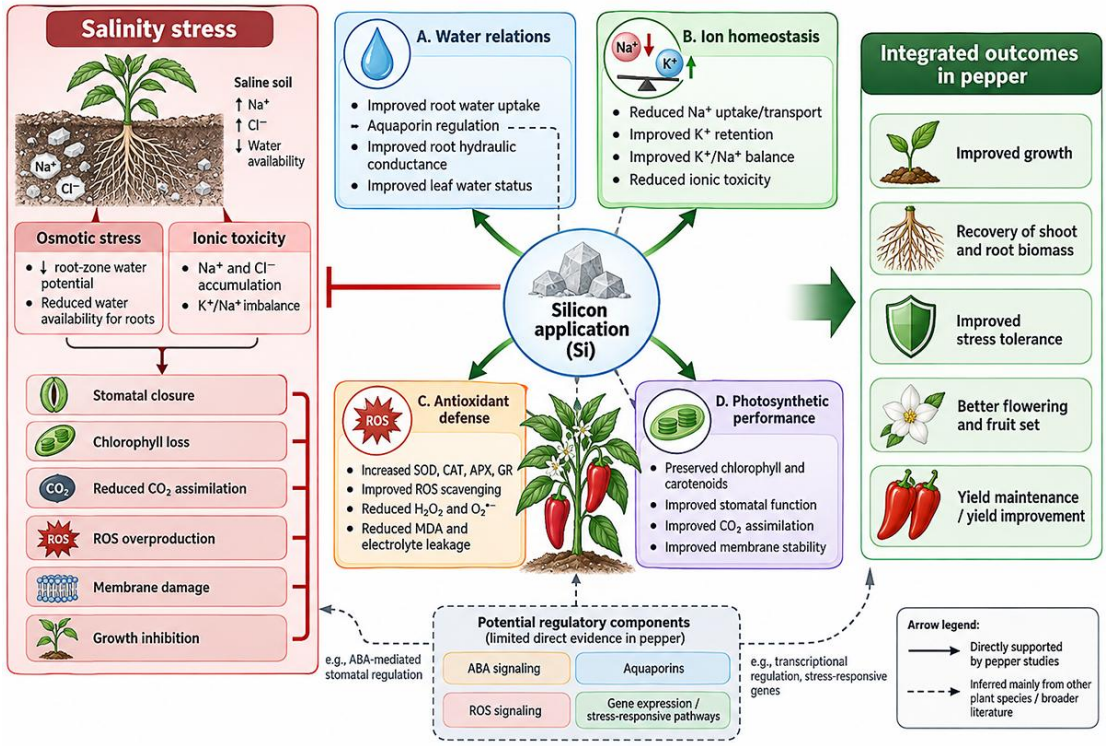


Figure 1 Proposed physiological framework of silicon-mediated salinity tolerance in pepper

Image caption: Salinity stress induces osmotic limitation, Na^+ and Cl^- accumulation, oxidative damage, and photosynthetic inhibition in pepper. Silicon application may alleviate these effects by improving root water uptake and leaf water status, maintaining ion homeostasis, enhancing antioxidant defense, stabilizing cellular membranes, and supporting photosynthetic performance. Solid pathways represent responses directly supported by pepper studies, whereas dashed pathways indicate mechanisms mainly inferred from evidence in other plant species

3.2 Root growth responses

Root responses show considerably greater variability. In 'Bugwang', individual root length was lower under the combined Si + salt treatment than under salt stress alone, whereas root number increased from 23.2 to 43.2, an increase of approximately 86%. This suggests that root system architecture may shift from a small number of relatively long roots toward a greater number of lateral roots. In the experiment of Altuntas et al. (2018), Si increased root dry weight by approximately 5%-39% across different genotypes under salinity stress. By contrast, Badem and Söylemez (2022) observed only a nonsignificant increase in root dry weight. Taken together, these results are more informative when changes in overall root system development are considered rather than root length alone.

Under saline conditions, roots are responsible for both water and mineral acquisition and are also the first organs directly exposed to NaCl. Si deposition and regulation of aquaporins may help root tissues maintain water uptake under high osmotic stress. At the same time, enhanced antioxidant capacity in roots may reduce membrane lipid damage and thereby help preserve selective ion uptake. Studies in other plant species have shown that Si can influence root hydraulic conductance and ABA-mediated regulation, providing a plausible explanation for the recovery of root biomass observed in pepper. However, direct measurements of root hydraulic parameters in pepper remain limited (Rios et al., 2017).

3.3 Biomass allocation and growth recovery

The root-to-shoot ratio does not necessarily increase consistently following Si application. A simple explanation is that both shoots and roots may recover, but at different rates. Under mild to moderate salinity stress, photosynthetic recovery may occur relatively rapidly, allowing a greater proportion of newly assimilated carbon to be allocated to leaves and stems. Under more severe salinity stress, maintaining root water uptake and ion exclusion becomes increasingly important. In a combined Si-K experiment, Bushra et al. (2025) reported that under a salinity level of 12 dS/m, the combined treatment increased root and shoot biomass by approximately 53% and 55%, respectively, compared with the corresponding control. This result indicates that the nutritional background can substantially modify the biomass response to Si. However, because potassium was applied together with Si, the entire increase cannot be attributed to Si alone.

The relative effect of Si often becomes more evident under moderate to relatively severe salinity stress, although excessively high salinity may eventually impose a biological limit on recovery. Altuntas et al. (2018) found that the sensitive cultivar 'Demre' showed a relatively pronounced improvement at 75 mM NaCl, whereas the salt-tolerant cultivar 'Karaisali' still responded well at 150 mM NaCl. Such crossover responses indicate that salinity intensity cannot be interpreted independently of genotype. In other words, a given Si dose does not produce a fixed percentage of growth recovery across different genotypes and salinity levels.

4 Effects of Exogenous Silicon on Photosynthesis and Water Relations in Pepper

4.1 Photosynthetic pigment responses

Chlorophyll is a relatively sensitive indicator of salinity stress. In a nanosilicon experiment using 'Mızrak' pepper, application of 1 mM nanosilicon (nSi) under 100 mM NaCl increased chlorophyll a from 1.672 to 2.171, corresponding to an increase of approximately 29.8%. Under 150 mM NaCl, chlorophyll a increased from 1.534 to 1.921, or by about 25.2% (Kusvuran et al., 2024). The recovery of chlorophyll b was even more pronounced, with increases of approximately 56.8% and 42.7% under 100 and 150 mM NaCl, respectively. These results suggest that the effects of Si are not limited to maintaining leaf water status, but also involve protection of the photosynthetic pigment system. Carotenoids function both as accessory pigments and as components of the chloroplast antioxidant system. The same study reported that 1 mM nSi increased carotenoid content by approximately 34% under 100 mM NaCl and by about 61% under 150 mM NaCl.

However, higher nanoparticle concentrations do not necessarily produce greater benefits. Overall, 0.5-1 mM nSi performed better than 2-3 mM. González-García et al. (2021) investigated sweet pepper (*Capsicum annuum* 'Kitrino') under 0, 25, and 50 mM NaCl and applied SiO_2 nanoparticles at 200 and 1 000 mg/L. Exposure to 50 mM NaCl alone reduced leaf chlorophyll a by approximately 54% relative to the non-saline control. At this salinity level, 200 mg/L SiO_2 increased chlorophyll a and raised total chlorophyll by approximately 52%, whereas 1 000 mg/L SiO_2 failed to improve chlorophyll a. In the fruit, the combination of 50 mM NaCl and 200 mg/L SiO_2 increased flavonoids by approximately 156%, yellow carotenoids by about 45%, and phenylalanine ammonia-lyase (PAL) activity by approximately 59%. In contrast, the 1 000 mg/L treatment did not show comparable advantages for these traits.

4.2 Gas exchange and photosynthetic efficiency

Altuntas et al. (2018) provided one of the more comprehensive datasets on gas exchange responses in pepper. Under 75 and 150 mM NaCl, application of 2 mM Si increased net photosynthetic rate in 'Karaisali' by 11.5% and 14.6%, respectively, and in 'Demre' by 21.8% and 11.1%, respectively. Across these four independent salinity-genotype comparisons, the median increase was approximately 13.0%. Stomatal conductance increased by about 20% in both cultivars under 75 mM NaCl, whereas under 150 mM NaCl the recovery was greater in the sensitive genotype.

The increase in transpiration following Si application does not necessarily mean that plants were "wasting" more water. Under salinity stress, excessive stomatal closure restricts both water loss and CO_2 entry. Partial reopening of stomata following Si treatment can therefore increase transpiration and CO_2 diffusion simultaneously. Available results indicate that Si increased transpiration rate in salt-stressed pepper by approximately 30%-55%,

while intercellular CO_2 concentration also partially recovered. A more plausible interpretation is that Si helped re-establish the balance between root water uptake and transpirational demand, rather than simply reducing water loss.

Based on the available evidence, Si appears to support photosynthetic performance through at least three pathways: protection of photosynthetic pigments and membrane structures, improvement of stomatal function and leaf water status, and alleviation of non-stomatal limitations associated with Na^+ toxicity and ROS accumulation. Singh et al. (2022) likewise observed recovery of photosynthetic pigments, gas exchange, and photochemical efficiency following Si treatment. However, in pepper, data on parameters such as Fv/Fm, electron transport rate, and photosystem I activity remain much more limited than gas-exchange measurements. Therefore, direct evidence that Si protects the photosystems themselves is still insufficient and requires further investigation.

4.3 Water relations and osmotic adjustment

Foliar Si experiments in sweet pepper have shown that salinity stress decreases relative water content, whereas Si treatment can partially restore it. Altuntas et al. (2018) reported a similar trend using leaf water potential as an indicator of plant water status. Across four salinity-genotype combinations, the improvement ranged from 9.2% to 26.8%, with a median of approximately 14%. The recovery of water status occurred broadly in parallel with increases in net photosynthetic rate, suggesting that water relations may represent an important link between root responses and the restoration of leaf photosynthesis in pepper.

The interpretation of proline and soluble sugar accumulation requires caution. Their concentrations often increase under salinity stress, but this increase may reflect either enhanced osmotic adjustment or greater stress injury. In sweet pepper, salinity markedly increased proline and soluble sugar contents, whereas some of these osmolytes declined after Si alleviated the stress. Badem and Söylemez (2022) also observed a tendency toward lower proline concentrations following Si application. Therefore, the assumption that "higher proline always indicates greater salt tolerance" is not appropriate when evaluating the effects of Si.

A more reliable assessment is to consider relative water content, leaf water potential, proline, soluble sugars, and stomatal parameters together. Si may promote the osmotic adjustment required to maintain cellular water relations, while at the same time reducing the overall severity of stress so that some stress-associated metabolites no longer need to remain at very high concentrations. Similar bidirectional changes were reported by Zhang et al. (2017). Thus, inconsistencies in proline responses among studies do not necessarily indicate contradictory effects of Si.

5 Effects of Exogenous Silicon on Antioxidant Defense and Cellular Protection

5.1 Regulation of antioxidant enzyme activities

Following the onset of salinity stress, superoxide dismutase (SOD) generally converts O_2^- to H_2O_2, which is subsequently scavenged by catalase (CAT). Data from nanosilicon experiments in pepper illustrate this response clearly. Under 100 mM NaCl, application of 1 mM nSi increased SOD activity from 182.47 to 300.46, corresponding to an increase of approximately 64.7%, while under 150 mM NaCl the increase was about 55.7%. The corresponding increases in CAT activity were approximately 70.2% and 65.6%, respectively (Kusvuran et al., 2024). By contrast, the increases in both enzymes were much smaller under 50 mM NaCl. These results suggest that Si-induced antioxidant responses may depend, at least in part, on stress intensity.

Ascorbate peroxidase (APX), peroxidase (POD), and glutathione peroxidase (GPX) further contribute to H_2O_2 detoxification, particularly in the chloroplast and cytosol. In 'Bugwang' pepper, Si application increased GPX, CAT, and APX activities relative to the salt-only treatment. In the nanosilicon study, 1 mM nSi increased APX activity by approximately 91% and 60% under 100 and 150 mM NaCl, respectively, while glutathione reductase (GR) increased by about 49% and 43% (Manivannan et al., 2016). Mycorrhiza-Si experiments have also shown that the responses of CAT, APX, and related enzymes vary among genotypes. Sensitive genotypes do not necessarily exhibit lower enzyme activities; in some cases, the opposite occurs because they experience stronger oxidative stress (Altuntas et al., 2025).

5.2 Alleviation of oxidative damage

Whether increased antioxidant enzyme activity is physiologically effective ultimately depends on whether ROS accumulation is actually reduced. In a foliar Si experiment with sweet pepper, both H_2O_2 and O_2^- increased markedly under 1 500 and 3 000 ppm NaCl, but declined after Si application (Abdelaal et al., 2020). Manivannan et al. (2016) likewise reported that Si reduced H_2O_2 accumulation in salt-stressed pepper by approximately 25.6%. Thus, based on the available direct evidence, Si treatment in pepper does not simply increase measured antioxidant enzyme activities; it is also accompanied by an actual reduction in oxidative load.

Malondialdehyde (MDA) is one of the more consistent indicators of oxidative damage reported in pepper studies involving Si. In 'Bugwang', Si application reduced MDA by 29.4% under salinity stress. In 'Mızrak' pepper exposed to 100 and 150 mM NaCl, 1 mM nSi reduced MDA from 10.59 to 7.05 and from 14.74 to 10.13, respectively, corresponding to decreases of 33.4% and 31.3% (Kusvuran et al., 2024). Across these three representative comparisons, the median reduction was approximately 31.3%. Compared with growth-related traits, the direction of the MDA response appears considerably more consistent.

Improved membrane integrity generally accompanies the reduction in MDA. In the study of Manivannan et al. (2016), salinity stress increased electrolyte leakage by 38.1%, whereas Si application reduced it by approximately 33.3% relative to the salt-only treatment. The effects reported by Abdelaal et al. (2020) were even more pronounced: under 1 500 ppm NaCl, electrolyte leakage decreased from 27% to 18%, a reduction of 33.3%, while under 3 000 ppm NaCl it fell from 49% to 25%, corresponding to a decrease of about 49%. The median reduction across comparable treatments was approximately 33%. Because these parameters directly reflect membrane injury, they are generally easier to interpret than changes in a single antioxidant enzyme.

5.3 Non-enzymatic antioxidant defense and stress-related metabolites

In addition to enzymatic defense, ascorbate (AsA), glutathione (GSH), and phenolic compounds contribute to the maintenance of cellular redox homeostasis. González-García et al. (2021) found that SiO_2 nanoparticles altered leaf GPX activity as well as fruit phenolic, flavonoid, and GSH levels in sweet pepper, although the direction and magnitude of these changes varied with Si concentration and salinity level. Salinity itself can also stimulate the synthesis of some phenolic compounds. These secondary metabolites are therefore better interpreted as components of a broader defense network rather than being classified simply as beneficial whenever their concentrations increase.

Proline can stabilize proteins and membrane structures and also contributes to osmotic adjustment. However, it often accumulates strongly under severe salinity stress. Consequently, in treatments where Si provides substantial stress alleviation, lower proline levels may actually indicate a reduction in the stress experienced by the plant. Studies in other species have likewise shown that Si can either increase or decrease proline accumulation depending on salinity intensity, plant organ, and duration of exposure (Zhang et al., 2017).

Taken together, the available evidence suggests that Si acts more by rebalancing the overall cellular redox system than by regulating any single antioxidant enzyme. SOD first detoxifies O_2^-, CAT and APX further remove H_2O_2, the AsA-GSH cycle replenishes reducing power, and phenolic compounds and carotenoids contribute to non-enzymatic scavenging and energy dissipation (Basu and Kumar, 2021). Whether these responses ultimately protect cells still needs to be verified through damage-related indicators such as MDA, ROS accumulation, and electrolyte leakage. At present, relatively few studies in pepper have measured this full set of parameters simultaneously.

6 Effects of Exogenous Silicon on Ion Homeostasis and Yield in Pepper

6.1 Regulation of Na^+ and K^+ homeostasis

Limiting Na^+ accumulation is one of the more convincing mechanisms by which Si may alleviate salinity damage. Abdelaal et al. (2020) reported that in sweet pepper exposed to 1500 ppm NaCl, tissue Na content was approximately 0.40%, but decreased to 0.19% following foliar Si application. Under 3000 ppm NaCl, Na content

declined from 0.48% to 0.30%. Across the two salinity levels, the average relative reduction was approximately 45%. Because this estimate is derived primarily from a single two-season experiment, it should not be interpreted as a universal effect size for pepper. Nevertheless, the direction of the response is consistent with evidence from other plant species showing that Si can restrict Na^+ uptake and its transport to aboveground tissues.

Under salinity stress, the K^+/Na^+ relationship is often more physiologically relevant than the absolute Na^+ concentration alone. As Na^+ competition increases, cellular enzyme activity and stomatal function can both be impaired. The salt-tolerant pepper genotype P300 maintained higher K^+ and lower Na^+ levels after salt treatment, indicating that K^+ retention itself is an important component of the salt-tolerance phenotype (Zhang et al., 2022). By reducing Na^+ load, preserving membrane function, and improving root performance, Si may indirectly increase the K^+/Na^+ ratio.

6.2 Effects on mineral nutrient balance

Ca^{2+} contributes to membrane stability and stress signaling, while Mg^{2+} is a central component of chlorophyll. Under high salinity, uptake of both nutrients may be disrupted by Na^+ competition and root injury. The effects of Si on mineral nutrition are not entirely consistent among crops, but they are generally more evident as a restoration of nutrient balance under salinity stress than as a universal increase in all mineral elements under non-stress conditions. Recent studies of Si-mediated salinity tolerance have also emphasized strong nutritional interactions between Si and K^+, Ca^{2+}, and Mg^{2+} (Dabravolski and Isayenkov, 2024).

Foliar Si application in sweet pepper increased N, P, and K concentrations under saline conditions while simultaneously reducing Na^+ accumulation (Abdelaal et al., 2020). This suggests that the improvement in mineral status cannot be explained solely by a dilution effect. However, particular attention is required when K_2SiO_3 is used as the Si source because potassium is supplied simultaneously. Although many experiments include appropriate comparison treatments, accompanying ions may still differ among Si sources. Bushra et al. (2025) further demonstrated a clear synergistic interaction between K and Si. Future meta-analyses should therefore distinguish the independent effect of Si from combined Si-nutrient effects whenever possible.

6.3 Yield and reproductive growth responses

Compared with studies focusing on seedling physiology, relatively few Si-salinity experiments in pepper have measured fruit yield directly. In the two-season sweet pepper experiment of Abdelaal et al. (2020), plants without Si produced approximately 7.1 and 5.4 fruits per plant under 1 500 and 3 000 ppm NaCl, respectively, whereas Si-treated plants produced 12.8 and 8.6 fruits per plant. These values correspond to relative increases of approximately 80.3% and 59.3%. The magnitude of these responses is substantial, but because they originate from a single experimental system, they are better interpreted as evidence that Si has the potential to restore reproductive growth rather than as estimates of a general effect size.

The same study reported that fruit fresh weight per plant increased from 495 to 781 g under 1 500 ppm NaCl and from 355 to 560 g under 3 000 ppm NaCl, with relative increases of nearly 58% at both salinity levels. This indicates that Si not only improved fruit set but also supported fruit growth. In contrast, Badem and Söylemez (2022) found no significant main effect of Si on marketable fruit yield, showing that improvements in physiological traits do not necessarily translate immediately into higher fruit production.

In the dataset of Abdelaal et al. (2020), total yield increased from 7.1 to 11.1 t/ha under 1 500 ppm NaCl and from 5.4 to 7.8 t/ha under 3 000 ppm NaCl, corresponding to relative increases of 56.3% and 44.4%, respectively. The median effect across the two salinity levels was approximately 50.4%. Although this result is notable, it should be treated conservatively in meta-analysis because the two effect estimates are derived from different salinity levels within the same study. Combined K + Si treatments have also been reported to improve yield substantially under 9 and 12 dS/m salinity, but these responses cannot be incorporated into estimates of the independent Si effect because of the interaction with potassium fertilization (Bushra et al., 2025).

Across the available comparisons, the magnitude of Si responses differed substantially among trait categories. Growth and photosynthetic traits generally showed moderate improvements, whereas oxidative damage and Na^+ accumulation exhibited larger and more consistent reductions (Figure 2).

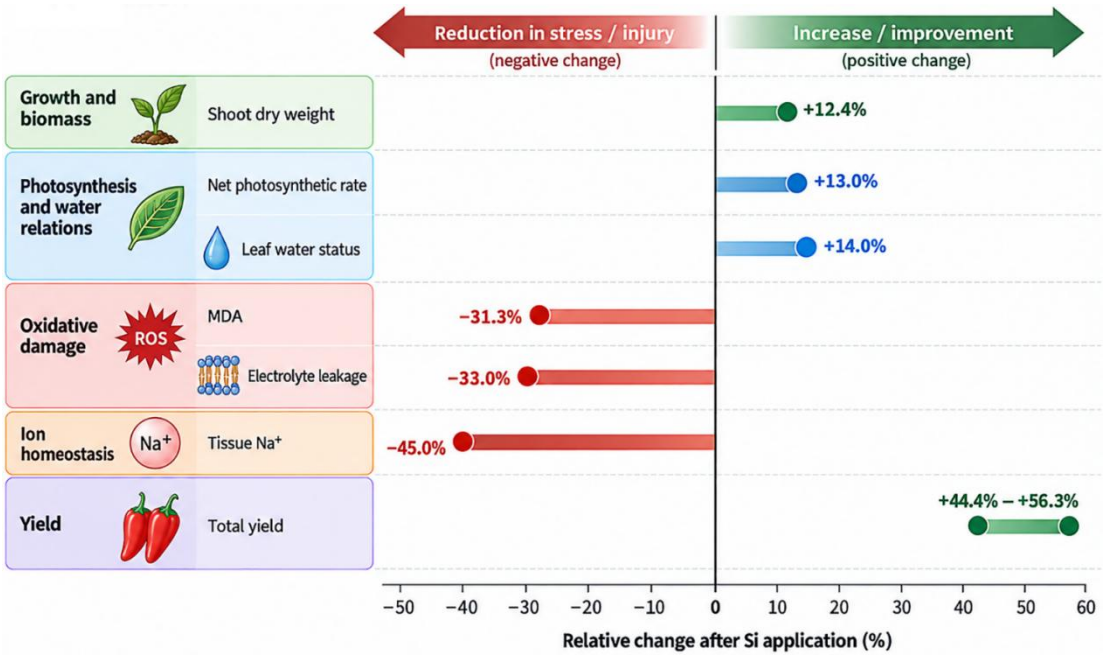


Figure 2 Exploratory summary of major responses of salt-stressed pepper to silicon application.

Image caption: Representative relative responses extracted from directly comparable Si-salinity treatments in pepper. Positive values indicate increases following Si application, whereas negative values indicate reductions in stress- or damage-related traits. Values for shoot dry weight, net photosynthetic rate, leaf water status, MDA, electrolyte leakage, and Na^+ represent exploratory median or representative responses derived from available comparisons. Yield responses should be interpreted cautiously because the available estimates are based on a limited number of experimental systems. These values are not variance-weighted pooled effect sizes

7 Factors Determining the Effectiveness of Exogenous Silicon in Pepper under Salinity Stress

7.1 Silicon source and application characteristics

Existing studies in pepper have used K_2SiO_3, foliar Si formulations, and SiO_2 nanoparticles. These treatments are not directly interchangeable. Potassium silicate supplies K simultaneously with Si, whereas nanosilicon has a larger specific surface area and differs in its uptake behavior and interfacial reactivity. In the 'Mızrak' experiment, 0.5-1 mM nanosilicon generally produced better responses, while increasing the concentration further to 2-3 mM did not result in a continued increase in effectiveness (Kusvuran et al., 2024). Similarly, marked differences were observed between 200 and 1 000 mg/L SiO_2 nanoparticle treatments in sweet pepper. A higher dose therefore cannot be assumed to be more effective (González-García et al., 2021).

Application through the nutrient solution is commonly used experimentally because it can directly influence root function and ion uptake. Foliar application, by contrast, is more relevant to some production systems and may also reduce the risk of Si immobilization in soil. Abdelaal et al. (2020) observed improvements in plant water status, oxidative damage, and yield following foliar Si application. Nanosilicon studies have likewise used both foliar and root-zone application. However, there are still too few studies in pepper directly comparing different application sites using the same Si source and dose. It is therefore not yet possible to determine which application method is consistently superior.

Based on the available evidence, soluble Si treatments in pepper are commonly applied at concentrations around 1.8-2 mM, whereas the effective concentration range of nanosilicon cannot be directly converted to that of conventional Si salts. Kusvuran et al. (2024) applied nanosilicon every 7 d and found that 1 mM generally performed well. In contrast, Badem and Söylemez (2022) used 2 mM Si while also evaluating the frequency of

nitric oxide (NO) application. Experimental protocols differ substantially in treatment frequency, leaf developmental stage, and the timing of stress initiation. These differences are likely to be important sources of heterogeneity in pooled effect estimates.

7.2 Salinity intensity and duration

Under mild salinity stress, endogenous defense systems may still retain sufficient capacity, and the absolute improvement following Si application can therefore be relatively small. As stress reaches moderate levels, Si effects often become more apparent. For example, in the nanosilicon experiment, the stimulation of SOD and CAT by 1 mM nSi was much greater under 100-150 mM NaCl than under 50 mM NaCl (Kusvuran et al., 2024). However, as salinity continues to increase, growth and yield may still decline substantially. Si can alleviate damage, but it cannot completely eliminate the effects of severe salinity stress.

Short-term seedling experiments lasting 15-30 d can produce clear physiological responses, but they do not necessarily represent the entire production cycle. Under prolonged salinity stress, Na^+ and Cl^- continue to accumulate, while flowering, pollination, and fruit expansion may also be affected. In a long-term study of two sweet pepper genotypes, Giorio et al. (2020) found that early changes in plant water status were not fully consistent with later yield responses. Future evaluations of Si should therefore distinguish short-term "leaf recovery" from long-term "yield recovery" rather than treating them as equivalent outcomes.

7.3 Genotype and growth environment

Genotype is likely to be an underappreciated moderator of Si effectiveness. Altuntas et al. (2018) found that the salt-sensitive cultivar 'Demre' responded strongly to Si under 75 mM NaCl, whereas the salt-tolerant cultivar 'Karaisali' still showed a clear benefit under 150 mM NaCl. Antioxidant studies have also shown that CAT, APX, and related responses differ between pepper cultivars exposed to the same Si and salinity treatments (Altuntas et al., 2025). Intrinsic differences in Na^+ exclusion, K^+ retention, and basal antioxidant capacity are all likely to influence the additional benefit that can be obtained from Si application (Figure 3).

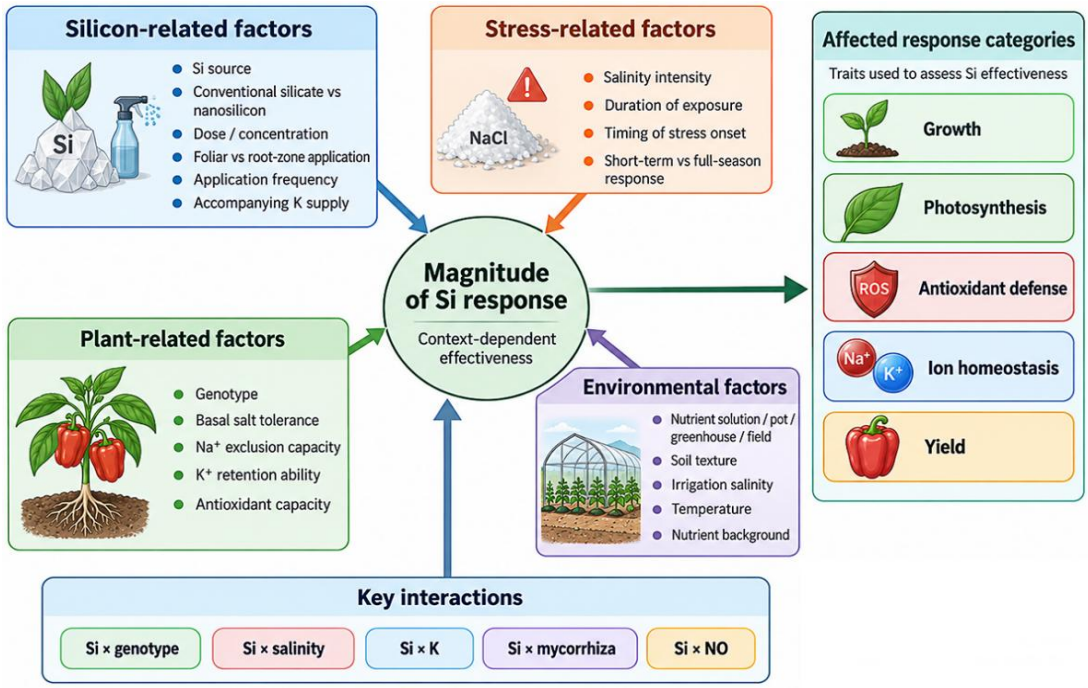


Figure 3 Major moderators of silicon effectiveness in pepper under salinity stress

Image caption: The magnitude of the response to Si is jointly determined by Si source and application characteristics, salinity intensity and duration, genotype, and growth environment. Interactions with nutrients and other treatments, including K, mycorrhizae, and NO, may further modify the observed response. These moderators should therefore be considered when interpreting pooled effects across studies

Most of the available evidence comes from nutrient solutions, pot experiments, perlite systems, or controlled greenhouse conditions. These designs are well suited to mechanistic studies because root-zone salinity can be maintained relatively uniformly. Field soils, however, show spatial variation in water availability, salinity, and plant-available Si, while temperature, fertilization, and soil texture introduce additional sources of variation. The study of Bushra et al. (2025) began to incorporate root responses and fruit yield into the evaluation, but overall, direct field evidence remains much more limited than controlled seedling experiments.

From a meta-analytic perspective, these interactions mean that future analyses should not focus only on the question of "how much Si improves performance on average". A more informative question is under which genotype, salinity level, and Si source the response is greatest. Existing studies already indicate interactions among genotype, salinity intensity, and Si treatment. The interpretation becomes even more complex when K, mycorrhizae, or NO are included (Altuntas et al., 2018). Therefore, simply pooling all treatments into a single overall mean effect may produce an apparently precise estimate with limited biological relevance.

8 Conclusions and Future Research Directions

Exogenous Si exerts beneficial effects on pepper under salinity stress, although the consistency of the response varies among traits. Among the biomass comparisons that could be quantified, the representative median increase in shoot dry weight was approximately 12%. Net photosynthetic rate increased by about 13%, while leaf water status improved by roughly 14%. Some individual studies reported much larger increases, particularly for fresh weight and plant height, but such values are not suitable as general conclusions when results are compared across experiments. Improvements in chlorophyll content, stomatal conductance, and transpiration rate were more consistent in direction.

Compared with growth-related traits, indicators of oxidative damage showed greater consistency. Representative comparisons indicated that Si reduced MDA by approximately 31% and electrolyte leakage by about 33%, while increasing the activities of SOD, CAT, APX, and GR. In sweet pepper, tissue Na^+ concentration declined by an average of approximately 45%. These responses form a physiologically coherent sequence: reduced Na^+ accumulation lowers oxidative pressure, while enhanced antioxidant capacity further limits membrane lipid peroxidation. At present, this constitutes one of the most complete lines of evidence for Si-mediated salinity tolerance in pepper. Positive yield responses have also been reported, and in some cases the magnitude was substantial. In one two-season sweet pepper experiment, Si increased total yield by approximately 56% and 44% under two salinity levels. By contrast, another study found no significant main effect of Si on marketable fruit yield. These findings are not necessarily contradictory. Rather, they indicate that production responses are strongly influenced by salinity level, genotype, application method, and experimental duration. A more appropriate conclusion at present is therefore that Si has clear potential to help maintain yield under salinity stress, but the available meta-analytic evidence in pepper is still insufficient to derive a stable overall yield effect size.

Existing studies have expressed salinity using 50-150 mM NaCl, ppm salt concentrations, or electrical conductivity in dS/m, while Si treatments have included conventional silicates, foliar Si formulations, and nanosilicon. Treatment duration has ranged from approximately two weeks to the full fruiting period. This methodological variation limits the applicability of rigorous variance-weighted meta-analysis. In particular, some studies report only treatment means or graphical results without complete information on SD, SE, or sample size. Pooling such data indiscriminately would create a false impression of precision. At present, data on chlorophyll, antioxidant enzymes, and MDA are much more abundant than data on fruit yield. This imbalance is important because a 50% increase in leaf SOD activity does not imply a 50% increase in yield. Physiological advantages can be translated into economic yield only if leaf area, photosynthetic activity, flowering, and fruit set are maintained throughout the crop cycle. Few pepper studies currently cover all of these stages simultaneously. Existing evidence has already shown that salt-tolerant and salt-sensitive genotypes respond differently, but the number of genotypes included in Si experiments remains limited. An "optimal Si concentration" derived from one or two commercial cultivars cannot be directly extrapolated to other pepper types. Transcriptomic evidence further indicates that cultivars inherently differ in ROS scavenging, SOS signaling, and hormonal responses.

Future studies should standardize the reporting of salinity level, electrical conductivity, actual NaCl concentration, effective Si concentration, Si source, pH, accompanying K content, application frequency, and tissue Si concentration. Means, SD or SE values, and the number of biological replicates should also be reported in full. Such information would make it possible to conduct rigorous random-effects meta-analyses and to examine dose-response relationships rather than merely comparing treatment and control groups. The next stage of research should also shift from an emphasis on seedling traits toward the entire crop cycle. Fruit number, mean fruit weight, marketable yield, total yield, water-use efficiency, and the cost of Si application should all be included. Multi-year and multi-location experiments across different soil textures and irrigation salinity levels are particularly needed. Only then will it be possible to determine whether Si functions mainly as a laboratory-scale "stress-alleviating agent" or can be developed into a reliable management practice for pepper production under saline conditions.

What is relatively clear at present is the phenotype: under many conditions, Si reduces Na^+ and MDA accumulation, improves plant water status, and enhances antioxidant defense. What remains less clear is where these responses are initiated. Future studies could integrate the tissue distribution of Na^+, K^+, Ca^{2+}, and Mg^{2+} with metabolomic, transcriptomic, and proteomic analyses, with particular attention to aquaporins, the SOS pathway, ABA signaling, and ROS signaling. A transcriptomic basis for salinity responses in pepper is already available. Incorporating Si treatments into such frameworks could move the field beyond the question of whether Si is effective toward explaining why it is more effective in a particular genotype and at a particular salinity level.

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Conflict of Interest Disclosure

The authors affirm 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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Effect of Herbicides on Weed Control, Growth and Yield of Direct Seeded Rice in Chitwan, Nepal

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Abstract A field experiment was conducted during the 2024 growing season in Chitwan, Nepal, to evaluate the effects of different herbicides and herbicide combinations on growth and yield of direct-seeded rice (DSR). The experiment was laid out in a randomized complete block design (RCBD) with nine treatments and three replications using the rice variety Hardinath-5. Treatments included pre-emergence herbicides, post-emergence herbicides, combinations with 2,4-D, a weedy check, and a weed-free treatment. Weed management treatments significantly affected plant height, dry matter production, crop growth rate (CGR), yield attributes, grain yield, straw yield, harvest index, and weed index. Bispyribac sodium alone and bispyribac sodium + 2,4-D produced the greatest values for effective tillers, panicle length, filled grains per panicle, and grain yield, but their grain yields were not significantly different. Grain yield was 6.1 t/ha with bispyribac sodium, 6.0 t/ha with bispyribac sodium + 2,4-D, and 5.9 t/ha with the weed-free treatment, whereas the weedy check produced 2.1 t/ha. The results indicate that both bispyribac sodium treatments were effective under the conditions of this single-location, single-season study. Multi-location, multi-season, and economic studies are needed before making a broader recommendation for DSR production in Nepal.

Keywords Direct-seeded rice; Weed management; Bispyribac sodium; 2,4-D; Grain yield; Weed index

1 Introduction

Rice is the principal staple cereal crop in Nepal. It occupies about 1.42 million hectares, with average productivity of 4.19 t/ha and annual production of approximately 5.955 million tons in 2024/25 (MoALD, 2026). Improving productivity on existing farmland is increasingly important because further expansion of cultivated area is constrained by conversion of agricultural land to non-agricultural uses and by increasing pressure on farm labor and production resources.

Conventional puddled transplanted rice has long been the dominant production system in Nepal. Rural-to-urban migration and associated labor shortages, particularly during transplanting, have encouraged interest in direct-seeded rice (DSR). Compared with transplanted rice, DSR can reduce labor demand and water use, promote earlier crop establishment and harvesting, and facilitate timely planting of succeeding crops. These advantages have increased interest in DSR as a resource-efficient production system in Nepal and other parts of Asia (Chauhan, 2012; Adhikari, 2021; Sharma et al., 2021).

Weed infestation is one of the most serious biological constraints in DSR because weeds and rice emerge together and compete for nutrients, water, light, and space. The absence of standing water during early crop establishment further favors weed emergence and growth (Hossain et al., 2016; Raj and Syriac, 2017). Yield losses can be severe when weed control is delayed or incomplete (Chauhan and Johnson, 2011). Chitwan, in the Inner Terai, provides a relevant rice-growing environment for evaluating DSR weed-management options, but herbicide performance cannot be assumed to be identical across locations because weed communities, soil conditions, weather, and field-management histories vary.

Herbicides are widely used in DSR because they can provide timely and economical weed control. However, reliance on a single application may not provide season-long suppression, and treatment response may vary with

application timing and weed spectrum. Pre-emergence herbicides such as pendimethalin, pretilachlor, and oxadiargyl and post-emergence bispyribac sodium have therefore been evaluated in different DSR systems (Mahajan et al., 2014; Selvaraj and Hussainy, 2020; Shekhawat et al., 2020; Dangol et al., 2020). Integrated weed management remains important because combining preventive, cultural, mechanical, and chemical practices can reduce weed shifts and delay herbicide resistance (Kaur and Singh, 2017; Gyawaly et al., 2021).

Previous studies in Nepal and elsewhere have reported treatment-specific effects of herbicides on weed management and rice productivity, but results from other locations or varieties do not directly establish the best option for Hardinath-5 under Chitwan conditions. Studies in Nepal have also demonstrated that weed-management practices can substantially influence weed dynamics and grain productivity in dry direct-seeded rice (Marasini et al., 2020).

A field comparison of pre-emergence and post-emergence treatments within the same RCBD was therefore needed. The objectives of this study were to: (i) compare the effects of selected herbicides and herbicide combinations on plant height, dry matter production, and CGR; (ii) evaluate their effects on effective tillers, panicle length, grain filling, sterility, test weight, grain yield, straw yield, and harvest index; and (iii) compare treatment performance with weedy-check and weed-free conditions using weed index. The study was intended to provide location-specific evidence for selecting herbicide treatments for DSR, while recognizing that broader recommendations require validation across seasons, locations, and production costs.

2 Materials and Methods

2.1 Experiment sites and conditions

The field experiment was conducted during the 2024 rice-growing season at Rampur, Chitwan District, Nepal, located in the Inner Terai region. The experimental site was situated at 27° 39′ 15″ N and 84° 21′ 17″ E at an elevation of 210 m above sea level. The soil at the experimental site was classified as sandy loam, with a pH of 6.4, organic matter content of 5.43% and total N, available P and K contents of 0.27%, 26.5 kg/ha and 30.5 g/ha respectively. The experimental field had been under a rice-fallow-wheat cropping sequence during the preceding two years (2022 and 2023). The field was relatively uniform in fertility and suitable for field experimentation.Weather conditions during the experimental period, including mean temperature and total rainfall, were 27 °C and 1,500 mm.

2.2 Experiment design and treatments

The experiment was conducted using a single-factor Randomized Complete Block Design (RCBD) with nine treatments and three replications (Table 1).

Table 1 Different treatments used in experiment

S.N.	Treatments	Symbol	Rate/ha (a.i.)
1	Weedy check	T1	-
2	Weedfree	T2	-
3	Pendimethalin (PE)	T3	1 kg
4	Pretilachlor (PE)	T4	0.75 kg
5	Bispyribac sodium (PoE)	T5	25 g
6	Pendimethalin +2,4-D	T6	1 kg + 0.5 kg
7	Pretilachlor+2,4-D	T7	0.75 kg +0.5 kg
8	Oxadiargyl (PE)	T8	90 g
9	Bispyribac Sodium+ 2,4-D (PoE)	T9	25 g + 0.5 kg

2.3 Crop establishment and field management

Nitrogen, phosphorus, and potassium were applied at 100:30:30 kg N:P_2O_5:K_2O per hectare. Half of the nitrogen and the full doses of phosphorus and potassium were incorporated as basal fertilizer during final land preparation;

the remaining nitrogen was top-dressed at panicle initiation. Seeds of Hardinath-5 were sown manually in shallow furrows at 40 kg/ha on 25 June 2024, using 20 cm × 10 cm spacing and a sowing depth of 4-5 cm. Pre-emergence treatments (pendimethalin, pretilachlor and oxadiargyl) were applied within 24 h after sowing, and post-emergence treatments (bispyribac sodium) were applied at 25 days after sowing (DAS). In the combination treatments, 2,4-D was applied as a post-emergence spray at 25 DAS. For pendimethalin + 2,4-D and pretilachlor + 2,4-D, the pre-emergence herbicide was applied within 24 h after sowing and 2,4-D was applied as a follow-up spray at 25 DAS to control broad leaf weeds and sedges that escaped the pre-emergence treatment. For bispyribac sodium + 2,4-D, the two herbicides were tank-mixed and applied together as a single post-emergence spray at 25 DAS. All herbicide sprays were applied with a knapsack sprayer fitted with a flat-fan nozzle. No weed-control measure was used in the weedy-check plots. Weed-free plots were maintained by manual weeding at frequent intervals. One pre-sowing irrigation and six subsequent irrigations were applied as required during the crop season.

2.4 Harvesting and yield determination

The crop was harvested manually with serrated sickles and sun-dried in the field for three days. Grain and straw yields were determined from the net plot. Grain yield was adjusted to a standard moisture content of 14% and expressed in kg/ha using the following equation:

$$\text{Grain yield (kg/ha)} = W_i \times \frac{100-M_i}{100-14} \times \frac{10{,}000}{A}$$

Where, W_i is the initial grain weight (kg), M_i is the initial grain moisture content (%), and A is the net plot area (m^2).

Straw yield was calculated as total biomass yield minus grain yield. To estimate dry straw yield, a 500-g fresh-straw sample was collected from each plot, sun-dried for more than 10 days, weighed, and used to adjust the total straw yield to t/ha. Biological yield was calculated as the sum of grain yield and straw yield using the following equation:

$$\text{Biological yield} = \text{Grain yield} + \text{Straw yield}$$

Harvest index (%) was calculated as follows:

$$\text{HI} = \frac{\text{Grain yield}}{\text{Biological yield}} \times 100\%$$

2.5 Observations recorded

2.5.1 Growth and yield measurements

Ten hills were randomly selected and tagged in each plot. Plant height was measured at 15-day intervals from 30 DAS to physiological maturity. Before heading, height was measured from the soil surface to the tip of the highest leaf; after heading, it was measured to the tip of the panicle. The mean of the ten plants represented the plot value.

Two hills were sampled destructively from the designated sampling rows of each plot at 15-day intervals from 30 DAS until harvest. Above-ground biomass, excluding roots, was collected and dried at 70 °C for 72 h in a hot-air oven. Dry matter production was expressed as gm^2. Crop growth rate (CGR) was calculated for each sampling interval following Brown (1984):

$$\text{CGR} = \frac{W_2-W_1}{t_2-t_1} \times \frac{1}{A}$$

Where, W_1 and W_2 are total dry weights at t_1 and t_2 DAS, respectively, and A is the sampled ground area in m^2.

2.5.2 Yield and yield attributing parameters

The number of effective tillers was recorded at crop maturity by counting all panicle-bearing tillers within a randomly selected 1 m² area of each net plot. The number was expressed as effective tillers per square meter. The average length of ten panicles from the base of rachis to the tip of panicle was measured and expressed as length of panicle in cm.

The number of grains per panicle was counted manually from the ten panicles in each plot and the average number of filled grain from ten panicles was taken as the number of filled grain per panicle. At the same time, the number of unfilled grains per panicle was also counted to find out the sterility percentage of each treatment. Thousand grains were counted from randomly selected grain yield of net plot and weighted.

The sterility percentage was taken from the total filled grains and unfilled grains of each panicle and the calculation is done by using the formula as follows:

$$\text{Sterility percentage} = \frac{\text{Number of unfilled grains per panicle}}{\text{Total number of grains per panicle}} \times 100$$

2.6 Weed index

It was calculated by using the formula:

$$WI = \frac{X-Y}{X} \times 100$$

Where, X = Yield from minimum weed competition plot; Y = Yield from the treatment for which WI is to be worked out.

2.7 Statistical analysis

Data for each sampling date or interval were analyzed separately using a randomized complete block design (RCBD) model, as follows:

$$Y_{ij}=\mu+\tau_i+\beta_j+\varepsilon_{ij}$$

Where, Y_{ij} represents the observed value for treatment i in block j, μ is the overall mean, τ_i is the effect of treatment i, β_j is the effect of block j, and ε_{ij} is the random experimental error.

Treatment was considered a fixed effect and block was included as a blocking factor. The plot was the experimental unit and there were three blocks (n = 3). Plant height and dry matter were analyzed separately at each sampling date, and CGR was analyzed separately for each sampling interval; no Treatment x Time model was fitted. Analyses were performed in R version 4.3.1 using agricolae package. When the treatment effect was significant at $p \leq 0.05$, means were separated using Duncan's multiple range test (DMRT) at the 5% level.

3 Results and Analysis

3.1 Plant height (cm)

Plant height increased from 30 DAS to harvest in all treatments. Treatment differences were significant at each measurement date. Bispyribac sodium + 2,4-D had the numerically greatest height from 30 to 90 DAS, while the weed-free and oxadiargyl treatments were in the same statistical group at most of these dates (Table 2). At harvest, the weed-free and bispyribac sodium + 2,4-D treatments had the greatest values (93.4 cm), and both were statistically grouped with pretilachlor, bispyribac sodium, oxadiargyl, and pretilachlor + 2,4-D. The weedy check had the lowest harvest height (87.4 cm).

Table 2 Effect of herbicides on plant height at different time interval on direct seeded rice cultivation at Chitwan during 2024

Treatments	Plant height (cm)					
	30 DAS	45 DAS	60 DAS	75 DAS	90 DAS	at Harvest
Weedy Check	44.7^{d}	52.9^{d}	65.1^{c}	81.0^{c}	85.9^{c}	87.4^{c}
Weedfree	49.5^{ab}	66.6^{a}	75.3^{a}	91.3^{a}	93.2^{a}	93.4^{a}
Pendimethalin	45.3^{cd}	66.1^{a}	71.7^{b}	81.8^{c}	86.4^{c}	91.1^{b}
Pretilachlor	46.0^{bcd}	64.8^{ab}	72.1^{b}	88.5^{b}	91.4^{ab}	92.2^{a}
Bispyribac sodium	45.7^{cd}	60.7^{c}	73.0^{b}	89.0^{b}	90.8^{b}	92.9^{a}
Pendi+2,4-D	43.5^{d}	61.6^{c}	70.5^{b}	86.4^{b}	90.7^{b}	91.5^{b}
Pretilachlor+2,4-D	40.5^{e}	60.6^{c}	71.5^{b}	88.1^{b}	91.5^{ab}	92.5^{a}
Oxadiargyl	48.3^{bc}	68.8^{a}	74.0^{a}	93.0^{a}	95.1^{a}	93.0^{a}
Bispyribac Sodium+ 2,4-D	50.5^{a}	73.5^{a}	76.5^{a}	94.0^{a}	95.7^{a}	93.4^{a}
SEm±	0.97	1.85	1.03	1.42	1.06	0.59
CV%	6.34	8.67	4.28	4.83	3.49	1.93
Mean	46.00	63.96	72.19	88.12	91.19	91.93

Note: DAS= Days after sowing, SEm = Standard error of mean and CV= Coefficient of variation

3.2 Dry matter production (g/m^2)

Dry matter production increased progressively from 30 to 90 DAS in all treatments. The weedy check had the lowest dry matter at every sampling date. Bispyribac sodium was numerically greatest at 30 DAS and 75 DAS, whereas bispyribac sodium + 2,4-D was numerically greatest at 45, 60, and 90 DAS. At 90 DAS, bispyribac sodium and bispyribac sodium + 2,4-D were in the same statistical group and had dry matter values of 2093.4 g/m^2 and 2120.8 g/m^2, respectively. The treatment differences and grouping letters are provided in Table 3.

Table 3 Effect of herbicides on dry matter production at different time interval on direct seeded rice cultivation at Chitwan during 2024

Treatments	Dry matter production (g/m^2)				
	30 DAS	45 DAS	60 DAS	75 DAS	90 DAS
Weedy Check	28.5^{d}	51.2^{d}	164.5^{c}	839.4^{d}	1114.5^{d}
Weedfree	44.3^{bc}	74.7^{ab}	357.7^{ab}	1343.5^{ab}	1786.6^{b}
Pendimethalin	40.7^{cd}	57.4^{cd}	256.9^{bc}	1210.7^{bc}	1670.6^{bc}
Pretilachlor	40.8^{cd}	70.4^{ab}	274.1^{bc}	1325.1^{ab}	1794.7^{b}
Bispyribac sodium	51.8^{a}	69.4^{ab}	342.2^{ab}	1431.7^{a}	2093.4^{a}
Pendi+2,4-D	46.3^{ab}	65.4^{bc}	315.9^{ab}	1147.4^{c}	1490.4^{c}
Pretilachlor+2,4-D	48.0^{ab}	56.7^{cd}	251.7^{bc}	1221.9^{bc}	1719.2^{bc}
Oxadiargyl	42.5^{bc}	73.5^{ab}	351.5^{ab}	1240.6^{bc}	1680.7^{bc}
Bispyribac Sodium+ 2,4-D	44.4^{bc}	76.0^{a}	380.0^{a}	1410.0^{a}	2120.8^{a}
SEm±	2.04	2.82	21.55	55.98	95.15
CV%	14.23	12.79	21.60	13.53	16.61
Mean	43.03	66.08	299.40	1241.14	1718.99

Note: Treatment means followed by the same letter (s) within the column are non-significantly different among each other at 5% level of significance. DAS= Days after sowing, SEm = Standard error of mean and CV= Coefficient of variation

3.3 Crop growth rate (CGR)

Crop growth rate followed a common temporal pattern across treatments: it was lower during 30-45 DAS, increased during 45-60 DAS, reached its maximum during 60-75 DAS, and declined during 75-90 DAS (Table 4). Bispyribac sodium + 2,4-D had the greatest CGR during the first three intervals, although it was statistically grouped with several treatments during 30-45 and 60-75 DAS. Bispyribac sodium and bispyribac sodium + 2,4-D had the greatest CGR during 75-90 DAS and were in the same statistical group. The weedy check had the lowest CGR during 45-60, 60-75, and 75-90 DAS.

Table 4 Effect of herbicides on CGR at different time interval on direct seeded rice cultivation at Chitwan during 2024

Treatments	Crop growth rate (g/m^2/day)			
	30-45 DAS	45-60 DAS	60-75 DAS	75-90 DAS
Weedy Check	2.22^{c}	10.6^{c}	48.0^{c}	25.1^{c}
Weedfree	3.12^{ab}	22.3^{ab}	74.3^{a}	40.7^{b}
Pendimethalin	2.62^{bc}	20.1^{b}	62.4^{b}	36.8^{b}
Pretilachlor	3.02^{ab}	20.1^{b}	70.3^{ab}	37.5^{b}
Bispyribac sodium	2.32^{c}	21.6^{ab}	75.6^{a}	50.9^{a}
Pendi+2,4-D	2.22^{c}	17.15^{b}	60.6^{b}	29.6^{c}
Pretilachlor+2,4-D	1.72^{d}	17.0^{b}	66.9^{ab}	36.6^{b}
Oxadiargyl	3.02^{ab}	19.2^{b}	70.4^{ab}	38.7^{b}
Bispyribac Sodium+ 2,4-D	3.40^{a}	22.8^{a}	72.7^{a}	52.0^{a}
SEm±	0.18	1.25	2.90	2.90
CV%	20.82	19.76	13.02	22.53
Mean	2.63	18.98	66.80	38.66

Note: Treatment means followed by the same letter (s) within the column are non-significantly different among each other at 5% level of significance. DAS= Days after sowing, SEm = Standard error of mean and CV= Coefficient of variation

3.4 Yield attributes

Treatment effects were significant for effective tillers, panicle length, filled grains, unfilled grains, and sterility percentage. Bispyribac sodium + 2,4-D and bispyribac sodium had the greatest effective-tiller values, with 287 and 284 tillers per square meter, respectively, and were statistically grouped together (Table 5). The weedy check had the lowest value, with 151 tillers per square meter. Panicle length was greatest with bispyribac sodium (25.8 cm) and bispyribac sodium + 2,4-D (25.7 cm), both in the same statistical group and both greater than the weedy check (22.9 cm).

Bispyribac sodium + 2,4-D had the greatest number of filled grains (161 grains per panicle), followed by bispyribac sodium (158 grains per panicle); these treatments were statistically grouped together. The weedy check had the lowest filled-grain value (132 grains per panicle). The weedy check had the highest unfilled-grain count (39 grains per panicle) and sterility (22.81%), while all weed-management treatments were in the same statistical group for these two variables.

3.5 Test weight (1000-grain weight)

1000-grain weight differed significantly among treatments. The weed-free treatment had the numerically greatest value (24.8 g) and was statistically grouped with bispyribac sodium + 2,4-D (24.2 g), bispyribac sodium (24.0 g), and oxadiargyl (24.0 g). The weedy check had the lowest value (21.1 g).

3.6 Grain yield, straw yield and harvest index

Grain yield was lowest under the weedy check (2.1 t/ha). Bispyribac sodium (6.1 t/ha) and bispyribac sodium + 2,4-D (6.0 t/ha) had the greatest numerical yields and were statistically grouped together. The weed-free treatment

(5.9 t/ha) was also in the same statistical group as these treatments. Pretilachlor produced 5.4 t/ha and was statistically grouped with the weed-free treatment, whereas pendimethalin + 2,4-D produced 3.7 t/ha.

Table 5 Effect of herbicides on effective tiller, panicle length, number of grain and sterility percent on direct seeded rice cultivation at Chitwan during 2024

Treatments	Effective tiller (m^2)	Panicle length (cm)	No. of grains per panicle filled	Unfilled	Sterility (%)
Weedy Check	151^{c}	22.9^{c}	132^{c}	39^{a}	22.81^{a}
Weedfree	272^{ab}	25.5^{ab}	155^{ab}	22^{b}	12.43^{b}
Pendimethalin	260^{ab}	24.1^{b}	150^{b}	21^{b}	12.28^{b}
Pretilachlor	267^{ab}	24.9^{ab}	152^{ab}	20^{b}	11.63^{b}
Bispyribac Sodium	284^{a}	25.8^{a}	158^{a}	19^{b}	10.73^{b}
Pendi+2,4-D	236^{b}	23.5^{bc}	149^{b}	27^{b}	15.34^{b}
Pretilachlor+2,4-D	248^{b}	24.6^{b}	150^{b}	25^{b}	14.29^{b}
Oxadiargyl	254^{ab}	24.3^{b}	151^{ab}	21^{b}	12.21^{b}
Bispyribac Sodium+2,4-D	287^{a}	25.7^{a}	161^{a}	17^{b}	9.55^{b}
SEm±	13.65	0.33	2.72	2.19	1.30
CV%	16.31	4.06	5.41	17.98	18.94
Mean	251	24.59	150.89	23.44	13.47

Note: Treatment means followed by the same letter (s) within the column are non-significantly different among each other at 5% level of significance. SEm = Standard error of mean and CV= Coefficient of variation

Straw yield was lowest under the weedy check (4.6 t/ha). Bispyribac sodium + 2,4-D produced the greatest numerical straw yield (7.1 t/ha), followed by the weed-free treatment (7.0 t/ha) and bispyribac sodium (6.9 t/ha); these three treatments were statistically grouped together.

Harvest index was lowest under the weedy check (31.3%). Bispyribac sodium had the greatest numerical harvest index (46.9%) and was statistically grouped with pretilachlor, weed-free, and bispyribac sodium + 2,4-D. The remaining treatment means are presented in Table 6.

Table 6 Effect of herbicides on TGW, grain yield, straw yield, HI and weed index on direct seeded rice cultivation at Chitwan during 2024

Treatments	TGW (g)	Grain yield (t/ha)	Straw yield (t/ha)	HI (%)	WI
Weedy Check	21.1^{b}	2.1^{c}	4.6^{c}	31.3^{c}	64.41^{a}
Weedfree	24.8^{a}	5.9^{ab}	7.0^{a}	45.7^{ab}	0.00^{b}
Pendimethalin	22.3^{b}	4.5^{b}	6.1^{b}	42.5^{b}	23.73^{b}
Pretilachlor	22.4^{b}	5.4^{ab}	6.3^{ab}	46.2^{ab}	8.47^{b}
Bispyribac sodium	24.0^{a}	6.1^{a}	6.9^{a}	46.9^{a}	−3.39^{b}
Pendi+2,4-D	21.5^{b}	3.7^{bc}	6.2^{b}	37.4^{bc}	37.29^{b}
Pretilachlor+2,4-D	22.0^{b}	4.6^{b}	5.9^{b}	43.8^{b}	22.03^{b}
Oxadiargyl	24.0^{a}	4.8^{b}	6.0^{b}	44.4^{b}	18.64^{b}
Bispyribac Sodium+ 2,4-D	24.2^{a}	6.0^{a}	7.1^{a}	45.8^{ab}	−1.69^{b}
SEm±	0.45	0.43	0.25	1.71	7.29
CV%	5.84	18.95	12.22	12.01	16.17
Mean	22.92	4.79	6.23	42.67	18.83

Note: Treatment means followed by the same letter (s) within the column are non-significantly different among each other at 5% level of significance. SEm = Standard error of mean and CV= Coefficient of variation

3.7 Weed index (WI)

The weed index clearly reflected the effectiveness of different weed management practices in reducing yield losses. The highest weed index (64.41%) was recorded in the weedy check, indicating severe yield reduction due to weeds. Negative weed index values observed under bispyribac sodium (−3.39%) and bispyribac sodium + 2,4-D (−1.69%) indicate slightly higher yields than the weed-free treatment, possibly due to reduced crop disturbance and better resource use efficiency under chemical control. Higher weed index values in pendimethalin + 2,4-D and pendimethalin alone treatments suggest comparatively lower weed control efficiency, especially against later-emerging weeds.

4 Discussion

4.1 Vegetative growth and biomass

Plant height, dry matter production, and CGR were greater under the more effective weed-management treatments than under the weedy check, especially during the later growth stages. The temporal pattern of CGR, with an increase toward 60-75 DAS followed by a decline during 75-90 DAS, is consistent with the changing balance between vegetative biomass accumulation and reproductive development. The present experiment did not measure weed density, weed biomass, nutrient uptake, or photosynthetic traits. Therefore, the greater growth observed under bispyribac sodium treatments may be associated with reduced crop-weed interference, but the mechanism was not directly demonstrated. Previous DSR research has similarly linked timely weed suppression with improved crop growth, although responses depend on weed spectrum, environment, and application timing (Chauhan and Johnson, 2011; Mahajan et al., 2014; Shekhawat et al., 2020).

4.2 Yield components

Bispyribac sodium and bispyribac sodium + 2,4-D produced the greatest effective-tiller and filled-grain means, and both treatments were statistically grouped together. Their lower sterility values were also numerically favorable, although all weed-management treatments were statistically grouped for sterility and unfilled grains. This pattern suggests that maintaining crop growth during tillering and reproductive development may partly reflect improved yield-component formation, but the study did not directly measure the physiological processes responsible. The response is directionally similar to reports from DSR systems in Nepal and South Asia, where timely weed-management treatments improved tiller formation and grain filling (Dangol et al., 2020; Poudel et al., 2020; Sharma et al., 2021). Direct comparison of response magnitude should nevertheless be made cautiously because the cited studies differed in location, variety, weed flora, and treatment schedule.

4.3 Grain yield and biomass partitioning

The most important result was that bispyribac sodium alone and bispyribac sodium + 2,4-D produced statistically similar grain yields, 6.1 and 6.0 t/ha, respectively. The weed-free treatment also belonged to the same statistical group at 5.9 t/ha. Thus, the data do not support the claim that adding 2,4-D increased grain yield over bispyribac sodium alone. The single-herbicide treatment may be operationally simpler and uses fewer active ingredients, whereas the combination could be considered only where the weed spectrum, label requirements, compatibility, and resistance-management strategy justify it. Because treatment costs and returns were not measured, no economic advantage can be assigned to either option. The greater straw yield and harvest index under effective treatments indicate improved total biomass production and partitioning, but these interpretations are based on yield measurements rather than direct measurements of assimilate allocation.

4.4 Weed-management implications

Under the conditions of this experiment, bispyribac sodium alone and bispyribac sodium + 2,4-D were the most promising treatments for grain yield and several yield attributes. However, a weed index based on grain yield does not replace direct measurements of weed density, species composition, or weed biomass. The negative weed-index values for the two bispyribac sodium treatments indicate that their numerical yields exceeded the weed-free treatment, but they do not by themselves demonstrate broader weed-spectrum control or long-term

sustainability. Herbicide selection should therefore be integrated with cultural and mechanical practices and should account for application safety, crop tolerance, resistance risk, and local label recommendations (Kaur and Singh, 2017; Gyawaly et al., 2021; Shekhawat et al., 2020).

4.5 Limitations and future research

This study has three important limitations. First, weed density, species composition, and weed biomass were not measured, so treatment effects on the weed community cannot be quantified directly. Second, the experiment was conducted at one location in one season with one rice variety and three replications, which limits generalization to other environments. Third, no economic analysis was conducted, so the relative profitability of the single and combination herbicide treatments is unknown. Multi-location and multi-season trials should include direct weed measurements, treatment-by-environment assessment, crop-safety observations, herbicide-resistance considerations, and partial-budget or full economic analysis.

5 Conclusion

The present study demonstrated that weed-management treatment affected the growth, yield attributes, and productivity of direct-seeded rice under the conditions of Chitwan in 2024. Bispyribac sodium alone and bispyribac sodium + 2,4-D produced the greatest numerical grain yields, 6.1 and 6.0 t/ha, respectively, and both were statistically comparable with the weed-free treatment. Because the two bispyribac sodium treatments did not differ significantly in grain yield, the present data do not justify recommending the combination as superior to the single herbicide. Bispyribac sodium alone may be considered an effective option, while the choice between treatments should consider weed spectrum, label compliance, resistance management, crop safety and cost.

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Feature Review Open Access

Regulation of Sugar-Acid Balance During Kiwifruit Fruit Development and Ripening

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Abstract Kiwifruit flavor and commercial quality are largely determined by sugar–acid balance, the formation of which involves complex regulation of carbon metabolism throughout fruit development, ripening, and postharvest stages. This study examines the dynamic changes in sugars and organic acids in kiwifruit and their metabolic, molecular, and environmental regulatory mechanisms. The results indicate that starch accumulation and organic acid formation are prominent during fruit development, whereas during ripening and post-ripening, starch is rapidly degraded and converted into sucrose, glucose, and fructose, while the decline in total acidity is mainly associated with citrate degradation. AGPase, BAM, SUS, SPS, INV, and genes involved in citrate synthesis, degradation, and vacuolar transport jointly participate in sugar and acid metabolism. Regulatory modules such as AcNAC1–AcALMT1 and AcPUB11–AcCTS1–AcBAM3 further elucidate the molecular basis of sugar–acid balance. Ethylene, ABA, temperature, light, water and fertilizer management, crop load, and postharvest treatments can regulate fruit flavor by affecting carbon allocation, starch degradation, and organic acid metabolism. Future studies should strengthen multi-omics analyses, spatiotemporal regulation, and germplasm-specific differences to provide a theoretical basis for flavor quality evaluation, molecular breeding, and precision cultivation of kiwifruit.
Keywords Kiwifruit; Sugar–acid balance; Sugar metabolism; Organic acid metabolism; Quality regulation

1 Introduction

Kiwifruit flavor and market quality are strongly shaped by sugar–acid balance, because soluble sugars, organic acids, and their ratio determine sweetness, sourness, overall flavor intensity, and consumer preference. Soluble sugars and organic acids are repeatedly identified as the principal contributors to kiwifruit flavor and palatability (Titeli et al., 2023). In kiwifruit, sweetness is especially important for overall eating quality, yet it is not perceived independently, because the sensory expression of sweetness is modified by concurrent acidity and volatile composition (Nardozza et al., 2013). Consumer studies further show that acceptance rises with improved ripe soluble solids and an appropriate acid background, whereas fruit with insufficient sweetness or unfavorable acid balance are judged less acceptable or more sour (Wang et al., 2025). Consistent with this, fruit differing in carbohydrate supply, orchard origin, cultivar, or storage condition show measurable differences in acidity, sugar accumulation, flavor perception, and eating quality, indicating that sugar–acid balance is not only a biochemical trait but also a practical determinant of commercial value (Lievre et al., 2021).

The sugar–acid ratio therefore serves as a key indicator of fruit maturity and market quality in kiwifruit. Studies on commercial and postharvest fruit show that soluble solids concentration is a primary ripening criterion, while the interaction between soluble solids and titratable acidity is closely linked to taste quality and consumer acceptance (Titeli et al., 2023). Early-harvest experiments in ‘Hayward’ demonstrated that fruit with higher ripe soluble solids were consistently preferred, and that acidity became especially important when sweetness remained low. At the same time, orchard comparisons showed that sugar/acid ratios differ during maturation and are associated with acceptable versus unacceptable eating quality, with poorly matured fruit showing weak flavor intensity and off-flavors. Recent sensory-metabolomic work also identifies sugar-acid ratio as a major driver of consumer preference among flesh-color types and as a metabolite-derived index elevated during post-ripening

(Bao et al., 2026). These findings support the view that monitoring sugar accumulation, acid decline or redistribution, and their resulting ratio provides a biologically meaningful and commercially useful framework for judging kiwifruit maturity, readiness to eat, and market performance.

The formation of this balance is highly dynamic across fruit development and ripening, reflecting coordinated changes in carbohydrate metabolism. Kiwifruit differs from many fruits because it stores substantial carbohydrate as starch during development and converts that reserve into soluble sugars only after physiological maturity or during ripening (Nardozza et al., 2013). Net starch accumulation begins after cell division, intensifies during the slower fruit growth phase, and is followed near maturity by rising sucrose and hexose pools together with increased activities or transcripts of starch- and sucrose-related enzymes such as AGPase, SPS, AMY, and BAM-associated genes (Tian et al., 2021). During postharvest ripening, glucose, fructose, and sucrose typically increase markedly, although the dominant sugar can vary among genotypes, with sucrose predominating in some cultivars and glucose/fructose in others (Mao et al., 2023). Carbohydrate supply from the vine also alters this trajectory: enhanced supply promotes earlier maturation and higher starch and soluble sugar accumulation, whereas restricted supply delays maturity and weakens flavor development. These results show that sugar formation in kiwifruit depends on developmental stage, sink strength, genotype, and the regulation of starch–sucrose interconversion rather than on simple linear sugar accumulation.

Organic acid metabolism is equally dynamic and is a major counterpart to sugar accumulation in shaping flavor during maturation and ripening. Across kiwifruit species and cultivars, quinic acid, citric acid, and malic acid are the major organic acids, but their relative abundance and developmental trajectories differ substantially by genotype and storage environment (Mao et al., 2023). In several developmental studies, quinic acid is more prominent early, whereas citric acid increases as fruits mature, while malic acid either remains comparatively stable or changes more modestly (Lin et al., 2022; Jia et al., 2023). During postharvest ripening, titratable acidity usually declines, and this decline is often driven mainly by citric acid degradation, although malic acid can remain stable or even increase under some storage temperatures, helping explain differences in acidity perception between ripening conditions (Mao et al., 2023). Mechanistically, citric and malic acid accumulation is linked to the TCA cycle and to the coordinated regulation of synthesis and degradation enzymes, including citrate synthase, aconitase, isocitrate dehydrogenase, malate dehydrogenase, and phosphoenolpyruvate carboxylase. The objective of the present study is to clarify how sugars and organic acids are coordinately regulated during kiwifruit fruit development and ripening, to identify the metabolic and molecular factors that determine sugar–acid balance, and to provide a basis for improving maturity evaluation, flavor quality, and breeding or postharvest management strategies.

2 Dynamic Changes in Sugars and Organic Acids During Kiwifruit Development

2.1 Sugar composition and accumulation patterns

The main soluble sugars in kiwifruit are sucrose, glucose, and fructose, but their relative abundance changes with developmental stage and genotype. During fruit growth, Nardozza et al. (2023) reported that sugar concentrations often decline during early cell division and then rise again during cell expansion and maturation, with glucose sometimes peaking before net starch accumulation begins. In later developmental and ripening stages, sucrose, glucose, and fructose all increase substantially and contribute directly to ripe-fruit sweetness (Mao et al., 2023). However, the dominant soluble sugar is not uniform across kiwifruit types: glucose and fructose predominate in some *A. chinensis* fruit such as ‘Jinyan’, whereas sucrose is more prominent in ‘Hongyang’, ‘Kuilv’, and some hardy kiwifruit backgrounds (Li et al., 2021).

Starch accumulation and conversion are central to sugar formation in kiwifruit because this fruit stores much of its carbon as starch before harvest and converts it to soluble sugars during maturation and postharvest ripening. Net starch accumulation begins after cell division is completed, increases during the slower fruit growth phase, and then declines when maturation starts and soluble sugars rise rapidly. This pattern is consistent across cultivars, although the timing differs: starch peaks earlier in fast-developing ‘Kuilv’ than in ‘Hongyang’ or ‘Hayward’, and

in hardy kiwifruit the accumulation period can also vary by cultivar (Lin et al., 2022). Enzyme and transcript data indicate that AGPase is a key determinant of starch accumulation, while AMY, BAM, SPS, SUS, and related enzymes regulate starch degradation and sugar production during maturation and ripening (Shu et al., 2023).

2.2 Organic acid composition and metabolic dynamics

The dominant organic acids in kiwifruit are citric acid, quinic acid, and malic acid, although their proportions vary among species, cultivars, and developmental stages. Quinic acid is often abundant in young fruit and contributes strongly to the characteristic acidity of fresh kiwifruit (Fu et al., 2023). During development, quinic acid generally declines, whereas citric acid accumulates progressively and becomes the major contributor to total acidity near harvest in several cultivars including 'Hongyang', 'Hayward', and 'Zesy002' (Lievre et al., 2021). Malic acid usually occurs at lower levels and shows a more variable pattern, including transient early peaks or stage-specific fluctuations rather than a single uniform trajectory.

Acid content also varies systematically across developmental phases. In early growth, glucose and quinic acid tend to accumulate together, whereas the transition to slower growth and maturation is associated with declining quinic acid and increasing citric acid (Lievre et al., 2021). During postharvest ripening, titratable acidity generally falls, and this decline is driven mainly by citrate loss rather than by major changes in malate (Mao et al., 2023). Even so, malic acid can remain stable or increase under some storage conditions, which helps explain differences in perceived acidity after ripening. Mechanistically, citrate and malate accumulation depend on coordinated regulation of synthesis, degradation, and transport, including citrate synthase, aconitase, isocitrate dehydrogenase, NAD-MDH, PEPC, and the citrate transporter AcALMT1 under AcNAC1 control (Jia et al., 2023).

2.3 Cultivar differences in sugar–acid profiles

Substantial cultivar variation exists in sugar–acid profiles among green-, yellow-, and red-fleshed kiwifruit. Comparative studies by Li et al. (2021) show that green-fleshed 'Hayward', red-fleshed 'Hongyang', and hardy 'Kuilv' share the broad pattern of starch accumulation followed by sugar increase, but differ in developmental duration, sugar composition, and acid trajectories. 'Kuilv' matures earlier, has lower late-stage glucose, fructose, quinic acid, and malic acid, but higher sucrose than 'Hongyang' and 'Hayward'. In broader market comparisons, red-fleshed cultivars tend to receive higher consumer preference, with sugar–acid ratio, soluble sugars, and malic acid among the major drivers of liking, while green- and yellow-fleshed cultivars appear more environmentally sensitive (Wang et al., 2025).

Genetic and cultivar-level variation in sugar–acid ratio is therefore a major basis for flavor diversity in kiwifruit. High-sugar or high-dry-matter genotypes accumulate more starch reserves and soluble sugars, while differences in citrate, quinate, and malate metabolism shift acidity and final taste balance (Nardozza et al., 2013). Orchard and carbohydrate-supply effects further modify these inherited tendencies, changing sugar/acid ratios, maturity timing, and sensory quality even within the same cultivar. Kiwifruit development is characterized by a transition from starch and organic acid accumulation to starch remobilization, soluble sugar accumulation, and progressive organic acid remodeling. Although the timing and relative abundance of individual sugars and organic acids vary among cultivars, the overall developmental pattern is relatively conserved (Figure 1).

3 Regulation of Sugar Metabolism in Developing and Ripening Kiwifruit

3.1 Starch metabolism and sugar release

During early fruit development, net starch synthesis begins after cell division and becomes a major feature of the slower enlargement phase (Kang et al., 2021). Comparative metabolic analyses identify AGPase as a key control point for starch accumulation, with high-starch genotypes showing 2- to 5-fold higher and more sustained AGPase activity than low-starch genotypes. Additional evidence indicates that SPS also contributes to maximizing starch accumulation, likely through sucrose cycling that supports carbon supply to the starch pathway (Nardozza et al., 2013). In hardy kiwifruit, expression correlations further suggest genotype-specific regulation, with neutral invertase positively associated with starch and fructokinase linked to the conversion of fructose into starch in some cultivars (Lin et al., 2022).

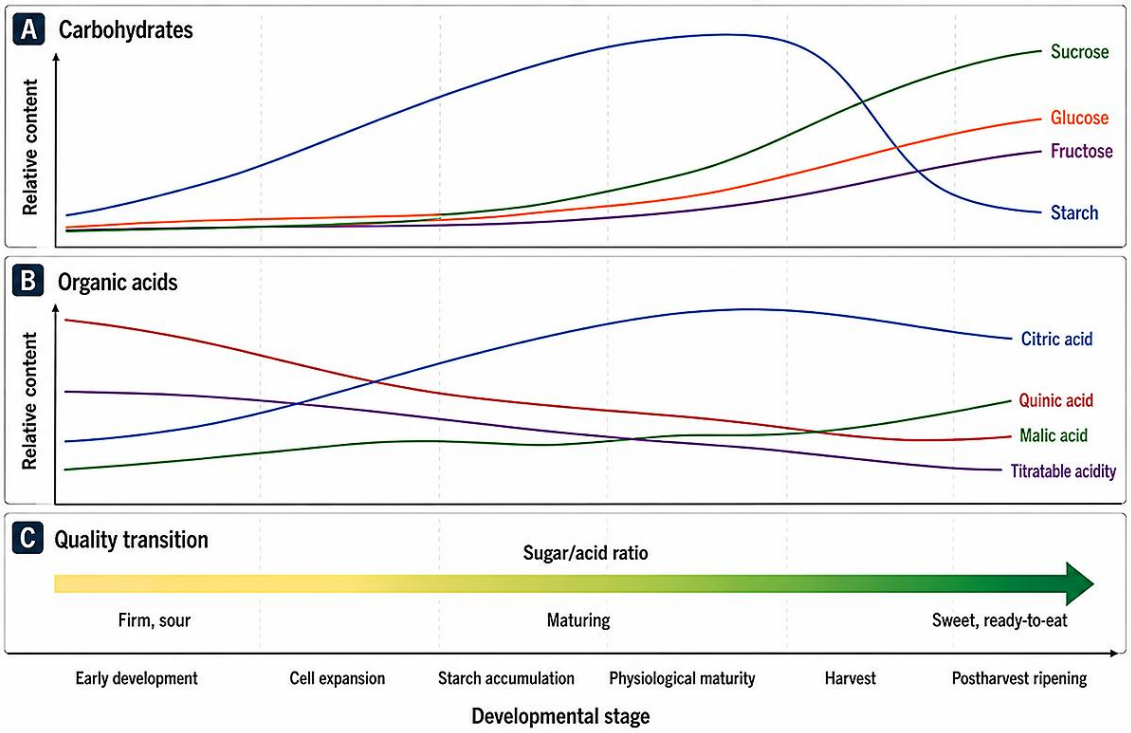


Figure 1 Dynamic changes in major sugars, organic acids, and quality attributes during kiwifruit development and ripening
Image caption: Relative changes in starch, sucrose, glucose, and fructose (A); Dynamic changes in citric acid, quinic acid, malic acid, and titratable acidity (B); As fruit development and ripening progress, the sugar–acid ratio gradually increases, accompanied by a transition from firm and sour fruit to sweet, ready-to-eat fruit (C). The curves shown in the figure represent general trends rather than specific quantitative values

During ripening, starch degradation becomes the main source of soluble sugar accumulation and is closely tied to the onset of softening. In postharvest fruit, starch breakdown precedes or accompanies strong increases in sucrose, glucose, and fructose, indicating that the conversion of reserve carbon into soluble sugars is a central ripening event. Enzyme and omics studies repeatedly implicate α-amylase, β-amylase, starch phosphorylase, and debranching enzymes in this process, with β-amylase emerging as a particularly important regulator (Tian et al., 2021). Regulation is not solely ethylene-dependent: cool temperatures at 5 °C–10 °C accelerate starch degradation and soluble solids accumulation even when ethylene perception is blocked, through an AcPUB11–AcCTS1–AcBAM3 module (Li et al., 2026). Ethylene still contributes, however, because treatment represses the transcriptional repressors AdVAL2 and AdKAN2 and upregulates BAM genes, thereby accelerating early starch degradation (Tong et al., 2024). Conversely, blue light delays ripening by suppressing starch degradation, amylase activity, and total soluble solids accumulation (Xu et al., 2024).

3.2 Sucrose metabolism and sugar interconversion

Sucrose metabolism in kiwifruit depends mainly on the balance between sucrose synthase and sucrose phosphate synthase, which together regulate sucrose cleavage, resynthesis, and cycling. Sucrose synthase shows high activity through much of fruit growth and is consistently higher than invertase during the growing season, supporting a dominant role in cleavage of imported sucrose (Chen et al., 2017). In growing 'Hayward' fruit, sucrose synthase activity is tightly associated with relative growth rate and is co-regulated with fructokinase and UDP-glucose pyrophosphorylase, linking sucrose cleavage directly to sink strength and carbon utilization. Nardozza et al. (2017) used *Actinidia chinensis* var. *deliciosa* 'Hayward' to compare CPPU-induced fruit enlargement under normal and high carbon supply conditions. The study found that CPPU significantly increased fruit fresh weight and elevated glucose and fructose levels. At 49 days after anthesis (49 DAA), the aquaporin gene *PIP2.4* was markedly upregulated. By contrast, SPS remains relatively low during earlier developmental stages and rises near maturity and ripening, when sucrose synthesis from starch-derived substrates intensifies (Kang et al., 2021). Feeding

studies and enzyme assays indicate that starch-to-sucrose conversion involves active sucrose cycling, rather than simple one-way accumulation (Nardozza et al., 2013). Cultivar comparisons support this developmental shift, with SS highly expressed in immature fruit and SPS increasing in mature stages, while SPS expression is positively associated with sugar accumulation in some genotypes (Lin et al., 2022).

Invertases provide a second route for sucrose cleavage and help shape the balance between sucrose and hexose accumulation. Invertases occur as cell wall, vacuolar, and neutral isoforms, and their functions differ by compartment and developmental stage (Huang et al., 2025). In kiwifruit fruit, neutral invertase is generally more important than acid invertase during development, and early changes in glucose and neutral invertase activity mark the transition into starch accumulation (Kang et al., 2021). During softening, acid and neutral invertase activities increase alongside amylase activities and correlate with sucrose, fructose, starch, and soluble solids, indicating a broader role in remobilizing carbon during ripening. Gene-expression data from 'Donghong' further suggest that specific NINV members participate in postharvest sugar accumulation, because several sugar-metabolism genes were upregulated during ripening but inhibited by 1-MCP (Yuan et al., 2023).

3.3 Sugar transport and sink strength

Sugar accumulation also depends on transport capacity and sink strength, because imported assimilates must be unloaded from the phloem and partitioned into storage parenchyma (Falchi et al., 2020). In general, sucrose can be unloaded symplasmically through plasmodesmata or apoplasmically into the cell wall space, after which SUTs, SWEETs, or hexose transporters mediate membrane transfer (Braun, 2022). Work across crops shows that these transporters strongly influence sink development, soluble sugar levels, and carbon allocation (Braun et al., 2014; Li et al., 2021). In kiwifruit leaves, Zhang et al. (2026) found that SPS in source tissues is itself a central regulator of sucrose synthesis and export capacity, and distinct SPS isoforms appear to differ in their contributions to whole-plant carbon allocation.

For kiwifruit fruit specifically, the strongest anatomical and tracer evidence supports predominantly apoplastic phloem unloading in the flesh during development. This conclusion contrasts with an earlier metabolite-based inference of symplastic unloading, showing that the unloading route remains somewhat debated (Nardozza et al., 2013). Within this apoplastic framework, low cell wall acid invertase but high sucrose synthase activity suggests that post-unloading sucrose is metabolized mainly through the sucrose synthase pathway rather than extensive extracellular hydrolysis (Chen et al., 2017). More broadly, sugar partitioning in fruit tissues depends on the interaction between unloading route, transporter function, and sucrose-cleaving enzymes that maintain concentration gradients and sustain sink activity.

4 Regulation of Organic Acid Metabolism in Kiwifruit

4.1 Biosynthesis and accumulation of major organic acids

Citrate in kiwifruit is formed through the tricarboxylic acid cycle in mitochondria, and its accumulation depends on both strong synthesis and restricted degradation (Baiquan et al., 2018). In developing kiwifruit, citrate often accumulates continuously and becomes the predominant contributor to total acidity by harvest, as shown in both 'Hongyang' and 'Hayward' backgrounds (Fu et al., 2023). Jia et al. (2023) conducted enzyme activity analyses in *Actinidia eriantha* and found that high citrate accumulation was associated with increased citrate synthase activity, accompanied by decreased activities of mitochondrial aconitase and NAD-dependent isocitrate dehydrogenase. These findings suggest that substantial citrate accumulation may result from the combined effects of enhanced biosynthetic flux and reduced citrate utilization. This interpretation is consistent with broader fruit studies showing that citrate synthesis is controlled by the pyruvate-to-acetyl-CoA-to-citrate pathway and that TCA-cycle protein abundance can shift citrate accumulation capacity (Zheng et al., 2021; Wu et al., 2025).

Malate and quinate show distinct developmental trajectories from citrate. In kiwifruit, malate often peaks earlier or accumulates less strongly than citrate, while quinate is high in young fruit and declines during development (Qi et al., 2025). In *A. eriantha*, malate accumulation increased during fruit development and was positively associated with titratable acidity, with NAD-MDH and PEPC identified as major synthetic drivers and AeMDH2

implicated as a key regulator (Jia et al., 2023). Qi et al. (2025), based on a study of 'Hongyang' kiwifruit, found that malate content declined rapidly between 6 and 12 weeks after full bloom and was significantly negatively correlated with the expression of the plastidial AcPNAD-MDH1. CRISPR mutagenesis of AcSQBP9 reduced both malate and citrate contents while increasing AcPNAD-MDH1 expression, indicating that malate regulation also involves transcriptional control. Quinate metabolism is less resolved mechanistically, but kiwifruit studies have linked its accumulation to DAHPS, DHQS, and QDH expression, and consistently show high early abundance followed by decline as citrate becomes dominant (Fu et al., 2023).

4.2 Organic acid degradation during ripening

During ripening, organic acid decline in kiwifruit reflects increased respiratory utilization and broader metabolic reprogramming rather than simple dilution. Postharvest analyses show that citric acid declines progressively and tracks titratable acidity closely, identifying citrate degradation as the main cause of acid loss during ripening (Mao et al., 2023). In 'Xuxiang' fruit, Chai et al. (2024) found that the outer pericarp shows faster citric acid reduction than the core together with higher ATP, ADP, AMP, and energy charge, linking stronger acid decline to higher local respiration and energy metabolism. Across fruits more generally, citrate can be consumed through aconitase- and NAD-IDH-dependent pathways in mitochondria or diverted into the GABA shunt, and low mitochondrial aconitase activity can favor citrate retention whereas higher GABA-pathway activity promotes citrate degradation (Baiquan et al., 2018).

Malate decline during ripening is more variable than citrate decline, but when it decreases it is typically associated with decarboxylation and recycling into other pathways (Shu et al., 2024). Broader fruit metabolism studies indicate that vacuole-released malate and citrate can be redirected through gluconeogenesis, amino acid biosynthesis, and respiratory carbon metabolism during the transition from acid-dominated to sugar-dominated fruit composition (Iglesias-Sanchez et al., 2026).

In apple, malate decomposition is associated with NADP-malic enzyme and PEPCK activity, and suppressing these pathways during storage preserves acidity, supporting the general model that malate decarboxylation contributes to acid decline in fleshy fruit (Shu et al., 2024). Evidence in kiwifruit suggests this process is integrated with ethylene-responsive and TCA-linked ripening programs, although citrate appears to be the main driver of titratable acid loss in postharvest fruit (Fu and Chen, 2026).

4.3 Transport and compartmentation of organic acids

The final acidity of kiwifruit depends not only on metabolism but also on compartmentation, because malate and citrate are largely accumulated in vacuoles and their storage depends on tonoplast transport and vacuolar acidification (Huang et al., 2021). Reviews across fleshy fruits conclude that vacuolar storage is often the dominant determinant of cellular malate and citrate accumulation, even when biosynthetic pathways are active (Huang et al., 2021; Fu and Chen, 2026). In kiwifruit specifically, AcALMT1 has been functionally identified as a citrate transporter: its expression correlates with citrate accumulation, overexpression increases citrate content, and CRISPR mutagenesis of the upstream transcription factor AcNAC1 causes a dramatic citrate decrease without substantially affecting malate or quinate (Fu et al., 2023). This finding is notable because ALMT family members in other systems are more often linked to malate or fumarate transport, highlighting diversification of transporter function in fruit acidity control (Doireau et al., 2024).

Acid homeostasis also requires proton pumps and additional tonoplast carriers that establish the electrochemical gradient for organic acid sequestration (Huang et al., 2021; 2023). In other fruit systems, P-type ATPases such as PH5 and Ma10, together with V-ATPase and V-PPase, promote vacuolar acidification and enhance malate or citrate storage, indicating a transport logic likely relevant to kiwifruit as well (Wu et al., 2025). Tonoplast exchangers and channels such as tDT, ALMT9/Ma1, and related carriers further regulate the balance among citrate, malate, and other dicarboxylates by controlling import, export, and exchange across the vacuolar membrane (Doireau et al., 2024).

5 Molecular Regulation of Sugar–Acid Balance in Kiwifruit

5.1 Key structural genes involved in sugar and acid metabolism

Genes controlling starch degradation and sucrose metabolism are major determinants of sugar accumulation during ripening. Multi-omics analyses identify *AMY*, *BAM*, *SUS*, *SPS*, *INV*, *HK*, and *FK* as core structural genes associated with soluble sugar metabolism in kiwifruit (Wang et al., 2021). Among them, *BAM* genes are repeatedly highlighted as the main drivers of starch-to-sugar conversion, and AcBAM3.5 shows especially strong ripening-associated expression in 'Hongyang' (Gong et al., 2025). Zhang et al. (2018) further demonstrated in an ethylene-response study of 'Hayward' kiwifruit that *AdBAM3L* is a key gene involved in starch degradation, and its overexpression reduces starch content, supporting a direct structural role for *AdBAM3L* in soluble sugar formation. Recent family-wide analysis also expanded the BAM repertoire to 17 *AcBAM* genes, with *AcBAM5* and *AcBAM13* most highly expressed during postharvest storage and strongly induced by ABA; silencing either gene increases starch content (Gong et al., 2025). In yellow-fleshed kiwifruit, Lin et al. (2024) pointed out six *AcBAM* genes are significantly upregulated during ripening, especially *AcBAM3.1* and *AcBAM3.2*, and their expression parallels rising β-amylase activity and sugar accumulation. Starch synthesis capacity also contributes to final sweetness, because AGPS1.1, AGPS1.2, and WAXY1 are upregulated during development in sweeter *A. eriantha* fruit, while BAM3.2, BAM3.3, PHO1, PHO2.2, SUS2.1, and SUS2.2 support subsequent remobilization (Li et al., 2024).

Genes associated with citrate and malate metabolism regulate the acid side of the balance through both metabolic flux and transport. For citrate, accumulation depends on strong synthesis and weak degradation, with citrate synthase, mitochondrial aconitase, and NAD-dependent isocitrate dehydrogenase identified as key enzymatic control points (Wang et al., 2021). A major kiwifruit-specific advance is the identification of AcALMT1 as a citrate transporter rather than a malate transporter in this context; its expression correlates with citrate levels, and transient overexpression increases citrate accumulation. Malate regulation appears partly distinct: AcPNAD-MDH1 is negatively correlated with malate content during 'Hongyang' development, and overexpression lowers both malate and citrate in leaves (Qi et al., 2025). In *A. eriantha*, malate accumulation is linked mainly to NAD-MDH and PEPC activity, with AeMDH2 implicated as an important regulator, while quinate metabolism has been associated with DAHPS, DHQS, and QDH expression.

Sugar and organic acid metabolism are interconnected through carbon allocation, respiratory metabolism, and intracellular compartmentation. The major structural genes and metabolic pathways involved in starch–sugar interconversion and citrate–malate metabolism collectively constitute the sugar–acid metabolic network in kiwifruit and contribute to the establishment of sugar–acid balance through coordinated carbon flux (Figure 2).

5.2 Transcriptional regulation of sugar–acid metabolism

MYB, bZIP, NAC, ERF, bHLH, C2H2, Dof, and related transcription factor families all contribute to sugar–acid regulation, but they do so through different targets and developmental signals. Network analysis places NAC, C2H2, AP2/ERF, MYB, and bHLH among the dominant candidate families associated with soluble sugar accumulation in kiwifruit (Song et al., 2025). Within sugar metabolism, AcERF182 directly emerges as a central positive regulator because it is tightly correlated with AcBAM3.5 and embedded in the soluble sugar regulatory network (Wang et al., 2021). Additional ripening regulators act upstream of BAM genes through different mechanisms: AdDof3 activates the AdBAM3L promoter in an ethylene-responsive pathway, while under cool temperature AcCTS1 directly activates AcBAM3.3 and AcBAM3.5 and is negatively controlled by the E3 ligase AcPUB11 (Zhang et al., 2018). Co-regulation can also be negative: spatiotemporal multiomics identified an A. chinensis ERF1 that negatively controls sugar accumulation and ethylene production, indicating that not all ERFs promote ripening sugar gain (Zeng et al., 2025).

On the acid side, NAC regulation is the clearest experimentally validated mechanism. AcNAC1 directly binds the AcALMT1 promoter and activates its expression, and CRISPR mutagenesis of AcNAC1 causes a dramatic citrate decline without major effects on malate or quinate (Fu et al., 2023). Malate control involves a different transcriptional module, because AcSQBP9 represses AcPNAD-MDH1 and its mutagenesis decreases both malate

and citrate while increasing AcPNAD-MDH1 expression (Qi et al., 2025). Broader kiwifruit studies on MYB and bZIP factors, although centered on ascorbate metabolism, show that these families form cooperative transcriptional complexes and are hormone responsive, making them plausible components of wider flavor-regulatory networks (Liu et al., 2022).

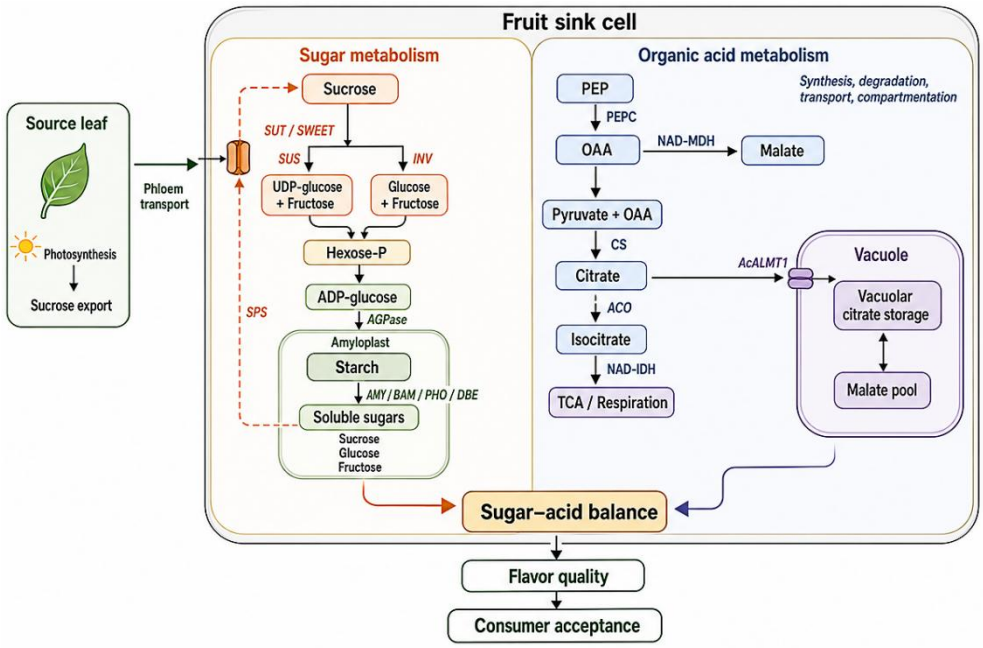


Figure 2 Integrated metabolic framework of sugar and organic acid metabolism underlying sugar – acid balance in kiwifruit
Image caption: Imported sucrose is unloaded into fruit tissues and enters sucrose cleavage, hexose metabolism, and starch biosynthesis pathways. During maturation and ripening, stored starch is remobilized through amylolytic pathways to support sucrose, glucose, and fructose accumulation. Organic acids are linked to central carbon metabolism through the TCA cycle, with citrate and malate levels determined by coordinated biosynthesis, degradation, transport, and vacuolar compartmentation. Key enzymes and transporters include AGPase, AMY, BAM, SUS, SPS, INV, PEPC, NAD-MDH, citrate synthase, aconitase, NAD-IDH, and AcALMT1

5.3 Hormonal regulation during kiwifruit ripening

Ethylene is the dominant hormonal regulator of sugar–acid conversion during postharvest ripening, but its effects are selective across traits and can interact with temperature. In climacteric kiwifruit, ethylene strongly accelerates ripening-associated transcriptional programs and starch degradation (Tipu and Sherif, 2024; Yang et al., 2025). Ethylene promotes sugar accumulation partly by inducing BAM-centered pathways: AdDof3–AdBAM3L, AcERF182–AcBAM3.5, and ethylene-upregulated AdBAM3-family genes all support faster starch loss and higher soluble solids (Zhang et al., 2018). Ethylene treatment also accelerates starch degradation and TSS accumulation, whereas 1-MCP suppresses these responses (Yang et al., 2025). However, Li et al. (2026) found that cool temperature can activate a partly ethylene-independent route, because AcCTS1 drives AcBAM3.3/3.5 expression and starch degradation under 5 °C–10 °C even when ethylene perception is blocked.

ABA and auxin appear to modulate maturation timing and flavor formation mainly through crosstalk with sugar and ethylene pathways rather than by replacing them. Across fruit systems, ABA usually rises during ripening and promotes flavor development, softening, and color, often in interaction with ethylene (Wu et al., 2023). In yellow-fleshed kiwifruit, ABA peaks early in postharvest ripening and participates with cytokinins and ethylene in a coordinated ripening model (Lin et al., 2024). Gong et al. (2025) reported that ABA also connects directly to sugar metabolism because AcBAM5 and AcBAM13 are strongly ABA induced, and their promoters contain ABRE elements. By contrast, auxin appears more associated with developmental timing: early-maturing *A. eriantha* germplasm has lower IAA, ABA, and ZR contents together with faster starch conversion and higher sucrose, glucose, and fructose at harvest (Liao et al., 2021). More generally, sugar signaling, ABA, and auxin are

increasingly viewed as interdependent ripening regulators, but the kiwifruit-specific auxin network remains less resolved than the ethylene and ABA pathways (Durán-Soria et al., 2020; Bai et al., 2021).

6 Environmental and Cultivation Factors Affecting Sugar–Acid Balance

6.1 Light and temperature effects

Canopy light conditions influence carbohydrate accumulation mainly by regulating photosynthesis, leaf sugar metabolism, and carbon export to the fruit. In kiwifruit, carbohydrate supply varies with leaf area, leaf position, light exposure, and leaf age, so canopy structure directly affects the amount of photosynthate reaching fruit sinks (Patiyal et al., 2024). Light quality also changes sugar metabolism at the source level: red or red–blue light increased leaf sucrose, glucose, and fructose compared with blue-dominant treatments, and the red–blue 3:1 treatment gave the highest sucrose content and SPS activity (Zhang et al., 2026). Promoter analysis of the AdSPS family further showed that light-responsive elements are abundant, supporting direct light regulation of sucrose metabolism genes in kiwifruit. Field management that improves light interception can therefore strengthen sugar accumulation indirectly through enhanced source activity, although excessive solar irradiance can become harmful rather than beneficial (Patiyal et al., 2024).

Temperature has equally strong effects on respiration and organic acid metabolism. High summer temperatures and heat load reduce dry matter, soluble solids, and starch-to-sugar conversion, while increasing acidity and delaying commercial ripening (Denaxa et al., 2023). Elevated temperature during starch accumulation also diverts carbohydrates toward vegetative growth and away from fruit sinks, weakening final sugar accumulation. By contrast, Mitalo et al. (2019) found that low-temperature storage can accelerate sugar accumulation and softening even without detectable ethylene production, and these changes occur faster at 5 °C than at 22 °C. Postharvest blue light has the opposite effect, reducing respiration, ethylene production, total soluble solids accumulation, and starch degradation, thereby delaying ripening (Xu et al., 2024). Organic acid behavior during ripening is closely tied to respiratory metabolism, with citrate decline being the main cause of titratable acidity (Mao et al., 2023).

6.2 Water and nutrient regulation

Water management affects both yield and flavor-related composition, but the response depends on irrigation intensity and growth stage. A recent meta-analysis by Ding et al (2025) showed that optimized water and fertilizer management increased soluble sugar by 6.35% and reduced titratable acidity by 4.35%, improving overall fruit quality. The same analysis found that excessive irrigation had a greater negative effect on yield and water-use efficiency, whereas reducing super-optimal water input increased yield by 16.24% and water-use efficiency by 20.06%. Stage-specific fertigation studies in ‘Jinyan’ further showed that moderate water deficit combined with potassium regulation can maintain yield while improving TSS and sugar/acid ratio, with late-stage HWHK treatment raising TSS by 30.58% and sugar/acid ratio by 24.91% (Cui et al., 2023).

Among nutrients, potassium has the clearest effect on flavor development because it regulates osmotic balance, carbon transport, and sugar–acid composition. Excess potassium can raise soluble solids and pH enough to disrupt acid balance and impair flavor, while overapplication also competes with Ca, Mg, and NH^{4+} uptake (Ding et al., 2025). In ‘Hayward’, increasing potassium generally reduced SSC and titratable acidity, and intermediate rates were more appropriate overall than the highest doses (Tarakçıoğlu and Öztürk, 2022). Potassium source also matters: basal K_2SO_4 followed by KCl topdressing improved fruit weight and vitamin C relative to single-source treatments (Ma et al., 2025). Nitrogen effects appear more conditional. Moderate nitrogen can increase fruit weight without large changes in sugars or acids, but excess N can disrupt nutrient balance and reduce fruit K and Ca status. Calcium mainly improves firmness and storability rather than sugar–acid composition: foliar Ca sprays increased fruit Ca and firmness, but did not significantly alter soluble solids or acidity (Sotiropoulos et al., 2021). In calcareous soils, Baldi et al. (2025) pointed out that soil-applied Ca was largely ineffective for improving fruit quality, whereas reflective films increased soluble solids at harvest and during storage.

6.3 Crop load and canopy management

Crop load and canopy management regulate sugar–acid balance by changing source–sink balance within the vine. General source–sink theory predicts that excessive fruit number increases demand for limited carbohydrates, while thinning and pruning improve carbon partitioning to the remaining fruit (Pawar and Rana, 2019). In 'Zesy002', experimentally increasing carbohydrate supply through girdling and thinning increased starch and soluble sugar concentrations and advanced maturation, whereas low carbohydrate supply delayed maturity and produced fruit perceived as more acidic and under-ripe (Lievre et al., 2021). Similar source–sink effects are reported more broadly in fruit crops, where thinning alters sugar and organic acid profiles early in development and predicts final quality (Paz Covarrubias et al., 2021).

Pruning and canopy regulation can improve the sugar–acid ratio when they optimize leaf area relative to fruit load. In 'Hayward', pruning up to 12 nodes per cane produced the highest TSS:acid ratio and total sugar content, and the combination of 12 nodes per cane with thinning to 6 fruits per shoot gave the highest ratio and sugars overall (Patiyal et al., 2024). Angami et al. (2022) showed that stronger thinning with regular pruning increased TSS and sugars and reduced titratable acidity, while moderate thinning maximized grade-A yield and profit.

7 Postharvest Regulation of Sugar–Acid Balance During Kiwifruit Ripening

7.1 Changes in sugar–acid metabolism during postharvest ripening

After harvest, kiwifruit enters a ripening program in which starch degradation precedes or accompanies rapid softening and the rise in soluble solids (Li et al., 2024). In 'Jinyan', starch fell rapidly from harvest onward, while SSC rose sharply during phase II softening and reached 14.4% by day 12 (Mao et al., 2023). The same general pattern appears across cultivars, including hardy kiwifruit, where high harvest starch gradually degrades into soluble sugars during storage and ripening (Lee et al., 2025). Proteomic and transcriptomic studies identify β-amylase-centered pathways as major drivers of this conversion, with BAM genes repeatedly induced during postharvest ripening (Tian et al., 2021; Lin et al., 2024).

Organic acid decline is slower and less uniform than sugar increase, but titratable acidity generally falls as fruit soften. In 'Jinyan', citrate, quinate, and malate remain the main organic acids during postharvest ripening, yet only citrate shows a steady decline that closely tracks the fall in titratable acidity (Mao et al., 2023). Quinate tends to rise first and then fall, whereas malate remains relatively stable in some cultivars, indicating that citrate degradation is the main source of acid loss during softening rather than a uniform depletion of all acids. Fruit ripened at room temperature also show a rising sugar–acid ratio as starch fragments, cells collapse, and texture softens, linking metabolic change directly to eating quality (Li et al., 2024).

7.2 Effects of ripening treatments

Ethylene or ethylene analog treatment accelerates sugar accumulation mainly by hastening starch degradation, ethylene biosynthesis, and softening. In 'Kosui', Mitalo et al. (2019) found that propylene rapidly increased sucrose, glucose, and fructose together with Acβ-AMY1, Acβ-AMY2, and AcINV3-1 expression, while 1-MCP strongly delayed these changes. Ethrel treatment similarly accelerated senescence in 'Hayward', and ready-to-eat studies show that direct ethylene treatment shortens shelf life by increasing respiration, ethylene bursts, and starch loss (Salazar et al., 2021). Exogenous sucrose can also promote this process by increasing endogenous ethylene production and accelerating softening, indicating that sugar signaling feeds into ethylene-mediated ripening (Fei et al., 2020).

Controlled ripening aims to gain sweetness without excessive softening or flavor imbalance. 1-MCP consistently suppresses softening, ethylene production, starch degradation, and sugar accumulation during shelf ripening (Liu et al., 2021). After cold storage, combining postharvest ripening with 1-MCP can retain soluble sugars while limiting rapid decay and over-ripening (Hongli et al., 2024). Alternative delaying treatments show similar preservation logic: blue light suppresses ethylene biosynthesis, starch degradation, and TSS accumulation (Xu et al., 2024); GA3 delays ripening by suppressing ACO and BAM expression (Yang et al., 2023); tenuazonic acid inhibits BAM activity and maintains higher starch (Yan et al., 2025); and GABA or melatonin restrain sugar increase while slowing organic acid loss (Niu et al., 2025). Ethylene-induced and naturally ripened fruit can still

be sensorially similar, although exogenous ethylene tends to shift the profile toward higher glucose, fructose, and quinate and lower sucrose, citrate, and malate.

7.3 Storage conditions and flavor stability

Low-temperature storage modifies sugar and acid metabolism in ways that are partly independent of ethylene. Mitalo et al. (2019) pointed out that kiwifruit can soften and accumulate sugars at 5 °C without detectable ethylene, and these changes occur faster at 5 °C than at 22 °C in ethylene-free air. Mechanistically, cool temperatures between 5 °C and 10 °C accelerate starch degradation and SSC increase even when ethylene perception is blocked by 1-MCP, through the AcCTS1–AcBAM3 pathway (Li et al., 2026). However, low-temperature-ripened fruit remain deficient in ethylene-dependent aroma volatiles, so faster sugar gain does not necessarily preserve the full flavor profile (Mitalo et al., 2019). In hardy kiwifruit, 1 °C delays ripening relative to 5°C, slows starch degradation, but can favor later soluble sugar accumulation while increasing chilling injury risk (Lee et al., 2025).

Controlled-atmosphere storage helps preserve sugar–acid balance chiefly by slowing softening, decay, and acid loss, but the gas composition must stay within a safe range. In 'Jinyan', storage at 1 °C under 5% O_2 + 4% CO_2 delayed losses of firmness, acidity, and vitamin C and reduced decay by 43.7% at 200 days, whereas 2% CO_2 caused abnormal softening (Zhang et al., 2026). In 'Hayward', later harvest maturity improved long-term RA and CA outcomes and slowed acidity decline during storage, showing that storage stability depends partly on preharvest maturity at harvest (Goldberg et al., 2021). For cold-sensitive 'Xuxiang', 1-MCP followed by ethylene alleviated chilling injury better than ethylene alone and maintained fruit quality during 0 °C storage (Liu et al., 2021). In addition to genetic and developmental regulation, sugar–acid balance can be substantially modified by preharvest source–sink management and postharvest ripening conditions (Figure 3).

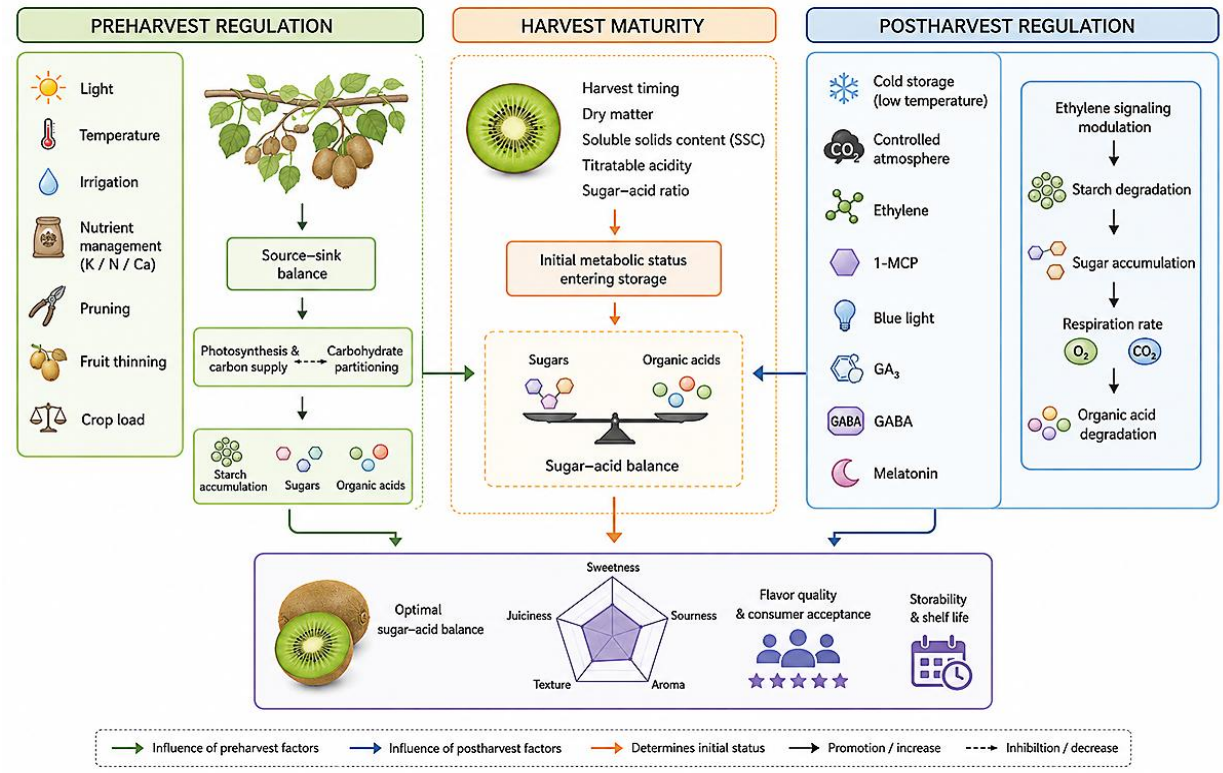


Figure 3 Integrated effects of environmental, cultivation, and postharvest factors on sugar–acid balance and flavor quality in kiwifruit
Image caption: Preharvest factors, including light, temperature, irrigation, nutrient management, pruning, thinning, and crop load, influence photosynthetic carbon supply and source-sink relationships. Harvest maturity determines the metabolic state entering storage, whereas postharvest temperature, atmospheric composition, ethylene-related treatments, light, and other regulators modify starch degradation, sugar accumulation, respiration, and organic acid loss. Their combined effects ultimately determine sugar–acid balance, flavor quality, and storage performance

8 Concluding Remarks

Sugar–acid balance in kiwifruit is regulated by a coordinated developmental program in which sugar accumulationand acid remodeling proceed together rather than independently. Across development and ripening, metabolome–transcriptome studies show that flavor formation reflects linked changes in soluble sugars, organic acids, and their regulatory genes, with network organization becoming clearer when fruit are sampled across many developmental stages. During postharvest ripening, starch reserves are converted into sucrose, glucose, and fructose while titratable acidity declines mainly through citrate degradation, producing the sensory shift from sour, firm fruit to sweet, edible fruit. This coordination is stage specific: early fruit development emphasizes starch and acid accumulation, whereas ripening activates starch breakdown, sugar release, respiratory carbon reallocation, and acid decline. Recent work also shows that this transition is not governed by ethylene alone, because cool temperature can directly activate AcBAM-centered starch degradation through the AcPUB11–AcCTS1–AcBAM3 module, linking environmental sensing to flavor formation.

Substantial progress has been made in identifying the structural genes, transcription factors, and hormonal cues involved in this process, but the regulatory architecture remains incomplete. Network studies in ‘Hongyang’ and red-fleshed kiwifruit have uncovered modules linking sugar metabolism, organic acid metabolism, and ripening-related transcription factors, yet these studies also emphasize that earlier work relied heavily on single-omics designs or limited metabolite coverage. Cultivar and species differences remain a major gap. ‘Hongyang’ and ‘Jinyan’ differ in their dominant sugar composition, *A. eriantha* shows distinctive high-acid behavior, early-maturing germplasm exhibits faster starch conversion under lower endogenous hormone levels, and species-level comparisons reveal divergent carbon allocation strategies between sweetness and other quality traits. Even postharvest flavor regulation can be strongly genotype dependent, as shown by varietal specificity in ‘Cuixiang’, *A. melanandra*, and CPPU-treated red-fleshed fruit.

Another unresolved issue is the still limited integration of metabolism, transport, and signaling across tissues and scales. Existing studies have largely succeeded in mapping changes in metabolites and candidate transcripts, but fewer have connected these data to tissue-specific transport, chromatin state, alternative splicing, long noncoding RNAs, or epigenetic regulation. This matters because flavor balance likely emerges from cross-compartment and cross-pathway coordination, not from enzyme abundance alone. Spatiotemporal networks already show that regulatory relationships differ among fruit skin, outer pericarp, inner pericarp, and core, while m6A studies show that epigenetic modifiers such as AcALKBH10 can simultaneously increase glucose, fructose, and sucrose and decrease citrate. More broadly, studies in other fruit systems indicate that integrated transcriptomic, chromatin, hormonal, and metabolomic analyses are effective for uncovering regulators of sugar and acid accumulation, suggesting a clear path forward for kiwifruit.

Future research should therefore move toward multi-omics dissection of sugar–acid regulatory networks across diverse *Actinidia germplasm*, tissues, environments, and postharvest conditions. Dense time-series sampling remains essential because regulatory peaks for transcripts, enzymes, and metabolites are stage dependent and may be missed by single-time-point studies. At the applied level, the field is now positioned to translate candidate genes, metabolite markers, and trait-linked SNPs into molecular breeding for flavor-balanced cultivars and into precision cultivation strategies that better align orchard climate, ripening management, and harvest timing with desired sugar–acid outcomes. Because consumers perceive flavor through the combined balance of sugars, acids, and other metabolites, breeding targets should shift from single traits such as SSC toward integrated flavor phenotypes supported by metabolomic and genetic markers.

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Conflict of Interest Disclosure

The authors affirm 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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