

ISSN 1925-2013

<https://genbreedpublisher.com/index.php/pgt>



Plant Gene and Trait

Vol.17 No.4 2026



Rhododendron simsi Planch.

OPEN  ACCESS

2026
04



Publisher

GenBreed Publisher

Edited by

Editorial Team of Plant Gene and Trait

Email: edit@pgt.genbreedpublisher.com

Website: <http://genbreedpublisher.com/index.php/pgt>

Address:

11388 Stevenston Hwy,

PO Box 96016,

Richmond, V7A 5J5, British Columbia

Canada

Plant Gene and Trait (ISSN 1925-2013) is an open access, peer reviewed journal published online by GenBreed Publisher.

The journal publishes articles that address the fundamental nature of genes and genomes at any level, either experimental or computational approaches, in plants as well as algae, including applications of novel techniques to plant biology and plant trait improvement. All papers chosen for publishing should be innovative research work in fields of plant genes or traits, plant protection, plant breeding, particular in the areas of functional genomics, genomic tools, genome technologies, transgene, genome sequencing analysis, molecular genetics, proteomics, genetic diversity, heterosis, genetic characteristics, genetic modification, genotype-phenotype relationships, stress resistance characteristics, QTL analysis, biochemistry, physiology and morphology.



GenBreed Publisher is an international Open Access publisher specializing in plant protection, plant breeding, molecular genetics, proteomics and genetic diversity registered at the publishing platform that is operated by Sophia Publishing Group (SPG), founded in British Columbia of Canada.

Open Access

All the articles published in Plant Gene and Trait are Open Access, and are distributed under the terms of the [Creative Commons Attribution License](#), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.



GenBreed Publisher uses CrossCheck service to identify academic plagiarism through the world's leading plagiarism prevention tool, iParadigms, and to protect the original authors' copyrights.



Latest Content

[Effects of Different Cultivation Management Models on Yield and Commercial Traits of Changshan Huyou](#)

Guofang Peng, Lijian Peng, Fangyuan Dong, Xi Cheng, Lixia Wang

Plant Gene and Trait, 2026, Vol. 17, No. 4, 235-244

[Molecular Genetic Regulation of Stamen Development: Insights from the ABC Model and Anther Ontogeny in *Arabidopsis* and Other Angiosperms](#)

Rimjhim Chandra

Plant Gene and Trait, 2026, Vol. 17, No. 4, 245-254

[Effects of Polyethylene Color and Thickness on the Retention of Some Minerals, Vitamins, and Antioxidant Activities of Stored Plantain \(*Musa paradisiaca*\) Flour](#)

Folasade Kemisola Olufemi-Salami, Olufemi Samson Salami, John Isa, Omolola Victoria Adefela, Mary Anuoluwapo Ajatta

Plant Gene and Trait, 2026, Vol. 17, No. 4, 255-263

[Effects of Planting Density on Plant Architecture, Fruit Setting and Yield Performance of Tomato](#)

Lingli Shen

Plant Gene and Trait, 2026, Vol. 17, No. 4, 264-276

[Effects of Canopy Management Practices on Fruit Development and Yield Stability of Fresh Table Grapes](#)

Feixue Pan

Plant Gene and Trait, 2026, Vol. 17, No. 4, 277-288

Research Report

Open Access

Effects of Different Cultivation Management Models on Yield and Commercial Traits of Changshan Huyou

Guofang Peng¹, Lijian Peng¹, Fangyuan Dong², Xi Cheng³, Lixia Wang⁴ ✉¹ Changshan County Dabaoshan Citrus Professional Cooperative, Changshan, 324204, Zhejiang, China² Changshan County Tonggong Township People's Government, Changshan, 324216, Zhejiang, China³ Changshan County Dong'an Township People's Government, Changshan, 324204, Zhejiang, China⁴ Development Center of Changshan Huyou Industry, Changshan, 324200, Zhejiang, China✉ Corresponding email: wanglixia809@126.comPlant Gene and Trait, 2026, Vol.17, No.4 doi: [10.5376/pgt.2026.17.0016](https://doi.org/10.5376/pgt.2026.17.0016)

Received: 20 May, 2026

Accepted: 25 Jun., 2026

Published: 02 Jul., 2026

Copyright © 2026 Peng et al., This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Peng G.F., Peng L.J., Dong F.Y., Cheng X., and Wang L.X., 2026, Effects of different cultivation management models on yield and commercial traits of Changshan Huyou, Plant Gene and Trait, 17(4): 235-244 (doi: [10.5376/pgt.2026.17.0016](https://doi.org/10.5376/pgt.2026.17.0016))

Abstract This study summarizes the effects of different management methods on the yield and quality of Changshan Huyou. It was found that conventional management could ensure stable yields, but it was prone to soil degradation and environmental pressure. Ecological and organic management can enhance fruit quality and also contribute to product differentiation, but it has higher requirements for environmental conditions and technical levels. Precise and integrated management, through intelligent irrigation, digital monitoring and nutrient regulation, has improved resource utilization and also made fruit quality more stable. The research also pointed out some problems, such as the trade-off between output and quality, differences in adaptability among different regions, and the lack of long-term comparative data. In the future, the development of Changshan Huyou should focus on the application of intelligent agriculture, the integration of breeding and management, as well as the promotion of sustainable cultivation models. This study aims to provide references for the efficient production, green development and brand building of Changshan Huyou.

Keywords Changshan Huyou; Cultivation management models; Yield and quality; Precision agriculture; Sustainable development

1 Introduction

Changshan Huyou (*Citrus changshan-huyou*) has an attractive fruit shape, mostly pear-shaped, spherical or flat-spherical, with a golden color. It is a characteristic product of Changshan County, Quzhou City, Zhejiang Province, and also a product with a geographical indication of China. It has received widespread attention due to its strong adaptability and high commercial value. At present, Changshan Huyou has been promoted and cultivated in Zhejiang, Hunan and other places, demonstrating good environmental adaptability and stable yield and flavor (Zhong, 2004; Tan et al., 2012; Yu et al., 2012).

The fruit of Changshan Huyou is rich in vitamins, 16 kinds of essential amino acids for the human body, as well as elements such as phosphorus, potassium, iron and calcium. It also contains flavonoids, coumarins and terpenoids. These substances not only enhance its nutritional value but also endow it with certain medicinal and health care functions. The unripe fruit dried product "Quzhou bitter orange pericarp" has been included in the Chinese Pharmacopoeia (Huang et al., 2025). In addition, the cultivation and processing of Changshan Huyou have played a significant role in promoting the local economy and increasing farmers' income (Zhong, 2004; Tan et al., 2012).

However, there are still many challenges in the production of Changshan Huyou. Factors such as climate, soil and management methods can affect output, causing fluctuations and thereby influencing the long-term stability of the industry (Yu et al., 2012). Fruits often vary in terms of flavor, nutrition and appearance, which limits the development of commercialization and branding (Huang et al., 2025). Meanwhile, with the increasingly fierce competition in the citrus market, Changshan Huyou needs new breakthroughs in variety improvement, cultivation techniques and deep processing and utilization (Zhong, 2004).

This study evaluated different cultivation and management models and compared their effects on the growth, yield and commercial traits of Changshan Huyou. The results show that optimizing management measures can enhance

the stability of yield and also improve the consistency of fruit quality. This research aims to provide theoretical basis and technical reference for the efficient cultivation of Changshan Huyou, industrial upgrading, and its sustainable development in modern fruit industry.

2 Biological and Commercial Characteristics of Changshan Huyou

2.1 Morphological and physiological traits of Huyou

Changshan Huyou (*Citrus changshan-huyou*) is a unique citrus fruit tree in China, mainly produced in Changshan County, Zhejiang Province and other places. It is a local specialty variety formed by the natural hybridization of pomelos and other citrus fruits, and belongs to evergreen subtropical fruit trees (Figure 1). Changshan Huyou grows fast, has strong adaptability, and is also cold-resistant and easy to store. The fruits enter the expansion period from June to July and September, and are ripe and harvested in November (Gao et al., 2022). In terms of morphology, the leaves of Changshan Huyou are relatively thick. The fruits are mostly spherical or flattened spherical, with golden peel and pale yellow flesh. It has a high yield and good stress resistance (Miao et al., 2024). In addition, polyploid Changshan Huyou (such as tetraploid) has larger fruits, larger leaves and flower organs, strong pollen viability and ovule viability, which is suitable for hybrid breeding (Huang et al., 2025).



Figure 1 Field view of Changshan Huyou trees laden with mature fruits

2.2 Commercial quality indicators: fruit size, weight, peel thickness, juice content, flavor, and storage ability

The fruit of Changshan Huyou is generally medium to large-sized, with a single fruit weighing about 300 grams. The peel is relatively thick but easy to peel off. The flesh is juicy and has a unique flavor, with a hint of sweetness, sourness and a touch of bitterness. The fruit contains rich active substances, such as naringin, hesperidin and limonin (Zhang et al., 2012). The peel also contains a large amount of volatile oil, flavonoids, coumarins and terpenoids, etc., which bring special aroma and certain medicinal value (Gao et al., 2022; Huang et al., 2025). Changshan Huyou is suitable for storage and can be preserved for a long time at room temperature, which is convenient for long-distance transportation and market sales (Miao et al., 2024). Furthermore, it has a high content of antioxidant activity and functional components, and its nutritional and health care value is prominent (Zhang et al., 2012; Gao et al., 2022).

2.3 Current cultivation practices in major producing regions

Changshan Huyou is mainly cultivated in places such as Quzhou, Kecheng and Longyou in Zhejiang Province, and has a cultivation history of over a hundred years (Gao et al., 2022; Miao et al., 2024). The current mainstream planting methods include high-density cultivation, scientific pruning, reasonable fertilization and integrated pest and disease management, emphasizing ecological and green production (Zhong, 2004). Changshan Huyou has strong adaptability. After being introduced to Hunan and other places, it has performed well, with stable growth, good yield and flavor maintenance, few diseases and pests and easy control. It has high economic and ecological value (Tan et al., 2012). In recent years, with the development of deep processing and functional foods, the industrial chain of Changshan Huyou has been continuously extended, promoting the process of commercialization and branding (Gao et al., 2022; Miao et al., 2024).

3 Cultivation Management Models

3.1 Conventional management: high-input practices, strengths, and drawbacks

Conventional management mainly relies on a large amount of chemical fertilizers, pesticides and water management, with the aim of pursuing high yields and stable fruit quality. Under this model, Changshan Huyou grows well in a suitable environment, with relatively stable yield and flavor, few pests and diseases, and easy control. Therefore, it has good economic and ecological value (Tan et al., 2012). However, this high-investment approach will also bring environmental pressure, consume resources and may even lead to soil degradation. Excessive reliance on chemical inputs may also affect the safety and market competitiveness of fruits.

3.2 Ecological and organic management: sustainability and product differentiation

Ecological and organic management places greater emphasis on reducing the use of chemicals, focusing on soil health, biodiversity and ecological balance. In suitable regions, Changshan Huyou can also achieve high yields and quality through ecological management, and enhance the ecological value and market differentiation advantages of the fruit (Tan et al., 2012). Organic management can reduce the occurrence of pests and diseases, increase the safety and added value of fruits, and make them more competitive in the high-end market. However, this model has high technical requirements, is more sensitive to environmental adaptability, may have a slightly lower output, and is easily affected by climate and soil conditions (Yu et al., 2012).

3.3 Integrated and precision management: technology-driven approaches (smart irrigation, nutrient management, digital monitoring)

Integrated and precision management combines new technologies such as intelligent irrigation, nutrient regulation and digital monitoring. By collecting data on meteorology, soil and crop growth in real time, irrigation and fertilization schemes can be optimized, resource utilization can be improved, and adaptability to extreme climates can be enhanced, thereby maintaining the stability of yield and quality (Yu et al., 2012; Yan et al., 2021). This approach can achieve efficient and sustainable production, but it requires a high level of technology and management, and is more suitable for large-scale and modern planting.

4 Effects on Yield Performance

4.1 Yield comparison among different cultivation models

Different cultivation and management methods will significantly affect the yield of Changshan Huyou. Research has found that reasonable management measures, such as dense planting, pruning, integrated water and fertilizer management, and comprehensive pest and disease control, can significantly increase the yield and commercial quality of citrus fruit trees. In the introduction adaptability test, Changshan Huyou showed good growth momentum, high yield, stable fruit flavor, few and easy-to-control diseases and pests under suitable climate and management conditions, demonstrating strong adaptability and promotion value. Among them, dense planting and scientific pruning can increase the yield per unit area, while precise water and fertilizer management can further enhance fruit quality and yield stability (Tan et al., 2012). Compared with the traditional extensive management, the efficient and integrated management model can simultaneously increase output and quality.

4.2 Factors influencing fruit set, maturation, and stability of annual production

The main factors influencing the fruit setting rate, maturity and annual yield stability of Changshan Huyou include: climatic conditions (temperature, precipitation, light), soil fertility, variety characteristics, cultivation density, pruning methods, water and fertilizer management and pest and disease control. Suitable climate and soil are conducive to flower bud differentiation and fruit development. Scientific water and fertilizer management can promote fruit enlargement and improve quality. Reasonable pruning can improve the structure of the tree, enhance ventilation and light penetration, reduce the occurrence of pests and diseases, and thereby increase the fruit setting rate and fruit uniformity. Integrated pest and disease control can also ensure the normal development and stable yield of fruits (Tan et al., 2012). In addition, the genetic characteristics of the variety itself can also affect its adaptability to environmental stress and yield stability.

4.3 Long-term yield sustainability and orchard productivity trends

In the long term, scientific management methods are conducive to enhancing the sustained output and overall productivity of Changshan Huyou orchards. Continuous optimization of water and fertilizer management,

reasonable planting density and pruning, and green prevention and control of diseases and pests can not only increase the current season's yield, but also maintain soil fertility and ecological environment, reduce yield fluctuations, and extend the high-yield and stable production period of orchards. In suitable ecological areas, Changshan Huyou demonstrates advantages such as strong adaptability and stable yield, with high economic and ecological value, making it suitable for large-scale promotion (Tan et al., 2012). However, if management is lax or soil and ecological protection is neglected, the yield and fruit quality may gradually decline, which requires attention.

5 Effects on Commercial Traits

5.1 Influence on fruit size, shape, and external appearance

Different cultivation and management methods will directly affect the size, shape and appearance of Changshan Huyou. Reasonable water and fertilizer management, appropriate dense planting and pruning can make the fruits grow more evenly, increase the weight of individual fruits, make the fruit shape more regular, and also reduce deformed and small fruits, thereby increasing the commercial fruit rate. Under suitable climate and soil conditions, scientific management can make the fruit skin color brighter, the fruit surface smoother, the fruit dots finer, the fruit look more beautiful and more market-attractive. Meanwhile, the integrated prevention and control of pests and diseases can reduce the spots and damage on the fruit surface and make the fruit appearance better. However, if the planting is overly dense or the management is lax, it is easy to have fruits of uneven size and irregular shape, which will affect the commercial traits (Tan et al., 2012).

5.2 Effects on flavor, sugar-acid ratio, nutritional content, and consumer preference

Cultivation management also plays a crucial role in terms of flavor and nutrition. Scientific fertilization, especially the reasonable combination of nitrogen, phosphorus and potassium, along with water regulation, can help accumulate sugar, adjust acidity, and make the sugar-acid ratio of fruits moderate, resulting in a better taste. The use of organic or bio-fertilizers can increase the content of vitamin C and soluble solids, making fruits more nutritious. Meanwhile, the harvest time and post-harvest treatment are also very important, directly affecting the retention of flavor and nutrition. Consumers usually prefer Changshan Huyou with a well-shaped fruit, bright color, rich flavor and a well-balanced sugar-acid ratio. Scientific management can effectively enhance these characteristics (Tan et al., 2012).

5.3 Postharvest traits: shelf life, storage, and transportability

In terms of postharvest traits, the differences among various management methods are also quite obvious. Moderate water control, reasonable fertilization and pest and disease prevention can enhance the toughness and thickness of the fruit peel, reduce post-harvest rot and mechanical damage, and thereby extend the storage time and shelf life. Seizing the right timing during harvest, along with post-harvest pre-cooling, grading and packaging, helps maintain the freshness and appearance of the fruits and enhance their adaptability during transportation. In addition, the use of biological preservatives or the proper control of storage temperature and humidity can also delay fruit senescence, reduce weight loss and rot, and increase the commercial fruit rate. Therefore, scientific post-harvest management is particularly important for the long-distance transportation and market sales of Changshan Huyou (Tan et al., 2012).

6 Economic and Environmental Considerations

6.1 Production cost and profitability analysis for each model

Different cultivation methods vary greatly in terms of input, output and returns. The input of traditional management is low, but the yield and fruit quality fluctuate greatly and the profit-making ability is limited (Ren et al., 2020; Abisheva and Mussin, 2023). Modern intensive management, such as high-density planting, precise fertilization and intelligent irrigation, can increase the yield per unit area and make the fruits more uniform. However, this approach is more costly and requires more fertilizers, pesticides, labor and equipment. Modern management can increase the yield of citrus and pomelo trees by 30% to 60%, but the cost often rises by 40% to 70%. The final revenue ratio should also be calculated in combination with market prices and policy subsidies (Chandra et al., 2024). Studies have found that if reasonable optimization is carried out, such as moderate planting

density, scientific fertilization, and pest and disease control, the yield and commercial fruit rate can be increased without significantly increasing the cost (Ren et al., 2020; Chandra et al., 2024). Although organic and ecological management has a slightly lower yield per unit area, they are still competitive in the long term because the products can be sold at a higher price and some input is saved (Szeląg-Sikora et al., 2019; Boschiero et al., 2023).

6.2 Environmental impacts: soil fertility, biodiversity, pesticide/fertilizer use

While intensive management increases production, it also brings about some environmental problems, such as the decline of soil fertility, the reduction of biodiversity, and the excessive use of chemical fertilizers and pesticides (Huang et al., 2024). Relatively speaking, organic and ecological management can improve the soil, increase organic matter and microorganisms, make the soil healthier and have better ecological functions (Martinez et al., 2024). Some systematic reviews and life cycle analyses have shown that organic/ecological management is significantly superior to conventional intensive models in terms of greenhouse gas emissions, nutrient loss and water pollution (Boschiero et al., 2023). In addition, hybrid management, such as precise fertilization, integrated pest and disease control, and crop cover, can balance yield and environmental protection. This type of approach can reduce the usage of chemical fertilizers and pesticides by 20% to 40%, while increasing soil organic matter and biodiversity (Martinez et al., 2024; Peng et al., 2024). However, some ecological measures may lead to a decrease in output in the short term, and the relationship between the economy and the environment needs to be balanced through technological improvements and policy subsidies (Szeląg-Sikora et al., 2019; Boschiero et al., 2023; Huang et al., 2024).

6.3 Farmer adoption, labor requirements, and policy support

Whether farmers are willing to adopt new management methods is influenced by multiple aspects such as income, labor force, technical threshold and policy environment (Huang et al., 2024). The intensive approach has high requirements for labor and technology and is more suitable for large-scale operation. The demand for ecologically-managed labor force is high, but it can be shared through cooperatives or socialized services (Chandra et al., 2024). Policy support is also important, such as green subsidies, technology promotion, insurance, etc., all of which will affect farmers' choices. At present, the main difficulties for farmers to adopt the new model are large initial investment, insufficient technical services and high market risk. Therefore, to promote the sustainable development of characteristic fruit trees such as Changshan Huyou, it is necessary to strengthen training, increase policy support, and improve the market system (Szeląg-Sikora et al., 2019; Chandra et al., 2024; Huang et al., 2024).

7 Case Study: Cultivation Management of Changshan Huyou

7.1 Background: study location, orchard characteristics, and climatic conditions

Changshan Huyou is a geographical indication fruit tree in Quzhou City, Zhejiang Province, with high ecological and economic value (Tan et al., 2012). Quzhou has a subtropical monsoon climate. The annual average temperature is about 17 °C, the precipitation is about 1 500 millimeters, the light conditions are good, and the soil is mainly red soil and yellow soil, which is very suitable for the growth of citrus fruit trees (Yu et al., 2012). Most orchards are located in hilly areas with undulating terrain and smooth drainage. The management methods of local orchards vary greatly. Some are still using the traditional extensive mode, while others have adopted modern and precise methods (Tan et al., 2012). In recent years, industrial upgrading has promoted the application of some new technologies and new varieties, such as natural tetraploids and superior grafted strains, to increase yield and fruit quality (Figure 2) (Du, 2001; Huang et al., 2025).

7.2 Methods: cultivation management treatments, monitoring, and data collection

This case study selected typical Changshan Huyou orchards in Quzhou City and designed multiple cultivation and management models, including: conventional management (control), optimized fertilization (controlled-release fertilizer or organic fertilizer combination), dense planting and sparse planting, scientific pruning, irrigation regulation, and the introduction of superior varieties (such as natural tetraploid, preferred grafted strains) (Tan et al., 2012). The experiment adopted a random block design, with duplicate cells set for each mode. The monitoring contents include yield per plant, yield per unit area, fruit size, color, shape, soluble solids, acidity, commercial

fruit rate and incidence of pests and diseases, etc. (Du, 2001). The data covers the entire growing season, and some indicators even extend to the post-harvest storage period. Some studies also combined meteorological data, soil properties, fruit metabolomics and transcriptomics to analyze the effects of management measures on fruit quality and stress resistance (Huang et al., 2025).

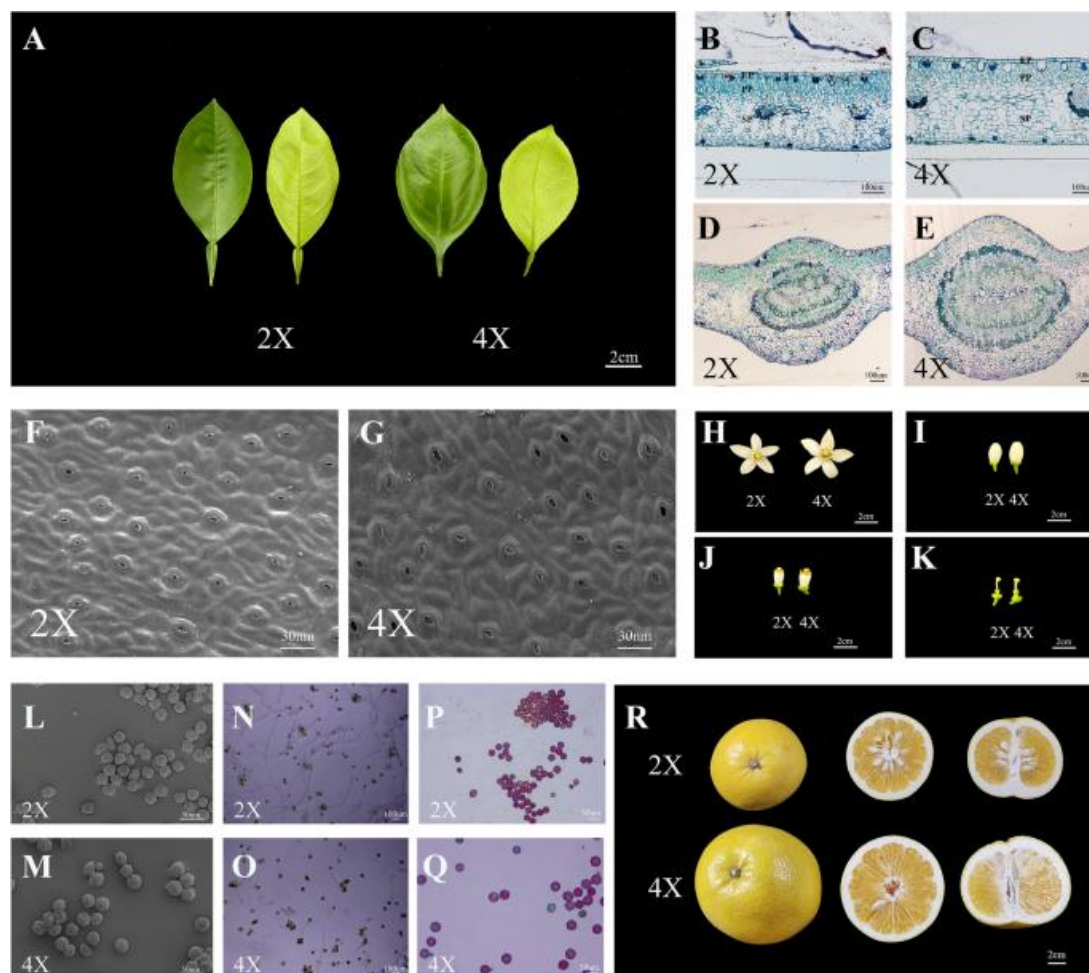


Figure 2 A Morphology of the leaves of the diploid (2X) and the tetraploid (4X) (Bar = 2 cm) (Adopted from Huang et al., 2025)
Image caption: The leaf was shown in both adaxial (upper) (left) and abaxial (lower) (right) surfaces. B-E Transversal sections of leaves (B-C) and midribs (D-E) of the diploid (2X) and the tetraploid (4X) (Bar = 100 μ m). F-G Scanning electron micrographs of stoma of the diploid (2X) and the tetraploid (4X) (Bar = 30 nm). EP: Epidermis, PP: Palisade parenchyma, SP: Spongy parenchyma. H-K Morphology of blooming flowers (H), floral buds (I), stamens (J), and pistils (K) of the diploid (2X) and the tetraploid (4X) (Bar = 2 cm). L, M Scanning electron micrographs of pollen grains of the diploid (2X) and the tetraploid (4X) (Bar = 50 nm). (N, O) The pollen germination of the diploid (2X) and the tetraploid (4X) (Bar = 100 μ m). P, Q Pollen staining activity of the diploid (2X) and the tetraploid (4X) (Bar = 50 μ m). R Morphological characteristics of fruits in the diploid (2X) and the tetraploid (4X) (Bar = 2 cm) (Adopted from Huang et al., 2025)

7.3 Results: yield outcomes, fruit quality improvements, and market acceptance

The results indicated that optimized fertilization and scientific irrigation could significantly increase the yield per plant and per unit area by 10% to 25% compared with conventional management (Huang et al., 2025). Dense planting can achieve early high yields in young orchards, but as the tree age increases, timely thinning is necessary; otherwise, it is prone to clogging, leading to a decrease in yield (Tan et al., 2012). Superior varieties such as natural tetraploid and preferred grafted lines have stronger growth vigor and higher yield potential (Du, 2001). Scientific pruning, reasonable fertilization and irrigation also make the fruit size more uniform, the fruit skin color brighter, the content of soluble solids higher and the flavor more stable (Tan et al., 2012). The fruit of the natural tetraploid is larger, the peel is thicker, and the contents of some metabolites such as flavonoids, terpenoids and amino acids are higher, with enhanced medicinal and processing values (Huang et al., 2025).

Under optimized management, the commercial fruit rate has increased, the fruit storage capacity has improved, and the incidence of pests and diseases has decreased. After the introduction of superior varieties and efficient management, both the appearance and internal quality of the fruits have improved, and the market acceptance has significantly increased. In some orchards, the commercial fruit rate exceeds 90%, and the economic benefits have significantly increased (Du, 2001; Tan et al., 2012). In addition, the development of the medicinal value of fruits has also expanded the industrial chain and increased the added value (Huang et al., 2025).

8 Challenges and Research Gaps

8.1 Lack of long-term comparative data across cultivation models

At present, research on different cultivation and management models of Changshan Huyou (such as organic, intensive, conventional, intelligent, etc.) is mostly short-term experiments or regional cases. Most studies only last for one quarter or 2 to 3 years, lacking systematic, long-term and multi-point comparative data. This leaves us with limited understanding of the sustained effects of management measures, interannual fluctuations, and their interactions with environmental factors such as climate and soil (Tan et al., 2012; Ren et al., 2020; Zhang et al., 2020; Li and Tao, 2023; Luo et al., 2023). For instance, some experiments have shown that optimizing dense planting, fertilization and water management can significantly increase yield and commercial traits. However, due to the short cycle, it is impossible to reflect the long-term cumulative effect and it is also difficult to assess the long-term changes in the orchard ecosystem.

8.2 Trade-offs between yield maximization and quality traits

In production, there is often a contradiction between “high yield” and “good quality”. For instance, intensive high-density planting and high nitrogen fertilizer input can increase the yield per unit area, but the fruits tend to be too large, the sugar-acid ratio decreases, the flavor becomes weak, and the risk of pests and diseases may also increase (Ren et al., 2020; Chen et al., 2023). In contrast, organic or ecological management can improve fruit quality and safety, but the increase in yield is limited and the management cost is higher. How to find the balance point between output and commercial traits under different modes is a difficult problem in current research and production. In addition, there are often complex interactions among varieties, environment and management measures, which makes the trade-off between yield and quality even more complicated (Zhang et al., 2020; Li and Tao, 2022; Li and Tao, 2023).

8.3 Insufficient region-specific optimization strategies

The ecological conditions in the main production areas of Changshan Huyou vary greatly, with different climates, soils and terrains. The responses of different regions to management models also differ significantly. However, most of the existing research focuses on a single region or unified management standards, lacking localized optimization plans for different ecological zones. For instance, there are significant differences in demands such as water and fertilizer management, pest and disease control, and fruit ripening regulation between the humid southern region and the subtropical northern region. A unified model is difficult to take into account the actual situation (Tan et al., 2012). In the context of frequent extreme climate events (such as high temperatures, heavy rain, and droughts), it is even more urgent to develop and promote adaptable regional management measures (Huang et al., 2020; Zhang et al., 2020; Yan et al., 2021; Li and Tao, 2023). At present, research on management optimization for different ecological zones, screening of adaptive varieties, and the synergy between management and varieties is still insufficient.

9 Future Perspectives

9.1 Application of smart agriculture and digital technologies in Huyou orchards

With the development of the Internet of Things, remote sensing, artificial intelligence and big data, smart agriculture is becoming an important method to increase the yield and quality of citrus fruits, including Changshan Huyou. Deep learning models can combine various types of data and perform well in aspects such as yield prediction, pest and disease monitoring, precise irrigation and fertilization. They can handle the complex relationships among the environment, plants and management, significantly improving prediction accuracy and management efficiency (Li et al., 2022a; Sun et al., 2022; Lu et al., 2024). Remote sensing and satellite data

combined with meteorological, soil and topographic information can achieve real-time monitoring of orchards, providing support for precise management and decision-making (Zhang et al., 2021; Li et al., 2022b; Ishaq et al., 2023). The prediction models based on machine learning have been verified in both large and small orchards, and can effectively improve the prediction accuracy and management scientificity (Guo et al., 2021; Li et al., 2022a; Liu et al., 2023; Sun et al., 2025). In the future, with the popularization of sensors, drones and automated equipment, the Changshan Huyou orchards will gradually achieve full-process digitalization and intelligence in planting, management and harvesting, promoting the industry to develop in the direction of high efficiency, greenness and sustainability.

9.2 Integration of breeding and management to improve both yield and quality

The yield and quality of Changshan Huyou are jointly influenced by multiple factors such as genetics, environment and management. The latest research indicates that the combination of molecular breeding and precise management is a key path to enhance the yield and quality of citrus fruits (Zhong, 2004; Huang et al., 2025). Through multi-environmental trials (METs), phenomics and genomic selection, high-yield, high-quality and stress-resistant varieties can be screened out. Combined with local climate and soil conditions, a reasonable match between varieties and management can be achieved (Guo et al., 2022; Li and Tao, 2022; Lee et al., 2023). Polyploid breeding, such as natural tetraploidization, can also enhance stress resistance, enrich secondary metabolites of fruits, and contribute to the development of diversified products such as seedless, medicinal and deep processing (Huang et al., 2025). Meanwhile, machine learning-based models can combine phenotypic, environmental and management data to provide decision support for breeding and cultivation, and promote the combination of variety innovation and efficient management (Zhong, 2004; Parmley et al., 2019; Yoosefzadeh-Najafabadi et al., 2021).

9.3 Scaling sustainable cultivation models for wider adoption and global competitiveness

Sustainable agriculture and large-scale management have been proven to significantly increase the yield, quality and ecological benefits of citrus crops (Tan et al., 2012; Yu et al., 2012; Yang et al., 2024). Crop rotation can increase soil fertility, reduce pests and diseases, increase the average yield by more than 20%, and adapt to various climatic and soil conditions (Zhao et al., 2020). Intercropping and diversified planting contribute to resource utilization and risk dispersion, and improve overall economic benefits and ecological stability (Yang et al., 2024). In the Changshan Huyou industry, regional suitability assessment and big data analysis can help achieve precise matching of varieties, management and environment, and promote the large-scale development of high-quality orchards (Yu et al., 2012). Meanwhile, promoting measures such as green prevention and control, water-saving irrigation and organic fertilizer substitution can also enhance the international competitiveness and brand influence of Changshan Huyou (Zhong, 2004; Tan et al., 2012).

Acknowledgments

The authors appreciate the modification suggestions from the anonymous peer reviewers on the manuscript of this study. The authors also thank the group members for helping to organize the research data.

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.

References

- Abisheva S., and Mussin N., 2023, Comparative study of traditional and modern cultivation practices on field crop yield, *International Journal of Advanced Academic Studies*, 5(5): 53-55.
<https://doi.org/10.33545/27068919.2023.v5.i5a.1129>
- Boschiero M., De Laurentiis V., Caldeira C., and Sala S., 2023, Comparison of organic and conventional cropping systems: a systematic review of life cycle assessment studies, *Environmental Impact Assessment Review*, 102: 107187.
<https://doi.org/10.1016/j.eiar.2023.107187>
- Chandra S.S.V., Hareendran S.A., and Albaaji G., 2024, Precision farming for sustainability: an agricultural intelligence model, *Comput. Electron. Agric.*, 226: 109386.
<https://doi.org/10.1016/j.compag.2024.109386>

- Chen Z., Li X., Liu T., Fu H., Yuan X., Cheng Q., Liao Q., Zhang Y., Li W., Sun Y., Yang Z., Ma J., and Li X., 2023, Strategies for fertilizer management to achieve higher yields and environmental and fertilizer benefits of rice production in China, *The Science of the Total Environment*, 904: 166325.
<https://doi.org/10.1016/j.scitotenv.2023.166325>
- Du H.L., 2001, Preliminary report on top grafting of 9 elite *Citrus changshan-huyou* Y.B.Chang, *sp. nov.*, *Journal of Zhejiang Forestry Science and Technology*, 2001: 28-30.
- Gao L., Zhang H., Yuan C., Zeng L., Xiang Z., Song J., Wang H., and Jiang J., 2022, *Citrus aurantium* 'Changshan-huyou' - an ethnopharmacological and phytochemical review, *Frontiers in Pharmacology*, 13: 983470.
<https://doi.org/10.3389/fphar.2022.983470>
- Guo S., Zhang Z., Zhang F., and Yang X., 2022, Optimizing cultivars and agricultural management practices can enhance soybean yield in Northeast China, *The Science of the Total Environment*, 857: 159456.
<https://doi.org/10.1016/j.scitotenv.2022.159456>
- Guo Y., Xiang H., Li Z., Ma F., and Du C., 2021, Prediction of rice yield in east China based on climate and agronomic traits data using artificial neural networks and partial least squares regression, *Agronomy*, 11(2): 282.
<https://doi.org/10.3390/agronomy11020282>
- Huang M., Wang J., Wang B., Liu D., Yu Q., He D., Wang N., and Pan X., 2020, Optimizing sowing window and cultivar choice can boost China's maize yield under 1.5°C and 2°C global warming, *Environmental Research Letters*, 15(2): 024015.
<https://doi.org/10.1088/1748-9326/ab66ca>
- Huang P., Xu T., Wang G., Zhang L., Yao Y., Zhang M., and Zhang C., 2025, Morphological and metabolic changes in Changshan Huyou (*Citrus changshan-huyou*) following natural tetraploidization, *BMC Plant Biology*, 25: 301.
<https://doi.org/10.1186/s12870-025-06293-4>
- Huang T., Döring T., Zhao X., Weiner J., Dang P., Zhang M., Zhang M., Siddique K., Schmid B., and Qin X., 2024, Cultivar mixtures increase crop yields and temporal yield stability globally, a meta-analysis, *Agronomy for Sustainable Development*, 44: 28.
<https://doi.org/10.1007/s13593-024-00964-6>
- Ishaq R., Zhou G., Tian C., Tan Y., Jing G., Jiang H., and Rehman O., 2023, A systematic review of radiative transfer models for crop yield prediction and crop traits retrieval, *Remote. Sens.*, 16(1): 121.
<https://doi.org/10.3390/rs16010121>
- Lee S., Lee H., Lee C., Ha S., Park H., Lee S., Kwon Y., Jeung J., and Mo Y., 2023, Multi-environment trials and stability analysis for yield-related traits of commercial rice cultivars, *Agriculture*, 13(2): 256.
<https://doi.org/10.3390/agriculture13020256>
- Li L., Wang B., Feng P., Liu D., He Q., Zhang Y., Wang Y., Li S., Lu X., Yue C., Li Y., He J., Feng H., Yang G., and Yu Q., 2022a, Developing machine learning models with multi-source environmental data to predict wheat yield in China, *Comput. Electron. Agric.*, 194: 106790.
<https://doi.org/10.1016/j.compag.2022.106790>
- Li Y., and Tao F., 2022, Interactions of genotype, environment and management on wheat traits and grain yield variations in different climate zones across China, *Agricultural Systems*, 203: 103521.
<https://doi.org/10.1016/j.agsy.2022.103521>
- Li Y., and Tao F., 2023, Changes in maize traits and yield under the cultivar, environment and management interactions across China's Maize Belt in the past two decades, *European Journal of Agronomy*, 151: 127008.
<https://doi.org/10.1016/j.eja.2023.127008>
- Li Z., Ding L., and Xu D., 2022b, Exploring the potential role of environmental and multi-source satellite data in crop yield prediction across Northeast China, *The Science of the Total Environment*, 815: 152880.
<https://doi.org/10.1016/j.scitotenv.2021.152880>
- Liu B., Liu Y., Huang G., Jiang X., Liang Y., Yang C., and Huang L., 2023, Comparison of yield prediction models and estimation of the relative importance of main agronomic traits affecting rice yield formation in saline-sodic paddy fields, *European Journal of Agronomy*, 148: 126870.
<https://doi.org/10.1016/j.eja.2023.126870>
- Lu J., Li J., Fu H., Tang X., Liu Z., Chen H., Sun Y., and Ning X., 2024, Deep learning for multi-source data-driven crop yield prediction in northeast China, *Agriculture*, 14(6): 794.
<https://doi.org/10.3390/agriculture14060794>
- Luo N., Meng Q., Feng P., Qu Z., Yu Y., Liu D., Müller C., and Wang P., 2023, China can be self-sufficient in maize production by 2030 with optimal crop management, *Nature Communications*, 14: 2637.
<https://doi.org/10.1038/s41467-023-38355-2>
- Martinez D., Gathorne-Hardy A., and Smith B., 2024, Impacts of polycultural cropping on crop yields and biodiversity: a systematic map protocol, *Ecological Solutions and Evidence*, 5(3): e12349.
<https://doi.org/10.1002/2688-8319.12349>
- Miao C., Wu Y., Wang L., Zhao S., Grierson D., Xu C., Chen W., and Chen K., 2024, Haplotype-resolved chromosome-level genome assembly of Huyou (*Citrus changshanensis*), *Scientific Data*, 11: 605.
<https://doi.org/10.1038/s41597-024-03437-3>

- Parnley K., Higgins R., Ganapathysubramanian B., Sarkar S., and Singh A., 2019, Machine learning approach for prescriptive plant breeding, *Scientific Reports*, 9: 17132.
<https://doi.org/10.1038/s41598-019-53451-4>
- Peng Y., Wang L., Jacinthe P., and Ren W., 2024, Global synthesis of cover crop impacts on main crop yield, *Field Crops Research*, 310: 109343.
<https://doi.org/10.1016/j.fcr.2024.109343>
- Ren H., Han K., Liu Y., Zhao Y., Zhang L., He Q., Li Z., Zhang J., Liu P., Wang H., Zhang J., and Zhao B., 2020, Improving smallholder farmers' maize yields and economic benefits under sustainable crop intensification in the North China Plain, *The Science of the Total Environment*, 763: 143035.
<https://doi.org/10.1016/j.scitotenv.2020.143035>
- Sun J., Tian P., Li Z., Wang X., Zhang H., Chen J., and Qian Y., 2025, Construction and optimization of integrated yield prediction model based on phenotypic characteristics of rice grown in small-scale plantations, *Agriculture*, 15(2): 181.
<https://doi.org/10.3390/agriculture15020181>
- Sun Z., Li Q., Jin S., Song Y., Xu S., Wang X., Cai J., Zhou Q., Ge Y., Zhang R., Zang J., and Jiang D., 2022, Simultaneous prediction of wheat yield and grain protein content using multitask deep learning from time-series proximal sensing, *Plant Phenomics*, 2022: 9757948.
<https://doi.org/10.34133/2022/9757948>
- Szeląg-Sikora A., Sikora J., Niemiec M., Gródek-Szostak Z., Kapusta-Duch J., Kuboń M., Komorowska M., and Karcz J., 2019, Impact of integrated and conventional plant production on selected soil parameters in carrot production, *Sustainability*, 11(20): 5612.
<https://doi.org/10.3390/su11205612>
- Tan B.T., Li M.J., Xu Y.X., and Zhang H.X., 2012, The introduction and cultivation technology of *Citrus changshan-huyou* and its adaptability analysis, *Hunan Forestry Science & Technology*, 39(2): 72-74.
- Yan H., Harrison M., Liu K., Wang B., Feng P., Fahad S., Meinke H., Yang R., Liu D., Archontoulis S., Huber I., Tian X., Man J., Zhang Y., and Zhou M., 2021, Crop traits enabling yield gains under more frequent extreme climatic events, *The Science of the Total Environment*, 808: 152170.
<https://doi.org/10.1016/j.scitotenv.2021.152170>
- Yang S., Zhao Y., Xu Y., Cui J., Li T., Hu Y., Qian X., Li Z., Sui P., and Chen Y., 2024, Yield performance response to field configuration of maize and soybean intercropping in China: a meta-analysis, *Field Crops Research*, 306: 109235.
<https://doi.org/10.1016/j.fcr.2023.109235>
- Yoosefzadeh-Najafabadi M., Tulpan D., and Eskandari M., 2021, Application of machine learning and genetic optimization algorithms for modeling and optimizing soybean yield using its component traits, *PLoS One*, 16(4): e0250665.
<https://doi.org/10.1371/journal.pone.0250665>
- Yu L.P., Li Z.Z., Jin Z.F., Li R.Z., and Huang J.F., 2012, Ecological adaptability of Huyou planting in Quzhou, Zhejiang Province of East China, *Chinese Journal of Ecology*, 31(11): 2762.
- Zhang J., Sun C., Yan Y., Chen Q., Luo F., Zhu X., Li X., and Chen K., 2012, Purification of naringin and neohesperidin from Huyou (*Citrus changshanensis*) fruit and their effects on glucose consumption in human HepG2 cells, *Food chemistry*, 135(3): 1471-1478.
<https://doi.org/10.1016/j.foodchem.2012.06.004>
- Zhang L., Zhang Z., Luo Y., Cao J., and Li Z., 2020, Optimizing genotype-environment-management interactions for maize farmers to adapt to climate change in different agro-ecological zones across China, *The Science of the Total Environment*, 728: 138614.
<https://doi.org/10.1016/j.scitotenv.2020.138614>
- Zhang L., Zhang Z., Luo Y., Cao J., Xie R., and Li S., 2021, Integrating satellite-derived climatic and vegetation indices to predict smallholder maize yield using deep learning, *Agricultural and Forest Meteorology*, 311: 108666.
<https://doi.org/10.1016/j.agrformet.2021.108666>
- Zhao J., Yang Y., Zhang K., Jeong J., Zeng Z., and Zang H., 2020, Does crop rotation yield more in China, a meta-analysis, *Field Crops Research*, 245: 107659.
<https://doi.org/10.1016/j.fcr.2019.107659>
- Zhong S.M., 2004, The status and tendency of research in *Citrus changshan-huyou*, *Economic Forest Researches*, 1: 64-67.

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Review Article

Open Access

Molecular Genetic Regulation of Stamen Development: Insights from the ABC Model and Anther Ontogeny in *Arabidopsis* and Other Angiosperms

Rimjhim Chandra ✉

Department of Botany, Government Degree College, Chamba, Himachal Pradesh, 176314, India

✉ Corresponding email: rimjhimchandra6@gmail.comPlant Gene and Trait, 2026, Vol.17, No.4 doi: [10.5376/pgt.2026.17.0017](https://doi.org/10.5376/pgt.2026.17.0017)

Received: 17 Apr., 2026

Accepted: 20 Jul., 2026

Published: 31 Jul., 2026

Copyright © 2026 Chandra, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Chandra R., 2026, Molecular genetic regulation of stamen development: insights from the ABC model and anther ontogeny in *Arabidopsis* and other angiosperms, Plant Gene and Trait, 17(4): 245-254 (doi: [10.5376/pgt.2026.17.0017](https://doi.org/10.5376/pgt.2026.17.0017))

Abstract Stamen development is a critical process governing male fertility in flowering plants and is tightly regulated by genetic and hormonal networks. The ABC model of floral organ identity, extended to include D and E functions, explains stamen specification through the combined activity of B-, C-, and E-class MADS-box genes such as *APETALA3*, *PISTILLATA*, and *AGAMOUS*. In *Arabidopsis thaliana*, anther development proceeds through fourteen stages involving coordinated cell division, differentiation, and tissue organization. Early developmental events are controlled by receptor-like kinases including CIKs, BAM1/2, and RPK2, which regulate archesporial cell fate and parietal layer formation. Additional regulators such as SPL/NZZ, EMS1 – TPD1 signaling, and MAP kinases contribute to microsporogenesis and tapetum function. Hormonal pathways involving jasmonates, gibberellins, and auxins further coordinate pollen maturation and anther dehiscence. Comparative studies in other angiosperms reveal both conserved and species-specific regulatory mechanisms.

Keywords Stamen development; ABC model; MADS-box genes; *Arabidopsis thaliana*; Anther development; Microsporogenesis; Tapetum; Hormonal regulation

1 Introduction

Flowering plants (angiosperms) possess highly specialized reproductive structures, with the flower representing one of the most complex organs in plant development. A typical hermaphroditic flower is organized into concentric whorls consisting of sepals, petals, stamens, and carpels, each arising from a determinate floral meristem. Among these, the stamen constitutes the male reproductive organ and plays a central role in pollen production and successful fertilization. Structurally, a stamen comprises a filament that supports the anther, where pollen grains are formed within specialized compartments known as microsporangia. Proper development of stamens is therefore essential for plant fertility and reproductive success.

The genetic basis of floral organ identity has been extensively explained by the ABC model, later expanded into the ABCDE model, which describes how combinations of MADS-box transcription factors specify distinct floral organs (Schwarz-Sommer et al., 1990). In this framework, stamens are specified by the combined action of B-, C-, and E-class genes, including *APETALA3* (*AP3*), *PISTILLATA* (*PI*), and *AGAMOUS* (*AG*) (Bowman et al., 1991; Pelaz et al., 2000; Ng and Yanofsky, 2001; Becker and Theissen, 2003). These genes regulate downstream targets that control organ identity as well as the initiation and differentiation of reproductive tissues (Shore and Sharrocks, 1995; Riechmann and Meyerowitz, 1997). Mutations in these regulatory genes often result in homeotic transformations, highlighting their fundamental role in floral patterning (Bowman et al., 1989; 1991; Coen and Meyerowitz, 1991; Pelaz et al., 2000; Pinyopich et al., 2003; Alvarez-Buylla et al., 2010).

The model plant *Arabidopsis thaliana* has provided critical insights into the molecular and cellular mechanisms underlying stamen and anther development (Ma, 2005; Bowman, 2012). Anther ontogeny in *Arabidopsis* is divided into fourteen distinct stages characterized by precise patterns of cell division, differentiation, and tissue organization (Owen and Makaroff, 1995; Sanders et al., 1999). Early developmental events involve the specification of archesporial cells and their differentiation into sporogenous and somatic cell lineages. This process is tightly regulated by receptor-like kinases such as CLAVATA3 INSENSITIVE RECEPTOR KINASEs (CIKs), BARELY

ANY MERISTEM (BAM1/2), and RECEPTOR-LIKE PROTEIN KINASE2 (RPK2), which coordinate cell fate determination and tissue patterning (DeYoung et al., 2006; Hord et al., 2006; Mizuno et al., 2007; Cui et al., 2018; Hu et al., 2018).

Further progression of anther development involves the formation of distinct somatic layers, including the epidermis, endothecium, middle layer, and tapetum, surrounding the microspore mother cells. Key regulators such as SPOROCTELESS/NOZZLE (SPL/NZZ) play a pivotal role in initiating sporogenesis (Schiefthaler et al., 1999; Yang et al., 1999; Ito et al., 2004), while signaling pathways involving EMS1–TPD1 and MAP kinases (MPK3 and MPK6) govern tapetum differentiation and function (Canales et al., 2002; Zhao et al., 2002; Yang et al., 2003; Jia et al., 2008; Zhao et al., 2017). The tapetum, in particular, is crucial for providing nutrients and materials required for pollen wall formation, and its proper development is essential for viable pollen production (Kapoor et al., 2002; Zheng et al., 2003; Zhang et al., 2006; Zhang and Yang, 2014).

In addition to genetic regulation, hormonal signaling pathways significantly influence stamen development. Phytohormones such as jasmonic acid (Feys et al., 1994; McConn and Browse, 1996; Sanders et al., 2000; Stintzi and Browse, 2000; Ishiguro et al., 2001; Ito et al., 2007), gibberellins (Cheng et al., 2004; Fleet and Sun, 2005; Hou et al., 2008; Iuchi et al., 2007), and auxins (Nagpal et al., 2005; Cecchetti et al., 2008) coordinate critical processes including filament elongation, pollen maturation, and anther dehiscence. The interplay between these hormonal pathways ensures the temporal synchronization of reproductive events necessary for successful pollination.

Comparative studies in other angiosperms, including genera such as *Salvia* and *Gerbera* (Kramer and Irish, 1999; Kotilainen et al., 2000; Kramer and Irish, 2000; Wetters, 2020), have revealed both conserved and divergent roles of floral regulatory genes, particularly MADS-box genes, in stamen development. These studies highlight the evolutionary conservation of core regulatory networks alongside species-specific adaptations that contribute to floral diversity.

Overall, stamen development is governed by a complex interplay of genetic, molecular, and hormonal factors. Understanding these regulatory networks not only provides insights into fundamental plant developmental biology but also has important implications for crop improvement, hybrid seed production, and fertility regulation.

Recent advances in plant molecular biology have substantially improved our understanding of the regulatory mechanisms governing stamen development. High-throughput multi-omics approaches, including transcriptomics, proteomics, and epigenomics, have enabled comprehensive identification of genes, proteins, and regulatory pathways involved in anther development and pollen formation. In particular, single-cell RNA sequencing (scRNA-seq) has provided unprecedented resolution of cell-type-specific gene expression during anther ontogeny, revealing dynamic regulatory networks underlying tapetum differentiation and microsporogenesis. Furthermore, CRISPR/Cas-mediated genome editing has emerged as a powerful tool for functional validation of candidate genes such as SPL/NZZ, EMS1, BAM1/BAM2, RPK2, and MADS-box transcription factors, facilitating precise investigation of their roles in reproductive development. Integration of these advanced genomic technologies with classical genetic studies is expected to accelerate the discovery of novel regulatory mechanisms and support future applications in crop improvement, hybrid breeding, and fertility regulation.

2 Results

2.1 Stamen specification through ABC model genes

Previous studies have demonstrated that floral organ identity is governed by the combinatorial activity of B-, C-, and E-class genes. The coordinated expression of APETALA3 (AP3), PISTILLATA (PI), and AGAMOUS (AG) is essential for proper stamen specification. Genetic studies have shown that disruption of these genes results in the loss or homeotic transformation of stamens, highlighting their critical role in reproductive organ identity and development (Figure 1) (Bowman et al., 1989; 1991; Coen and Meyerowitz, 1991; Pelaz et al., 2000).

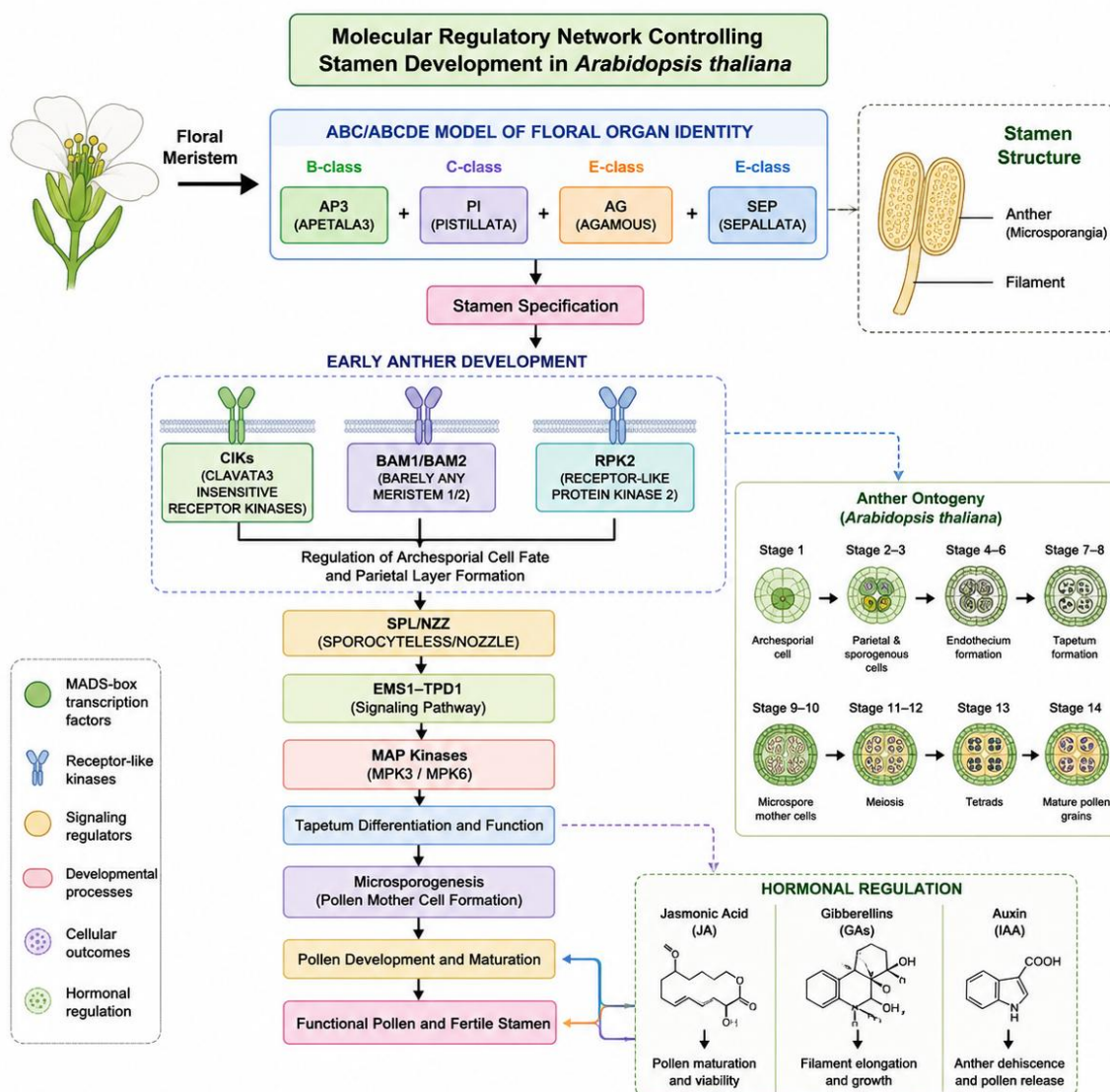


Figure 1 Molecular regulatory network controlling stamen development in *Arabidopsis thaliana*

Image caption: Floral organ identity is established through the coordinated activities of the ABC/ABCDE floral homeotic genes, including APETALA3 (AP3), PISTILLATA (PI), AGAMOUS (AG), and SEPALLATA (SEP). Early anther development is regulated by receptor-like kinases (CIKs, BAM1/BAM2, and RPK2) that control archesporial cell specification and anther patterning. Subsequent activation of the SPL/NZZ, EMS1-TPD1, and MAPK (MPK3/MPK6) signaling pathways promotes tapetum differentiation and microsporogenesis. Plant hormones, including jasmonic acid (JA), gibberellins (GAs), and auxin (IAA), regulate pollen maturation, filament elongation, and anther dehiscence, ultimately leading to the formation of functional pollen and male fertility. The diagram summarizes the major molecular and hormonal regulatory pathways described in this review

2.2 Stages of anther development in *Arabidopsis thaliana*

Previous developmental studies have shown that anther development in *Arabidopsis thaliana* proceeds through fourteen distinct stages characterized by sequential cellular and morphological changes. Early stages (1~5) involve the formation of anther primordia and differentiation of archesporial cells into primary sporogenous and parietal cells. Intermediate stages (6~8) are characterized by meiosis of microspore mother cells and tetrad formation, followed by release of microspores. Late stages (9~14) include pollen maturation and anther dehiscence, completing the reproductive process (Owen and Makaroff, 1995; Sanders et al., 1999; Ma, 2005).

2.3 Role of receptor-like kinases in early anther development

Accumulated evidence indicates that CLAVATA3 INSENSITIVE RECEPTOR KINASEs (CIKs), BARELY ANY MERISTEM (BAM1/BAM2), and RECEPTOR-LIKE PROTEIN KINASE2 (RPK2) play essential roles in early

anther cell fate determination. Previous studies have reported that mutations in these genes result in defective archesporial cell division and improper specification of parietal layers. Higher-order mutants lacking CIKs and RPK2 exhibit severe developmental defects, including the absence of somatic cell layers and overproduction of sporogenous cells, suggesting that these kinases function within a common signaling pathway (Albrecht et al., 2005; Colcombet et al., 2005; Hord et al., 2006; Mizuno et al., 2007; Cui et al., 2018; Hu et al., 2018).

2.4 Regulation of sporogenesis and tapetum development

Previous studies have demonstrated that SPOROCTELESS/NOZZLE (SPL/NZZ) is indispensable for the initiation of sporogenesis (Yang et al., 1999; Schiefthaler et al., 1999; Ito et al., 2004). Loss-of-function mutants fail to produce microsporogenous cells and tapetal tissues. In addition, the EMS1–TPD1 signaling pathway together with MAP kinases (MPK3/MPK6) plays a crucial role in tapetum differentiation and function (Canales et al., 2002; Zhao et al., 2002; Yang et al., 2003; Jia et al., 2008; Zhao et al., 2017). Disruption of these pathways results in abnormal tapetal development and impaired pollen formation.

2.5 Genetic control of anther morphogenesis

Previous studies have demonstrated that JAGGED (JAG) and NUBBIN (NUB) regulate the growth and structural organization of microsporangia. Mutant analyses indicate that these genes primarily promote tissue growth rather than floral organ identity specification.

2.6 Hormonal regulation of stamen development

Several studies have shown that jasmonic acid, gibberellins, and auxins play crucial roles in coordinating the later stages of stamen development. Jasmonic acid is required for pollen maturation and anther dehiscence, whereas gibberellins promote filament elongation. Auxin regulates the timing of pollen release and prevents premature anther dehiscence (Yang et al., 2007). Mutants deficient in these hormonal pathways frequently exhibit male sterility (Mandaokar et al., 2006) or delayed reproductive development (Feys et al., 1994; Ishiguro et al., 2001; Cheng et al., 2004; Cecchetti et al., 2008).

2.7 Comparative insights from other angiosperms

Comparative studies across angiosperms have demonstrated conserved expression patterns of B- and C-class MADS-box genes in stamen tissues. However, species-specific differences in gene expression dynamics and regulatory mechanisms have also been reported. In *Gerbera*, the GRCD1 gene plays a critical role in stamen identity, and its downregulation results in the homeotic transformation of stamens into petal-like structures. These findings highlight both the evolutionary conservation and diversification of floral developmental regulatory networks.

2.8 Integration of regulatory networks

Collectively, previous studies indicate that stamen development is regulated by an integrated network of genetic regulators, receptor-mediated signaling pathways, and phytohormonal cues. These components interact in a coordinated manner to regulate cell division, tissue differentiation, tapetum development, microsporogenesis, pollen maturation, and anther dehiscence, thereby ensuring successful male reproductive development in flowering plants (Figure 2).

3 Discussion

Stamen development represents a highly coordinated developmental program integrating genetic, molecular, and hormonal controls. The present synthesis highlights that the ABC (ABCDE) model remains a central framework for understanding floral organ identity, with B-, C-, and E-class MADS-box genes (*APETALA3*, *PISTILLATA*, and *AGAMOUS*) functioning as key determinants of stamen specification (Coen and Meyerowitz, 1991; Pelaz et al., 2000; Alvarez-Buylla et al., 2010). The conservation of this regulatory module across angiosperms underscores its evolutionary significance, while variations observed in other species indicate adaptive diversification of floral structures.

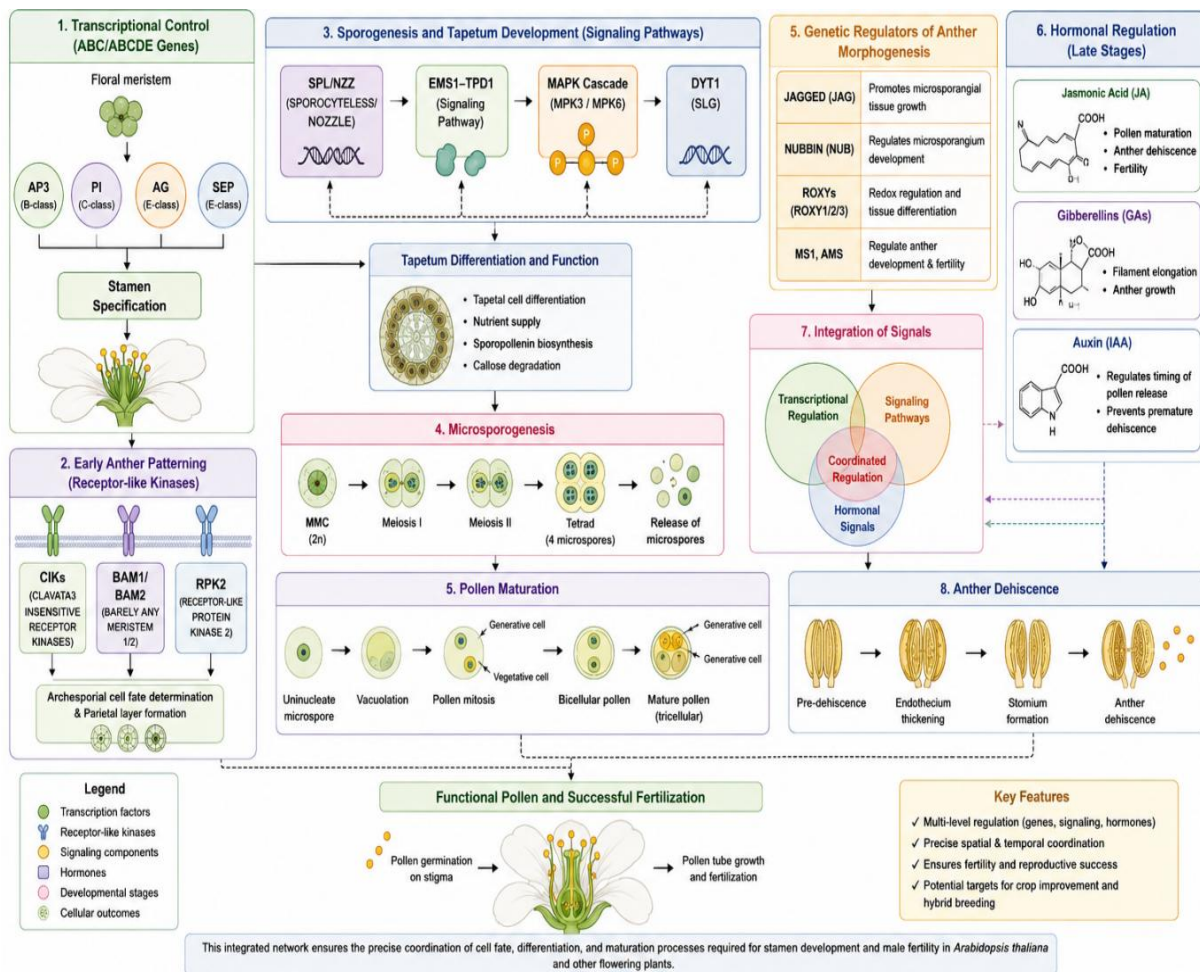


Figure 2 Integrated regulatory network governing anther development, pollen maturation, and male fertility in flowering plants

Image caption: The figure illustrates the coordinated regulation of male reproductive development by transcription factors, receptor-like kinases, signaling pathways, and phytohormones. Early anther patterning is regulated by *CIKs*, *BAM1/BAM2*, and *RPK2*, followed by activation of *SPL/NZZ*, *EMS1-TPD1*, MAP kinase signaling, and additional regulators controlling tapetum differentiation and microsporogenesis. Hormonal pathways involving jasmonic acid, gibberellins, and auxin regulate pollen maturation, filament elongation, and anther dehiscence. The integration of these molecular networks ensures successful pollen development, fertilization, and male fertility, providing potential targets for functional genomics, hybrid breeding, genome editing, and crop improvement

The staged progression of anther development in *Arabidopsis thaliana* provides a valuable model for dissecting the cellular and molecular mechanisms underlying male reproductive development. Early events, particularly archisporial cell specification and parietal layer formation, are tightly regulated by receptor-like kinases such as *CIKs*, *BAM1/2*, and *RPK2* (Hord et al., 2006; Mizuno et al., 2007; Cui et al., 2018). The phenotypic similarities observed in higher-order mutants suggest that these kinases operate within interconnected signaling pathways to maintain stem cell homeostasis and ensure proper tissue differentiation (Albrecht et al., 2005; Hu et al., 2018). Their interaction and phosphorylation dynamics further emphasize the importance of signal transduction in early anther patterning.

Transcriptional regulators such as *SPOROCTELESS/NOZZLE* (*SPL/NZZ*) play a pivotal role in initiating sporogenesis, acting downstream of floral identity genes (Yang et al., 1999; Ito et al., 2004). In parallel, the *EMS1-TPD1* signaling module and MAP kinase pathways (*MPK3/MPK6*) are essential for tapetum differentiation and function (Jia et al., 2008; Zhao et al., 2017). The tapetum emerges as a critical tissue, not only supporting pollen development but also influencing fertility outcomes, as evidenced by numerous mutants exhibiting male sterility due to tapetal defects (Zhang et al., 2006; Zhang and Yang, 2014). These findings reinforce the concept that successful microsporogenesis depends on precise coordination between sporogenous and somatic tissues.

Genes such as JAGGED (JAG) and NUBBIN (NUB) contribute to anther morphogenesis by promoting microsporangial growth rather than identity specification, indicating the existence of parallel regulatory pathways governing structural development.

Hormonal regulation adds another layer of complexity to stamen development. Jasmonic acid, gibberellins, and auxins act in a coordinated manner to regulate filament elongation, pollen maturation, and anther dehiscence. The crosstalk between these hormones ensures temporal synchronization of developmental events, which is crucial for successful fertilization. Mutant analyses further confirm that disruption in hormonal balance leads to defects in fertility, emphasizing their integrative role (Ishiguro et al., 2001; Cheng et al., 2004; Cecchetti et al., 2008).

These comparative studies indicate that the core molecular mechanisms governing stamen development have been largely conserved during angiosperm evolution. Nevertheless, lineage-specific modifications in gene expression patterns, regulatory interactions, and duplication of MADS-box genes have contributed to the remarkable diversity of floral morphology and reproductive strategies observed among flowering plants. Future comparative genomic and evolutionary developmental (evo-devo) studies will further clarify the origin and diversification of these regulatory networks.

Beyond its fundamental biological significance, understanding the molecular regulation of stamen development has important applications in modern crop improvement and sustainable agriculture. Genes regulating tapetum differentiation and anther development, including *SPL/NZZ*, *EMS1-TPD1*, *BAM1/BAM2*, and *DYT1*, have been widely investigated for the development of stable genetic male-sterility systems used in hybrid seed production (Mariani et al., 1990; Mariani et al., 1991; Denis et al., 1993). Recent advances in CRISPR/Cas-mediated genome editing have further enabled precise manipulation of floral regulatory genes for fertility control, functional validation, and de novo crop domestication. In addition, hormone-regulated pathways involving jasmonic acid, auxin, and gibberellins provide promising targets for improving pollen fertility and reproductive performance under abiotic stresses such as heat and drought. Comparative studies across diverse crop species are expected to accelerate molecular breeding strategies for the development of climate-resilient cultivars with enhanced reproductive efficiency. Furthermore, the integration of multi-omics technologies, including transcriptomics, proteomics, metabolomics, and single-cell sequencing, will facilitate the identification of novel regulatory genes and signaling networks controlling male reproductive development. These advances will not only improve our understanding of the molecular basis of stamen development but also support the development of next-generation crop varieties with enhanced yield, reproductive stability, and resilience under changing climatic conditions. Moreover, integrating artificial intelligence-assisted data analysis with functional genomics and genome editing is expected to accelerate the discovery of novel regulatory genes and improve predictive breeding strategies. Such interdisciplinary approaches will enhance the translation of fundamental knowledge into practical applications for sustainable agriculture and global food security.

4 Conclusion

Stamen development is a complex and tightly regulated process essential for plant reproduction, controlled by the coordinated action of floral identity genes, signaling pathways, and hormonal networks. The ABCDE model provides a robust framework for understanding stamen specification, while studies in *Arabidopsis thaliana* and other species have revealed intricate mechanisms governing anther development, microsporogenesis, and pollen maturation. Key regulators, including receptor-like kinases, transcription factors, and phytohormones, function in an integrated manner to ensure proper tissue differentiation and reproductive success. Advances in molecular genetics and genomics continue to deepen our understanding of these processes, offering potential applications in crop improvement, hybrid seed production, and fertility regulation.

Future research integrating multi-omics approaches, including transcriptomics, proteomics, metabolomics, and single-cell sequencing, together with CRISPR/Cas-mediated genome editing, is expected to further elucidate the molecular mechanisms underlying stamen development. These emerging technologies will facilitate the identification of novel regulatory genes and signaling networks, enabling precision breeding strategies for enhanced pollen fertility, hybrid seed production, and climate-resilient crop development. Continued integration of molecular

genetics, functional genomics, and comparative evolutionary studies will strengthen our understanding of male reproductive development and support sustainable agricultural production under changing environmental conditions.

5 Materials and Methods

5.1 Literature survey and data sources

The present study is based on a comprehensive review of published literature related to stamen and anther development in angiosperms. Peer-reviewed research articles, review papers, and experimental studies were collected from standard scientific databases, including Google Scholar, PubMed, and Web of Science. Emphasis was placed on studies involving *Arabidopsis thaliana* as a model system, along with comparative data from other plant species such as *Salvia* and *Gerbera*.

5.2 Selection criteria

Relevant studies were selected based on their focus on:

- Floral organ identity and the ABC/ABCDE model
- Genetic regulation of stamen development
- Anther ontogeny and cellular differentiation
- Role of receptor-like kinases and transcription factors
- Hormonal regulation of reproductive development

Only studies providing clear experimental evidence on gene function, signaling pathways, and developmental processes were included.

5.3 Data extraction and organization

Information from selected studies was systematically extracted and categorized into key thematic areas, including:

- Floral organ identity genes (A, B, C, D, E classes)
- Stages of anther development
- Molecular regulators (e.g., SPL/NZZ, EMS1, BAM1/2, RPK2, CIKs)
- Signaling pathways (MAP kinase pathways, receptor kinase signaling)
- Hormonal regulation (jasmonic acid, gibberellins, auxins)

The extracted data were organized to establish a logical sequence from early stamen specification to late-stage pollen development.

5.4 Comparative analysis

Comparative evaluation was performed across different plant species to identify conserved and divergent mechanisms of stamen development. Gene expression patterns and functional studies in *Arabidopsis*, *Salvia*, and *Gerbera* were analyzed to highlight evolutionary conservation and species-specific variations.

5.5 Synthesis of information

The collected data were critically analyzed and integrated to construct a unified framework describing the molecular and genetic regulation of stamen development. Special attention was given to linking classical genetic models (ABC model) with recent findings in signaling pathways and genomics.

5.6 Limitations

As this study is based on previously published data, no new experimental work was conducted. The conclusions are therefore dependent on the accuracy and scope of the cited literature.

Author's Contributions

RC conceived the review topic, designed the structure of the manuscript, conducted the literature review, performed literature collection and critical analysis, synthesized the published findings, prepared the figures and tables, and wrote, revised, and approved the final version of the manuscript.

Acknowledgments

The author declares that no specific funding was received for this work. The author thanks all researchers whose published work contributed to this review. The author also acknowledges the valuable comments and suggestions provided by the reviewers and the editorial team, which greatly improved the quality and clarity of this manuscript.

Conflict of Interest Disclosure

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

References

- Albrecht C., Russinova E., Hecht V., Baaijens E., and de Vries S., 2005, The *Arabidopsis thaliana* SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASES1 and 2 control male sporogenesis, *The Plant Cell*, 17(12): 3337-3349.
<https://doi.org/10.1105/tpc.105.036814>
- Alvarez-Buylla E.R., Benítez M., Corvera-Poiré A., Chaos Cador Á., de Folter S., Gamboa de Buen A., Garay-Arroyo A., García-Ponce B., Jaimes-Miranda F., Pérez-Ruiz R.V., Piñeyro-Nelson A., and Sánchez-Corrales Y.E., 2010, Flower development, *The Arabidopsis Book*, 8: e0127.
<https://doi.org/10.1199/tab.0127>
- Becker A., and Theissen G., 2003, The major clades of MADS-box genes and their role in the development and evolution of flowering plants, *Molecular Phylogenetics and Evolution*, 29(3): 464-489.
[https://doi.org/10.1016/S1055-7903\(03\)00207-0](https://doi.org/10.1016/S1055-7903(03)00207-0)
- Bowman J., ed., 2012, *Arabidopsis: an atlas of morphology and development*, Springer, New York, USA, pp.1-418.
- Bowman J.L., Smyth D.R., and Meyerowitz E.M., 1989, Genes directing flower development in *Arabidopsis*, *The Plant Cell*, 1(1): 37-52.
<https://doi.org/10.1105/tpc.1.1.37>
- Bowman J.L., Smyth D.R., and Meyerowitz E.M., 1991, Genetic interactions among floral homeotic genes of *Arabidopsis*, *Development*, 112(1): 1-20.
<https://doi.org/10.1242/dev.112.1.1>
- Canales C., Bhatt A.M., Scott R., and Dickinson H., 2002, EXS, a putative LRR receptor kinase, regulates male germline cell number and tapetal identity and promotes seed development in *Arabidopsis*, *Current Biology*, 12(20): 1718-1727.
[https://doi.org/10.1016/S0960-9822\(02\)01151-X](https://doi.org/10.1016/S0960-9822(02)01151-X)
- Cecchetti V., Altamura M.M., Falasca G., Costantino P., and Cardarelli M., 2008, Auxin regulates *Arabidopsis* anther dehiscence, pollen maturation, and filament elongation, *The Plant Cell*, 20(7): 1760-1774.
<https://doi.org/10.1105/tpc.107.057570>
- Cheng H., Qin L., Lee S., Fu X., Richards D.E., Cao D., Luo D., Harberd N.P., and Peng J., 2004, Gibberellin regulates *Arabidopsis* floral development via suppression of DELLA protein function, *Development*, 131(5): 1055-1064.
<https://doi.org/10.1242/dev.00992>
- Coen E.S., and Meyerowitz E.M., 1991, The war of the whorls: genetic interactions controlling flower development, *Nature*, 353(6339): 31-37.
<https://doi.org/10.1038/353031a0>
- Colcombet J., Boisson-Dernier A., Ros-Palau R., Vera C.E., and Schroeder J.I., 2005, *Arabidopsis* somatic embryogenesis receptor kinases1 and 2 are essential for tapetum development and microspore maturation, *The Plant Cell*, 17(12): 3350-3361.
<https://doi.org/10.1105/tpc.105.036731>
- Cui Y., Hu C., Zhu Y., Cheng K., Li X., Wei Z., Xue L., Lin F., Shi H., Yi J., Hou S., He K., Li J., and Gou X., 2018, CIK receptor kinases determine cell fate specification during early anther development in *Arabidopsis*, *The Plant Cell*, 30(10): 2383-2401.
<https://doi.org/10.1105/tpc.17.00586>
- Denis M., Delourme R., Gouret J.P., Mariani C., and Renard M., 1993, Expression of engineered nuclear male sterility in *Brassica napus*: genetics, morphology, cytology, and sensitivity to temperature, *Plant Physiology*, 101(4): 1295-1304.
<https://doi.org/10.1104/pp.101.4.1295>
- DeYoung B.J., Bickle K.L., Schrage K.J., Muskett P., Patel K., and Clark S.E., 2006, The CLAVATA1-related BAM1, BAM2 and BAM3 receptor kinase-like proteins are required for meristem function in *Arabidopsis*, *The Plant Journal*, 45(1): 1-16.
<https://doi.org/10.1111/j.1365-3113X.2005.02592.x>
- Feys B.J., Benedetti C.E., Penfold C.N., and Turner J.G., 1994, *Arabidopsis* mutants selected for resistance to the phytotoxin coronatine are male sterile, insensitive to methyl jasmonate, and resistant to a bacterial pathogen, *The Plant Cell*, 6(5): 751-759.
<https://doi.org/10.2307/3869877>
- Fleet C.M., and Sun T.P., 2005, A DELLAcate balance: the role of gibberellin in plant morphogenesis, *Current Opinion in Plant Biology*, 8(1): 77-85.
<https://doi.org/10.1016/j.pbi.2004.11.015>

- Hord C.L., Chen C., DeYoung B.J., Clark S.E., and Ma H., 2006, The BAM1/BAM2 receptor-like kinases are important regulators of *Arabidopsis* early anther development, *The Plant Cell*, 18(7): 1667-1680.
<https://doi.org/10.1105/tpc.105.036871>
- Hou X., Hu W.W., Shen L., Lee L.Y.C., Tao Z., Han J.H., and Yu H., 2008, Global identification of DELLA target genes during *Arabidopsis* flower development, *Plant Physiology*, 147(3): 1126-1142.
<https://doi.org/10.1104/pp.108.121301>
- Hu C., Zhu Y., Cui Y., Cheng K., Liang W., Wei Z., Zhu M., Yin H., Zeng L., Xiao Y., Lv M., Yi J., Hou S., He K., Li J., and Gou X., 2018, A group of receptor kinases are essential for CLAVATA signalling to maintain stem cell homeostasis, *Nature Plants*, 4(4): 205-211.
<https://doi.org/10.1038/s41477-018-0123-z>
- Ishiguro S., Kawai-Oda A., Ueda J., Nishida I., and Okada K., 2001, The DEFECTIVE IN ANTHR DEHISCENCE1 gene encodes a novel phospholipase A1 catalyzing the initial step of jasmonic acid biosynthesis, which synchronizes pollen maturation, anther dehiscence, and flower opening in *Arabidopsis*, *The Plant Cell*, 13(10): 2191-2209.
<https://doi.org/10.1105/tpc.010192>
- Ito T., Ng K.H., Lim T.S., Yu H., and Meyerowitz E.M., 2007, The homeotic protein AGAMOUS controls late stamen development by regulating a jasmonate biosynthetic gene in *Arabidopsis*, *The Plant Cell*, 19(11): 3516-3529.
<https://doi.org/10.1105/tpc.107.055467>
- Ito T., Wellmer F., Yu H., Das P., Ito N., Alves-Ferreira M., Riechmann J.L., and Meyerowitz E.M., 2004, The homeotic protein AGAMOUS controls microsporogenesis by regulation of SPOROCTELESS, *Nature*, 430(6997): 356-360.
<https://doi.org/10.1038/nature02733>
- Iuchi S., Suzuki H., Kim Y.C., Iuchi A., Kuromori T., Ueguchi-Tanaka M., Asami T., Yamaguchi I., Matsuoka M., Kobayashi M., and Nakajima M., 2007, Multiple loss-of-function of *Arabidopsis* gibberellin receptor AtGID1s completely shuts down a gibberellin signal, *The Plant Journal*, 50(6): 958-966.
<https://doi.org/10.1111/j.1365-313X.2007.03098.x>
- Jia G., Liu X., Owen H.A., and Zhao D., 2008, Signaling of cell fate determination by the TPD1 small protein and EMS1 receptor kinase, *Proceedings of the National Academy of Sciences*, 105(6): 2220-2225.
<https://doi.org/10.1073/pnas.0708795105>
- Kapoor S., Kobayashi A., and Takatsuji H., 2002, Silencing of the tapetum-specific zinc finger gene TAZ1 causes premature degeneration of tapetum and pollen abortion in petunia, *The Plant Cell*, 14(10): 2353-2367.
<https://doi.org/10.1105/tpc.003061>
- Kotilainen M., Elomaa P., Uimari A., Albert V.A., Yu D., and Teeri T.H., 2000, GRCD1, an AGL2-like MADS box gene, participates in the C function during stamen development in *Gerbera hybrida*, *The Plant Cell*, 12(10): 1893-1902.
<https://doi.org/10.1105/tpc.12.10.1893>
- Kramer E.M., and Irish V.F., 1999, Evolution of genetic mechanisms controlling petal development, *Nature*, 399(6732): 144-148.
<https://doi.org/10.1038/20172>
- Kramer E.M., and Irish V.F., 2000, Evolution of the petal and stamen developmental programs: evidence from comparative studies of the lower eudicots and basal angiosperms, *International Journal of Plant Sciences*, 161(S6): S29-S40.
<https://doi.org/10.1086/317576>
- Ma H., 2005, Molecular genetic analyses of microsporogenesis and microgametogenesis in flowering plants, *Annual Review of Plant Biology*, 56(1): 393-434.
<https://doi.org/10.1146/annurev.arplant.55.031903.141717>
- Mandaokar A., Thines B., Shin B., Lange B.M., Choi G., Koo Y.J., Yoo Y.J., Choi Y.D., and Browse J., 2006, Transcriptional regulators of stamen development in *Arabidopsis* identified by transcriptional profiling, *The Plant Journal*, 46(6): 984-1008.
<https://doi.org/10.1111/j.1365-313X.2006.02756.x>
- Mariani C., Beuckeleer M.D., Truettner J., Leemans J., and Goldberg R.B., 1990, Induction of male sterility in plants by a chimaeric ribonuclease gene, *Nature*, 347(6295): 737-741.
<https://doi.org/10.1038/347737a0>
- Mariani C., Goldberg R.B., and Leemans J., 1991, Engineered male sterility in plants, *Symposia of the Society for Experimental Biology*, 45: 271-279.
- McConn M., and Browse J., 1996, The critical requirement for linolenic acid is pollen development, not photosynthesis, in an *Arabidopsis* mutant, *The Plant Cell*, 8(3): 403-416.
<https://doi.org/10.2307/3870321>
- Mizuno S., Osakabe Y., Maruyama K., Ito T., Osakabe K., Sato T., Shinozaki K., and Yamaguchi-Shinozaki K., 2007, Receptor-like protein kinase 2 (RPK2) is a novel factor controlling anther development in *Arabidopsis thaliana*, *The Plant Journal*, 50(5): 751-766.
<https://doi.org/10.1111/j.1365-313X.2007.03083.x>
- Nagpal P., Ellis C.M., Weber H., Ploense S.E., Barkawi L.S., Guilfoyle T.J., Hagen G., Alonso J.M., Cohen J.D., Farmer E.E., Ecker J.R., and Reed J.W., 2005, Auxin response factors ARF6 and ARF8 promote jasmonic acid production and flower maturation, *Development*, 132(18): 4107-4118.
<https://doi.org/10.1242/dev.01955>
- Ng M., and Yanofsky M.F., 2001, Function and evolution of the plant MADS-box gene family, *Nature Reviews Genetics*, 2(3): 186-195.
<https://doi.org/10.1038/35056041>
- Owen H.A., and Makaroff C.A., 1995, Ultrastructure of microsporogenesis and microgametogenesis in *Arabidopsis thaliana* (L.) Heynh. ecotype *Wassilewskija* (*Brassicaceae*), *Protoplasma*, 185(1): 7-21.
<https://doi.org/10.1007/BF01272749>

- Pelaz S., Ditta G.S., Baumann E., Wisman E., and Yanofsky M.F., 2000, B and C floral organ identity functions require SEPALLATA MADS-box genes, *Nature*, 405(6783): 200-203.
<https://doi.org/10.1038/35012103>
- Pinyopich A., Ditta G.S., Savidge B., Liljegren S.J., Baumann E., Wisman E., and Yanofsky M.F., 2003, Assessing the redundancy of MADS-box genes during carpel and ovule development, *Nature*, 424(6944): 85-88.
<https://doi.org/10.1038/nature01741>
- Riechmann J.L., and Meyerowitz E.M., 1997, MADS domain proteins in plant development, *Biological Chemistry*, 378(10): 1079-1101.
- Sanders P.M., Bui A.Q., Weterings K., McIntire K.N., Hsu Y.C., Lee P.Y., Truong M.T., Beals T.P., and Goldberg R.B., 1999, Anther developmental defects in *Arabidopsis thaliana* male-sterile mutants, *Sexual Plant Reproduction*, 11(6): 297-322.
<https://doi.org/10.1007/s004970050158>
- Sanders P.M., Lee P.Y., Biesgen C., Boone J.D., Beals T.P., Weiler E.W., and Goldberg R.B., 2000, The *Arabidopsis* DELAYED DEHISCENCE1 gene encodes an enzyme in the jasmonic acid synthesis pathway, *The Plant Cell*, 12(7): 1041-1061.
<https://doi.org/10.1105/tpc.12.7.1041>
- Schieffhale U., Balasubramanian S., Sieber P., Chevalier D., Wisman E., and Schneitz K., 1999, Molecular analysis of NOZZLE, a gene involved in pattern formation and early sporogenesis during sex organ development in *Arabidopsis thaliana*, *Proceedings of the National Academy of Sciences*, 96(20): 11664-11669.
<https://doi.org/10.1073/pnas.96.20.11664>
- Schwarz-Sommer Z., Huijser P., Nacken W., Saedler H., and Sommer H., 1990, Genetic control of flower development by homeotic genes in *Antirrhinum majus*, *Science*, 250(4983): 931-936.
<https://doi.org/10.1126/science.250.4983.931>
- Shore P., and Sharrocks A.D., 1995, The MADS-box family of transcription factors, *European Journal of Biochemistry*, 229(1): 1-13.
<https://doi.org/10.1111/j.1432-1033.1995.tb0430.x>
- Stintzi A., and Browse J., 2000, The *Arabidopsis* male-sterile mutant, opr3, lacks the 12-oxophytodienoic acid reductase required for jasmonate synthesis, *Proceedings of the National Academy of Sciences*, 97(19): 10625-10630.
<https://doi.org/10.1073/pnas.190264497>
- Wetters S., 2020, Evo-devo of flowers and flowering genes: *Salvia* as a case study, Karlsruhe Institute of Technology (KIT), 2020: 1-92.
- Yang C., Xu Z., Song J., Conner K., Vizcay Barrena G., and Wilson Z.A., 2007, *Arabidopsis* MYB26/MALE sterile35 regulates secondary thickening in the endothecium and is essential for anther dehiscence, *The Plant Cell*, 19(2): 534-548.
<https://doi.org/10.1105/tpc.106.046391>
- Yang S.L., Xie L.F., Mao H.Z., Puah C.S., Yang W.C., Jiang L., Sundaresan V., and Ye D., 2003, Tapetum determinant1 is required for cell specialization in the *Arabidopsis* anther, *The Plant Cell*, 15(12): 2792-2804.
<https://doi.org/10.1105/tpc.016618>
- Yang W.C., Ye D., Xu J., and Sundaresan V., 1999, The SPOROCTELESS gene of *Arabidopsis* is required for initiation of sporogenesis and encodes a novel nuclear protein, *Genes & Development*, 13(16): 2108-2117.
<https://doi.org/10.1101/gad.13.16.2108>
- Zhang D., and Yang L., 2014, Specification of tapetum and microsporocyte cells within the anther, *Current Opinion in Plant Biology*, 17: 49-55.
<https://doi.org/10.1016/j.pbi.2013.11.001>
- Zhang W., Sun Y., Timofejeva L., Chen C., Grossniklaus U., and Ma H., 2006, Regulation of *Arabidopsis* tapetum development and function by dysfunctional tapetum1 (DYT1) encoding a putative bHLH transcription factor, *Development*, 133(16): 3085-3095.
<https://doi.org/10.1242/dev.02463>
- Zhao D.Z., Wang G.F., Speal B., and Ma H., 2002, The excess microsporocytes1 gene encodes a putative leucine-rich repeat receptor protein kinase that controls somatic and reproductive cell fates in the *Arabidopsis* anther, *Genes and Development*, 16(15): 2021-2031.
<https://doi.org/10.1101/gad.997902>
- Zhao F., Zheng Y.F., Zeng T., Sun R., Yang J.Y., Li Y., Ren D.T., Ma H., Xu Z.H., and Bai S.N., 2017, Phosphorylation of sporocyteless/nozzle by the MPK3/6 kinase is required for anther development, *Plant Physiology*, 173(4): 2265-2277.
<https://doi.org/10.1104/pp.16.01765>
- Zheng Z., Xia Q., Dauk M., Shen W., Selvaraj G., and Zou J., 2003, *Arabidopsis* AtGPAT1, a member of the membrane-bound glycerol-3-phosphate acyltransferase gene family, is essential for tapetum differentiation and male fertility, *The Plant Cell*, 15(8): 1872-1887.
<https://doi.org/10.1105/tpc.012427>

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Research Report

Open Access

Effects of Polyethylene Color and Thickness on the Retention of Some Minerals, Vitamins, and Antioxidant Activities of Stored Plantain (*Musa paradisiaca*) FlourFolasade Kemisola Olufemi-Salami ¹ ✉, Olufemi Samson Salami ², John Isa ³, Omolola Victoria Adefela ¹, Mary Anuoluwapo Ajatta ¹¹ Department of Food Science and Technology, Bamidele Olumilua University of Education, Science and Technology, Ikere, P.M.B. 250, Ikere-Ekiti State, Nigeria² Department of Biotechnology and Molecular Biology, Federal University of Health Science, Ila-Orangun, P.M.B. 204, Osun State, Nigeria³ Department of Agricultural and Environmental Engineering, Federal University of Technology, Akure, P.M.B. 704, Ondo State, Nigeria✉ Corresponding email: kemisade@yahoo.comPlant Gene and Trait, 2026, Vol.17, No.4 doi: [10.5376/pgt.2026.17.0018](https://doi.org/10.5376/pgt.2026.17.0018)

Received: 10 Jul., 2026

Accepted: 12 Aug., 2026

Published: 22 Aug., 2026

Copyright © 2026 Olufemi-Salami et al., This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.**Preferred citation for this article:**Olufemi-Salami F.K., Salami O.S., Isa J., Adefela O.V., and Ajatta M.A., 2026, Effects of polyethylene color and thickness on the retention of some minerals, vitamins, and antioxidant activities of stored plantain (*Musa paradisiaca*) Flour, Plant Gene and Trait, 17(4): 255-263 (doi: [10.5376/pgt.2026.17.0018](https://doi.org/10.5376/pgt.2026.17.0018))

Abstract Food packaging is critical for sustaining nutritional and functional quality of stored food. Polyethylene serves as a major packaging material in food industries. However, empirical evidence regarding how specific polyethylene characteristics dictate micronutrient stability during storage remains scarce. This study evaluated the effects of polyethylene color (black vs. transparent) and gauge thickness (0.03 mm vs. 0.15 mm) on the retention of essential minerals (Fe, Ca, Zn, P), vitamins, and antioxidant properties in stored plantain flour. French plantain (*Musa paradisiaca*) fruits were obtained, processed into flour. Samples of flour were packaged and stored under ambient conditions of 25 ± 5 °C temperature and $75 \pm 5\%$ relative humidity for 4 weeks in the laboratory. After the storage period, standard assays were used to quantify Fe, Ca, Zn, P, vitamins, and antioxidant properties in stored plantain flour. The results showed that both packaging color and thickness significantly influenced ($p < 0.05$) nutrient retention in the stored flours. Vitamin B6 was better preserved in black high-density polyethylene (BHP), whereas vitamin B9 stability was maximized in transparent high-density polyethylene (THP). Flour stored in transparent low-density polyethylene (TLP) exhibited the highest 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical scavenging activity (664.65 mg/kg) but the lowest total phenolic content (36.86 mg/kg). The preservation of Fe, Ca, and P was observed to be better in BHP. These findings demonstrate that no single packaging configuration optimally preserved the entire nutritional indices monitored; rather, packaging optimization must be strategically aligned with the specific target micronutrients of interest.

Keywords Polyethylene; Color; Vitamins; Antioxidant activities; Plantain flour**1 Introduction**

Plantain (*Musa paradisiaca*) serves as a foundational staple crop across tropical and subtropical regions, particularly within West and Central Africa, the Caribbean, and South America (Ajijolakewu et al., 2021). The crop is vital to household food security, rural and peri-urban economic sustainability (Abiola et al., 2024). Plantains are regularly converted into various value-added products, including pastes, chips, and flours (Udomkun et al., 2021). Plantain flour has attracted considerable research and commercial interest due to its prolonged shelf stability, ease of transportation, nutritional value and versatility in food formulation (Mundéné-Timothée et al., 2025). Notably, it represents a functionally viable gluten-free alternative to wheat flour and is extensively utilized in traditional thick pastes (“swallow”), porridges, and functional bakery products. Moreover, its low glycemic content makes it appealing to diabetic patients (Mundéné-Timothée et al., 2025).

Biochemically, plantain is a rich matrix of carbohydrates, dietary fiber, essential minerals, and diverse bioactive compounds. It contains structurally and metabolically significant concentrations of iron (Fe), calcium (Ca), zinc (Zn), and phosphorus (P), which modulate hematopoiesis, skeletal mineralization, enzymatic catalysis, and systemic metabolic homeostasis (Rotimi and Adeyemi, 2023a). Plantain fruit is rich in nutrients, it provides carbohydrates, dietary fiber, vitamins A, C, and B6, and vital minerals like potassium and magnesium (Emmanuel et al., 2025; Taak and Awasthi, 2025). Beyond basic nutrition, plantains are exceptionally high in bioactive antioxidants, including carotenoids, flavonoids, and vitamin C. These powerful compounds combat oxidative stress by neutralizing harmful free radicals in the body, protecting cells from damage. Consequently, regular

consumption helps reduce the risk of chronic illnesses such as cardiovascular disease and inflammation (Oladele and Adefegha, 2022). Furthermore, the matrix contains essential micronutrients, predominantly B-complex vitamins such as pyridoxine (vitamin B6) and folate (vitamin B9), which act as critical coenzymes in cellular metabolism and neurological functions (Oyeyinka and Afolayan, 2020). The presence of endogenous phenolic compounds imparts distinct antioxidant activity, neutralizing reactive oxygen species (ROS) and potentially mitigating oxidative stress-linked chronic pathologies (Rotimi and Adeyemi, 2023b). However, this nourishing food is highly susceptible to post-harvest handling, processing modalities, and environmental dynamics during storage (Ofosu et al., 2023).

In developing nations, post-harvest plantain losses remain critically high, driven by elevated initial moisture content, rapid senescent physiology, and susceptibility to microbial spoilage. Consequently, processing fresh pulp into shelf-stable flour is widely deployed as a post-harvest mitigation strategy (Pathare and Al-Dairi, 2022). Dehydration and subsequent particle size reduction diminish water activity (*aw*), thereby suppressing microbial proliferation and extending physical shelf life. Nevertheless, dehydrated plantain flour matrices remain highly susceptible to micronutrient degradation during storage (Mund  n  -Timoth  e et al., 2025). Photo-exposure, atmospheric oxygen, ambient relative humidity, and thermal fluctuations trigger the oxidative degradation of labile vitamins and systematically diminish radical scavenging capacity (Lalita et al., 2025). These biochemical transformations concurrently degrade the product's nutritional profile, functional properties, and organoleptic quality.

Sarkar and Kuna (2020) established that packaging configurations dictate the degree of product isolation from destructive vectors and some environmental factors. Polyethylene polymers are preferentially utilized as packing material globally in food supply chains due to their cost-effectiveness, low density, mechanical flexibility, and commercial accessibility (Saha et al., 2022). In small- and medium-scale food processing systems, particularly in low-resource settings, simple polyethylene bags are commonly used to package flours and dry food products (Garavito et al., 2024). Polyethylene films vary widely in color, thickness, light transmission and gas permeability. These properties influence energy transfer and biochemical processes in the packaged materials.

While many studies have documented the effects of storage kinetics on cereal and tuber flour quality (Solano and de Gante, 2014; Hemery et al., 2020; Awol et al., 2024), there is a paucity of data and literature, elucidating how discrete polyethylene characteristics influence the micronutrient retention in stored plantain flour. This research is therefore aimed at investigating the effects of the color and thickness of polyethylene on some vitamins and minerals retention in plantain flour, packed in polythene bags (of different colors and thickness) and stored in the laboratory environment for 4 weeks.

2 Results

The results of the effects of different polyethylene packaging materials on vitamin A, B6 and B9 preservation are shown in Table 1. The highest quantity (4 147.03 mg/kg) of preserved vitamin A in the stored flour was observed in the flour packed in TLP, although this quantity (4 147.03 mg/kg) was not statistically different from 4 033.99 and 3 929.31 mg/kg quantities of vitamin A observed in flour stored in THP and BLP respectively. Black high-density polyethylene bag preserved vitamin B6 better than the other packaging materials (TLP, THP and BLP) used. Flour stored in TLP, THP and BLP recorded 6.15, 9.72 and 8.78 mg/kg vitamin B6 respectively. These values (6.15, 9.72 and 8.78 mg/kg) were significantly lower than 10.77 mg/kg recorded in flour stored in BHP. Vitamin B9 preservation was significantly higher in flour stored in THP.

The results of the effect of colour and thickness of polyethylene packaging films on the DPPH content of stored plantain flour are presented in Figure 1. The highest DPPH was observed in flour stored in TLP. Flour stored in THP, BLP and BHP recorded 499.77, 597.58 and 396.67 mg/kg of DPPH respectively and these values were significantly lower than 664.65 mg/kg recorded in flour packed in TLP.

Table 1 The vitamin contents of the packaged and stored plantain flour compared with the baseline

Packaging Material	Vitamin A	Vitamin B6	Vitamin B9
Baseline	7692.74 ± 13.03 ^c	24.51 ± 0.54 ^e	55.63 ± 1.33 ^e
TLP	4147.03 ± 99.33 ^b	6.15 ± 0.10 ^a	22.50 ± 0.54 ^c
THP	3929.31 ± 94.11 ^b	9.72 ± 0.19 ^e	26.09 ± 0.63 ^d
BLP	4033.99 ± 96.59 ^b	8.78 ± 0.16 ^b	15.23 ± 0.37 ^b
BHP	3587.18 ± 85.92 ^a	10.77 ± 0.21 ^d	11.94 ± 0.29 ^a

Note: Means followed by the same superscript letter within the same column are not significantly different ($P > 0.05$) according to Duncan's multiple range test. TLP: Transparent Low-Density Polyethylene, THP: Transparent High-Density Polyethylene, BLP: Black Low-Density Polyethylene, BHP: Black High-Density Polyethylene

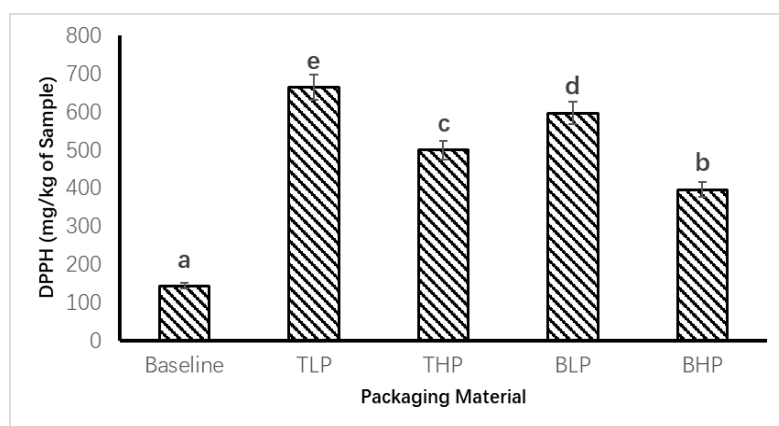


Figure 1 The DPPH content of the packaged and stored plantain flour compared with the baseline

Image caption: Bars with the same superscript letter are not significantly different ($P > 0.05$) according to Duncan's multiple range test. TLP: Transparent Low-Density Polyethylene, THP: Transparent High-Density Polyethylene, BLP: Black Low-Density Polyethylene, BHP: Black High-Density Polyethylene

The phenolic content of the stored flour varied across the packing material and was significantly lower when compared with the phenolic content of the baseline (flour before packaging and storage). At 4 weeks of storage, flour stored in TLP, THP, BLP and BHP recorded values of 36.86, 54.98, 44.23 and 66.34 mg/kg respectively (Figure 2).

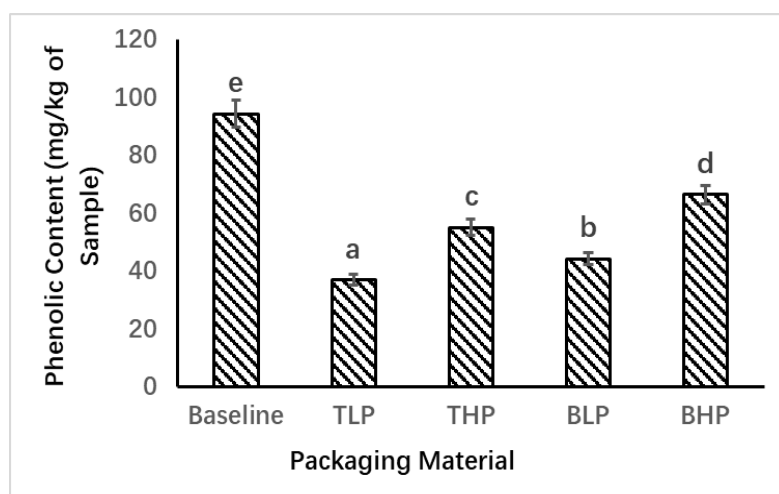


Figure 2 The Phenol content of the packaged and stored plantain flour compared with the baseline

Image caption: Bars with the same superscript letter are not significantly different ($P > 0.05$) according to Duncan's multiple range test. TLP: Transparent Low-Density Polyethylene, THP: Transparent High-Density Polyethylene, BLP: Black Low-Density Polyethylene, BHP: Black High-Density Polyethylene

The effects of colour and thickness of polyethylene packs on the retention of Fe, P, Ca and Zn in stored plantain flour are described in Table 2. The results show that mineral contents of the stored plantain flour decreases with time. Moreover, flour packed in BHP recorded 1.11, 697.27 and 20.5 mg/kg values of Fe, P and Ca respectively. The calcium and phosphorus retained in flour stored in BHP were significantly higher. Similarly, the Zn retention in the flour stored in TLP polyethylene is significantly higher than Zn contents of flour stored in THP, BLP and BHP. The amount of Zn retained in flour stored in THP, BLP and BHP were 0.92, 0.10 and 0.73 mg/kg respectively.

Table 2 The mineral content of the packaged and stored plantain flour compared with the baseline

Packaging material	Fe (mg/kg)	P (mg/kg)	Ca (mg/kg)	Zn (mg/kg)
Baseline	2.61 ± 0.71a	709.77 ± 28.10d	24.6 ± 0.72e	1.83 ± 0.14d
TLP	0.82 ± 0.00b	571.37 ± 14.47c	10.1 ± 0.14a	1.13 ± 0.00c
THP	0.80 ± 0.00b	470.66 ± 12.06b	17.7 ± 0.14c	0.92 ± 0.00b
BLP	0.63 ± 0.00b	420.30 ± 10.86a	16.1 ± 0.14b	0.10 ± 0.00bc
BHP	1.11 ± 0.00b	697.27 ± 17.49d	20.5 ± 0.14d	0.73 ± 0.00a

Note: Means followed by the same superscript letter within the same column are not significantly different ($P > 0.05$) according to Duncan's multiple range test. TLP: Transparent Low-Density Polyethylene, THP: Transparent High-Density Polyethylene, BLP: Black Low-Density Polyethylene, BHP: Black High-Density Polyethylene

3 Discussion

Polyethylene material is widely used as a mechanical barrier to micro-organisms and macro-organisms causing spoilage to food. Polyethylene also provides a barrier to some abiotic materials such as light, wind, water etc. that are capable of causing spoilage to food. The characteristics of the polyethylene may have direct significant effects on the protective properties of stored food. Luangtana-anan et al. (2017) reported an enhancement of moisture protective properties and stability of pectin via plastic protection. The investigation of the different properties of polyethylene revealed that the properties of the polyethylene have different effects on the retention of the nutritional composition of the stored plantain flour. Vitamin A retention in the plantain flour was favored by transparent low-density polyethylene (TLP). The heat production of TLP might be lower when compared to other polyethylene types considered for storage and this might have contributed to the retention of vitamin A in the flour stored in it. This observation is consistent with the report of Anand et al. (2022), who reported that plant vitamin A, β -carotene are heat-labile therefore its preservation must be in low heat environment. Black high-density polyethylene retains the highest amount of vitamin B6. Plant vitamin B6 (pyridoxine) has been reported to be light sensitive (Gorelova et al., 2022). The black colour of the BHP might have aided the barrier of the plastic to light energy to preserve pyridoxine better than the other types of the polyethylene examined.

Vitamin B9 (folate) is highly water-soluble and is important for DNA synthesis and cell division. The observation of the preservation of folate in the plantain flour packaged in THP (showed the highest folate retention) is slightly contradictory to the report of Liu et al. (2022) who reported that folate is sensitive to photooxidation. Although THP might have favoured folate preservation via heat reduction; owing to the fact that transparent materials could be poor radiator of heat energy (Salimian and Onwukwe, 2023).

Increase in antioxidant activities was also observed in all the polyethylene used (observed through increase in DPPH). High density of the polyethylene could have influenced the production of DPPH positively thereby extending the shelf life of the stored flour. A report by Rojas-Lema et al. (2021) indicated that high density polyethylene favors antioxidant activities in stored food. Although the antioxidant activities were observed to an increase in all plantain flour samples packed in polyethylene, it was also observed that the phenolic content of the flour reduced greatly. The phenol in the flour might have been highly susceptible to degradation forming new products in the period of storage in the polyethylene, this could have resulted in the reduction in its quantity (Rojas-Lema et al., 2021). Similarly, Liang et al. (2023) reported a significant decrease in the phenolic contents of some fermented foods in the process of antioxidant activities in food. The increase in the DPPH could have also

been as a result of some of the products from the breakdown of phenolic compounds involvement in the scavenging activities of free radicals that could cause spoilage of the stored flour (Ali et al., 2022).

Iron, calcium, zinc, and phosphorus are vital minerals essential for human health. Iron is crucial for oxygen transport in the blood and energy metabolism. Calcium supports strong bones and teeth, muscle function, and nerve signaling (Soetan et al., 2010). Zinc plays a key role in immune function, wound healing, and enzyme activity. Phosphorus is important for bone mineralization, energy production through ATP, and cell membrane integrity. Adequate intake of these minerals through food is necessary to prevent deficiencies, support growth, maintain physiological functions, and promote overall well-being (Serna and Bergwitz, 2020). The preservation of iron, calcium and phosphorus in plantain flour was observed to be better in BHP, this might be as a result of the black colour of the BHP reducing photo-oxidation of these elements as earlier reported (Wang et al., 2022).

4 Conclusion

The colour and thickness of polyethylene packaging materials significantly influence the retention of minerals, vitamins, and antioxidant properties of stored plantain flour. Across all treatments, storage resulted in measurable nutrient losses compared with baseline values; however, the extent of degradation varied with packaging characteristics. Transparent low-density polyethylene (TLP) favoured the retention of vitamin A and zinc and exhibited the highest DPPH antioxidant activity, suggesting enhanced radical scavenging potential under this packaging condition. In contrast, black high-density polyethylene (BHP) provided superior protection for vitamin B6 and key minerals such as iron, calcium, and phosphorus, highlighting the role of increased thickness and reduced light permeability in limiting nutrient degradation. Vitamin B9 was best preserved in transparent high-density polyethylene (THP), indicating that both density and optical properties interact to affect nutrient stability. Although antioxidant activity increased during storage, a concurrent decline in total phenolic content suggests phenolic degradation or transformation into other antioxidant compounds over time. Overall, the findings confirm that no single packaging material optimally preserves all nutrients; rather, packaging choice should be guided by the target nutritional components of interest. The study underscores the importance of selecting appropriate polyethylene colour and thickness to enhance shelf life, maintain nutritional quality, and support food security in plantain flour processing and storage systems, particularly in low-resource settings.

5 Materials and Methods

The unripe French plantain (*Musa paradisiaca*) fruits used for this research were of the same species and sourced from a local farm at Ikere, Ekiti State, Nigeria. The French plantain is called “Ogede agbagba” in Yoruba language. It is characterized by a complete, dense bunch carrying many hands and numerous smaller fingers, topped with a large, persistent male bud at maturity (Orluchukwu and Ogburia, 2014). The fruits were carefully sorted so that those used for the experiment were devoid of visible phytopathogenic defects and of length 20 ± 5 cm. The fruits were manually de-skinned, and the remaining pulp matrices were systematically sliced into small pieces to accelerate sun drying. The pulp slices were subjected to conventional open-air solar drying until they reached constant weight equilibrium and were subsequently pulverized using a heavy-duty 750-watt Solitaire Mixer Grinder. The powder was allowed to be thermally stable to ambient temperature. The resulting flour was passed through a standard 250 μ m sieve to remove extraneous particulate matter, fibrous fractions, and oversized plantain particles.

5.1 Experimental design and storage conditions

The packaging bags used for this experiment were of polythene materials and measured 15 cm by 15 cm. The bags were categorized into four distinct groups based on pigment profile (transparent and black) and thickness {0.03 mm (low-density polyethylene) and 0.15 mm (high-density polyethylene)}. The bags were divided into four groups: transparent low-density polyethylene (TLP), transparent high-density polyethylene (THP), black low-density polyethylene (BLP) and black high-density polyethylene (BHP). Aliquots of 50 g of the processed plantain flour were measured using electronic scale weighing balance (LCD type) and transferred into each type of polythene bag in triplicates, making a total of 12 bags of 50 g plantain flour. Samples of the flour were analyzed for minerals (Fe, Ca, Zn and P), vitamins (A, B6 and B9) and antioxidant properties (total phenolic

content (TPC) and 2,2-diphenyl-1-picrylhydrazyl (DPPH) measurement) at the beginning of the storage, to serve as control/baseline experiments. The packed polythene bags containing 50 g plantain flour were carefully placed on table so that approximately equal amount of white light can reach the twelve bags in the laboratory of Food Science and Technology Department, Bamidele Olumilua University of Education, Science and Technology, Ikere-Ekiti for 4 weeks. At 4 weeks of storage, samples were analyzed for minerals, vitamins and antioxidant properties.

Analytical reagents and polyethylene used were of analytical grade, sourced via Bisolamb Chemical and Pascal Scientific Equipment networks.

5.2 Minerals quantification

From each sample, 10 g was weighed into a crucible and ashed in a furnace at 600 °C for 8 h. The ash obtained was brought to 25 mL with HNO₃ 0.5 N under continuous stirring until the ash completely dissolved in the acid. Out of the product obtained, 1:10 dilutions were made in order to determine Fe, P, Ca and Zn. Atomic absorption spectrophotometry was used to determine Fe, Ca, and Zn. The determination was made using a “control AA 300” atomic absorption spectrophotometer with C₂H₂/air flame type. The standard solution was made with distilled water. The quantity of each metal was determined using the formula: $Me = m_{me} \times (25/m_p) \times D$ [mg/kg] where Me = the quantity of metal contained, in mg/kg; m_{me} = the quantity of metal read at the spectrophotometer, in mg/L; 25 = the volume of the solution of HNO₃ 0.5 N, in mL; m_p = the mass of the sample for analysis (10 g), in g; D = the dilution of the sample (1:10) (Nicoleta et al., 2006).

Phosphorus was determined and quantified by UV-Vis spectrophotometry (colorimetric method using Murphy and Riley reagents), and absorbance measurement at 660 nm wavelength. The results were expressed as mg P/kg of flour using a phosphorus standard curve (Salami et al., 2018).

5.3 Vitamins

Vitamin A quantification was done by measuring 0.2 g of the sample, 6 mL of ethanol and 0.6 mL of 5 % KOH into a test tube. The test tube was plugged with cotton wool and boiled for 25 min. 6 mL of distilled water was added. Hexane was then added to the water to separate vitamin A. The absorbance was measured at 400 nm using spectrophotometer (Kumar and Kamboj, 2021).

Also, for vitamin B6 measurement, 0.5 g of the sample was weighed into a test tube. 2 mL of 0.1 M sodium carbonate was added and shaken vigorously for 30 min. 100 mL of Folin was added and then the absorbance was measured at 580 nm using spectrophotometer (Khudhair et al., 2019).

For vitamin B9 measurement, 0.2 g of the sample was measured into a test tube. Two milliliters (2 mL) of KMnO₄ was added, and the mixture was left for 1 min. 2 mL of sodium nitrate was added to the mixture followed by 2 mL of 5% HCl, the mixture was shaken gently. 2 mL of sulphuric acid (5%) was then added as well as 2 mL of sodium acetate. The whole mixture was stirred and allowed to stand for 10 min. Finally, 2 mL of Azo dye (0.1%) was added to the mixture and allowed to stand for 10 min. Then the absorbance was measured at 550 nm. The quantity was determined using a standard curve (Najm et al., 2022).

5.4 Antioxidant measurement

The total phenolic content (TPC) in the sample was determined by using the method as described by Folin-Ciocalteu. The phenol in the food sample was extracted using methanol. The extracted mixture was allowed to incubate for 30 min after the addition of 1 mL of Folin-Ciocalteu and 1 mL of 0.5 M Na₂CO₃. The absorbance of the incubated mixture was measured at 750 nm and expressed in mg gallic acid equivalent (GAE) per gram of flour (Li et al., 2015).

The antioxidant 2,2-diphenyl-1-picrylhydrazyl, 0.5 mL of methanolic extract of plantain flour was mixed with DPPH solution and then kept in a dark place for 30 min (a purple chemical). If antioxidants are present, the purple colour fades. The change in colour was measured to know the antioxidant activity. After 30 min of incubation in the dark, absorbance was measured at 517 nm using a UV-Vis spectrophotometer (Sherma, 2017).

5.5 Statistical analysis

The data obtained from the results of the experiments were subjected to analysis of variance using IBM Statistical Package for the Social Sciences (SPSS) version 27. The means of the three replicates were separated from other treatment for significant difference using Duncan's multiple range test.

Abbreviations

Baseline: Flour before storage

TLP: Transparent Low-Density Polyethylene

THP: Transparent High-Density Polyethylene

BLP: Black Low-Density Polyethylene

BHP: Black High-Density Polyethylene

DPPH: 2,2-Diphenyl-1-Picrylhydrazyl

Authors' Contributions

FKO: Conceptualization, Methodology, Validation, Supervision. OSS: Formal analysis, Data curation, Writing—original draft. JI: Methodology, Validation, Formal analysis. OVA: Project administration, finance. MAA: Writing—review & editing. All authors read and approved the submitted version.

Acknowledgments

The authors would like to thank Dr. A.F. Akinbisoye of the department of Food Science and Technology, Bamidele Olumilua University of Education, Science and Technology, Ikere, Ekiti state, Nigeria, for her support during the drying process of the plantain.

Ethical approval

Not applicable.

Consent to participate

Not applicable.

Consent to publication

Not applicable.

Availability of data and materials

The datasets that support the findings of this study are available from the corresponding author upon reasonable request.

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.

References

- Abiola A., Adégbola Y.P., Zandjanakou-Tachin M., Crinot G.F., and Biaou G., 2024, Toward tailored interventions in plantain (*Musa paradisiaca* L.) industry: insights from heterogeneity and constraints to plantain-based cropping systems in South-Benin, *Social Sciences & Humanities Open*, 9: 100895.
<https://doi.org/10.1016/j.ssaho.2024.100895>
- Ajijolakewu K.A., Ayoola A.S., Agbabiaka T.O., Zakariyah F.R., Ahmed N.R., Oyedele O.J., and Sani A., 2021, A review of the ethnomedicinal, antimicrobial, and phytochemical properties of *Musa paradisiaca* (plantain), *Bulletin of the National Research Centre*, 45(1): 86.
<https://doi.org/10.1186/s42269-021-00549-3>
- Ali A., Kumar R.R., Vinutha T., Singh T., Singh S.P., Satyavathi C.T., and Goswami S., 2022, Grain phenolics: critical role in quality, storage stability and effects of processing in major grain crops—a concise review, *European Food Research and Technology*, 248(8): 2197-2213.
<https://doi.org/10.1007/s00217-022-04026-7>
- Anand R., Mohan L., and Bharadvaja N., 2022, Disease prevention and treatment using β -carotene: the ultimate provitamin A, *Revista Brasileira de Farmacognosia*, 32(4): 491-501.
<https://doi.org/10.1007/s43450-022-00262-w>
- Awol S.M., Kuyu C.G., Bereka T.Y., and Abamecha N., 2024, Physicochemical stability, microbial growth and sensory quality of refined wheat flour as affected by packaging materials during storage, *Journal of Stored Products Research*, 105: 102217.
<https://doi.org/10.1016/j.jspr.2023.102217>
- Emmanuel J.K., Mtashobya L.A., and Mgeni S.T., 2025, Potential contributions of banana fruits and residues to multiple applications: an overview, *Natural Product Communications*, 20(2): 1934578X251320151.
<https://doi.org/10.1177/1934578X251320151>

- Garavito J., Peña-Venegas C.P., and Castellanos D.A., 2024, Production of starch-based flexible food packaging in developing countries: analysis of the processes, challenges, and requirements, *Foods*, 13(24): 4096.
<https://doi.org/10.3390/foods13244096>
- Gorelova V., Colinas M., Dell'Aglio E., Flis P., Salt D.E., and Fitzpatrick T.B., 2022, Phosphorylated B6 vitamers deficiency in SALT OVERLY SENSITIVE 4 mutants compromises shoot and root development, *Plant Physiology*, 188(1): 220-240.
<https://doi.org/10.1093/plphys/kiab475>
- Hemery Y.M., Fontan L., Laillou A., Jallier V., Moench-Pfanner R., Avallone S., and Berger J., 2020, Influence of storage conditions and packaging of fortified wheat flour on microbial load and stability of folate and vitamin B12, *Food Chemistry: X*, 5: 100076.
<https://doi.org/10.1016/j.fochx.2019.100076>
- Khudhair A.F., Saeed S.I., Marhoon A.A., and Alesary H.F., 2019, A new spectrophotometric method to determine vitamin B6 in pharmaceutical formation samples using a micelle form, *Journal of Physics: Conference Series*, IOP Publishing, 1234(1): 012087.
<https://doi.org/10.1088/1742-6596/1234/1/012087>
- Kumar A., and Kamboj M., 2021, A review on photometric methods for the quantitation of vitamin A, *Microchemical Journal*, 171: 106791.
<https://doi.org/10.1016/j.microc.2021.106791>
- Lalita A.W., Hamad R., Manik S., and Mohapatra D., 2025, Processing-mediated changes, In: Purewal S.S., and Singh R.S. (eds.), *Colored Cereals: Properties, Processing, Health Benefits, and Industrial Uses*, CRC Press, Florida, USA, pp.170-194.
<https://doi.org/10.1201/9781003454922-8>
- Li Y., Ma D., Sun D., Wang C., Zhang J., Xie Y., and Guo T., 2015, Total phenolic, flavonoid content, and antioxidant activity of flour, noodles, and steamed bread made from different colored wheat grains by three milling methods, *The Crop Journal*, 3(4): 328-334.
<https://doi.org/10.1016/j.cj.2015.04.004>
- Liang Z., Huang Y., Zhang P., and Fang Z., 2023, Impact of fermentation on the structure and antioxidant activity of selective phenolic compounds, *Food Bioscience*, 56: 103147.
<https://doi.org/10.1016/j.fbio.2023.103147>
- Liu Z., Farkas P., Wang K., Kohli M.O., and Fitzpatrick T.B., 2022, B vitamin supply in plants and humans: the importance of vitamin homeostasis, *The Plant Journal*, 111(3): 662-682.
<https://doi.org/10.1111/tpj.15859>
- Luangtana-anan M., Soradech S., Saengsod S., Nunthanid J., and Limmatvapirat S., 2017, Enhancement of moisture protective properties and stability of pectin through formation of a composite film: effects of shellac and plasticizer, *Journal of Food Science*, 82(12): 2915-2925.
<https://doi.org/10.1111/1750-3841.13956>
- Mundéné-Timothée J.L., Nougou Bissoué A., Nguimbou R.M., Bissim S.M., Bouelet Ntsama I.S., Bouopda Tamo S.P., Fokam L., Mouangue R., and Njintang Yanou N., 2025, Plantain flour: production processes, technological characteristics, and its potential use in traditional African dishes-a review, *Journal of the Science of Food and Agriculture*, 105(9): 4741-4752.
<https://doi.org/10.1002/jsfa.13900>
- Najm M.A., Abd-Alrassol K.S., Qasim Q.A., Hussein H.H., and AL-Salman H.N.K., 2022, Spectrophotometric determination of folic acid using 1, 10-phenanthroline materials with ninhydrin reagent, *Materials Today: Proceedings*, 61: 865-872.
<https://doi.org/10.1016/j.matpr.2021.09.453>
- Nicoleta R.D., Gherhen I., and Furdí F., 2006, Determination of the metal content in some flours and pastes obtained from different wheat species, *Buletin USAMV-CN*, 62: 343-345.
- Ofosu D.O., Martinson F., Frimpong G.K., Asare I.K., and Darfour B., 2023, Pre-harvest and post-harvest practices along the plantain (*Musa* spp. AAB) fruit value chain in Ghana that predispose them to ripening, *Ghana Journal of Agricultural Science*, 58(2): 75-82.
- Oladele E.O.P., and Adefegha S.A., 2022, Plantain bioactives: an underutilised food resource in Africa, In: Babalola O.O., Ayangbenro A.S., and Ojuederie O.B. (eds.), *Food security and safety volume 2: African perspectives*, Springer International Publishing, Cham, Switzerland, pp.187-211.
https://doi.org/10.1007/978-3-031-09614-3_9
- Orluchukwu J.A., and Ogburia M.N., 2014, The relationship of growth and yield components of different plantain (*Musa* spp.) cultivars in a humid area of southern Nigeria, *Advances in Life Sciences*, 4(2): 37-43.
- Oyeyinka B.O., and Afolayan A.J., 2020, Potentials of *Musa* species fruits against oxidative stress-induced and diet-linked chronic diseases: in vitro and in vivo implications of micronutritional factors and dietary secondary metabolite compounds, *Molecules*, 25(21): 5036.
<https://doi.org/10.3390/molecules25215036>
- Pathare P.B., and Al-Dairi M., 2022, Effect of mechanical damage on the quality characteristics of banana fruits during short-term storage, *Discover Food*, 2(1): 4.
<https://doi.org/10.1007/s44187-022-00007-7>
- Rojas-Lema S., Lascano D., Ivorra-Martinez J., Gomez-Caturla J., Balart R., and Garcia-Garcia D., 2021, Manufacturing and characterization of high-density polyethylene composites with active fillers from persimmon peel flour with improved antioxidant activity and hydrophobicity, *Macromolecular Materials and Engineering*, 306(11): 2100430.
<https://doi.org/10.1002/mame.202100430>
- Rotimi D.E., and Adeyemi O.S., 2023a, Comparative evaluation of the antioxidant activity, trace elements, and phytochemical analysis of the extracts of unripe plantain whole fruit and pulp, *Karabala International Journal of Modern Science*, 9(2): 2.
<https://doi.org/10.33640/2405-609X.3290>

- Rotimi D.E., and Adeyemi O.S., 2023b, Plantain-based diet decreases oxidative stress and inflammatory markers in the testes of rats exposed to atrazine, *Molecular and Cellular Biochemistry*, 478(9): 2041-2056.
<https://doi.org/10.1007/s11010-022-04639-2>
- Saha N.C., Ghosh A.K., Garg M., and Sadhu S.D., 2022, Flexible packaging material-manufacturing processes and its application, In: Saha N.C., Ghosh A.K., Garg M., and Dey Sadhu S. (eds.), *Food packaging: materials, techniques and environmental issues*, Springer Nature Singapore, Singapore, pp.47-87.
https://doi.org/10.1007/978-981-16-4233-3_2
- Salami O.S., Akomolafe O.M., and Olufemi-Salami F.K., 2018, Quantification of cyanide and major nutrients of soil around cassava (*Manihot esculenta* C.) processing industries within Akure, Ondo State, Southwest Nigeria, *Molecular Soil Biology*, 9(2): 12-17.
<https://doi.org/10.5376/msb.2018.09.0002>
- Salimian A., and Onwukwe U., 2023, Development of a transparent thermal reflective thin film coating for accurate separation of food-grade plastics in recycling process via AI-based thermal image processing, *Coatings*, 13(8): 1332.
<https://doi.org/10.3390/coatings13081332>
- Sarkar S., and Kuna A., 2020, Food packaging and storage, In: Singh P., and Saini V. (eds.), *Research trends in home science and extension*, AkiNik Publications, New Delhi, India, 3: 27-51.
- Serna J., and Bergwitz C., 2020, Importance of dietary phosphorus for bone metabolism and healthy aging, *Nutrients*, 12(10): 3001.
<https://doi.org/10.3390/nu12103001>
- Sherma J., 2017, Studies on the antioxidant activity of foods and food ingredients by thin-layer chromatography-direct bioautography with 2, 2'-diphenyl-1-picrylhydrazyl radical (DPPH*), In: Grinberg N., and Carr P.W. (eds.), *Advances in chromatography*, CRC Press, Florida, USA, pp.229-244.
<https://doi.org/10.1201/9781315158075-9>
- Soetan K.O., Olaiya C.O., and Oyewole O.E., 2010, The importance of mineral elements for humans, domestic animals and plants: a review, *African Journal of Food Science*, 4(5): 200-222.
- Solano A.C.V., and de Gante C.R., 2014, Development of biodegradable films based on blue corn flour with potential applications in food packaging. Effects of plasticizers on mechanical, thermal, and microstructural properties of flour films, *Journal of Cereal Science*, 60(1): 60-66.
<https://doi.org/10.1016/j.jcs.2014.01.015>
- Taak K., and Awasthi M., 2025, Plantain as a functional food: a comprehensive review of its nutritional and therapeutic attributes, *Advances in Food Sciences*, 47(1): 2-8.
- Udomkun P., Masso C., Swennen R., Innawong B., Fotso Kuate A., Alakonya A., Lienou J., Ibitoye D.O., and Vanlauwe B., 2021, Consumer preferences and socioeconomic factors decided on plantain and plantain-based products in the central region of Cameroon and Oyo State, Nigeria, *Foods*, 10(8): 1955.
<https://doi.org/10.3390/foods10081955>
- Wang A., Ma S., Zhu Y., Zou L., and Zhao G., 2022, Evaluation of photo-oxidation in full-fat milk under different light spectra: a laboratory experiment in food chemistry, *Journal of Chemical Education*, 99(3): 1420-1427.
<https://doi.org/10.1021/acs.jchemed.1c00650>

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Research Insight

Open Access

Effects of Planting Density on Plant Architecture, Fruit Setting and Yield Performance of Tomato

Lingli Shen^{1,2} ¹ Tongxiang Hangji Ecological Agriculture Technology Co. Ltd., Tongxiang, 314500, Zhejiang, China² Zhejiang Agronomist College, Hangzhou, 310021, Zhejiang, China Corresponding email: 55983288@qq.comPlant Gene and Trait, 2026, Vol.17, No.4 doi: [10.5376/pgt.2026.17.0019](https://doi.org/10.5376/pgt.2026.17.0019)

Received: 15 Jul., 2026

Accepted: 19 Aug., 2026

Published: 28 Aug., 2026

Copyright © 2026 Shen, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:Shen L.L., 2026, Effects of planting density on plant architecture, fruit setting and yield performance of tomato, Plant Gene and Trait, 17(4): 264-276 (doi: [10.5376/pgt.2026.17.0019](https://doi.org/10.5376/pgt.2026.17.0019))

Abstract Planting density is an important cultivation factor affecting tomato plant architecture, fruit set characteristics, and yield performance. This study analyzed the effects of planting density on tomato population structure, reproductive characteristics, and yield formation. Previous studies showed that planting density regulated tomato canopy development by influencing plant height, internode length, stem diameter, leaf area index, and canopy light distribution. Moderate increases in planting density generally improved light interception per unit area and land-use efficiency, whereas excessive density intensified plant competition, resulting in reduced biomass accumulation per plant, canopy closure, and decreased photosynthetic efficiency. During the reproductive growth stage, an appropriate planting density maintained the balance between vegetative and reproductive growth, maintained favorable fruit set, and enhanced fruit development. However, excessive planting density increased the risk of flower and fruit abortion due to insufficient assimilate supply and negatively affected fruit quality. In terms of yield formation, planting density regulated yield per unit area by balancing individual plant productivity and population productivity. Future tomato density management should integrate cultivar characteristics, environmental conditions, and cultivation practices, and utilize canopy monitoring, modeling prediction, and intelligent regulation technologies to achieve dynamic and precise density management. This study provides a theoretical basis for efficient tomato cultivation, population structure optimization, and precision production in protected agriculture.

Keywords Planting density; Tomato; Plant architecture; Fruit set characteristics; Yield formation

1 Introduction

Tomato production depends strongly on planting density regulation because density determines how efficiently a crop captures light, water, nutrients, and cultivation space, while also shaping fruit yield, fruit quality, and economic return. Tomato is a major crop for fresh and processing markets worldwide, and growers increasingly seek management practices that raise productivity per unit area without compromising marketability (Caradonia et al., 2023; Francesca et al., 2026). Across production systems, planting density is recognized as a core agronomic factor because excessive crowding intensifies intraspecific competition for solar radiation, water, nutrients, and physical space, whereas overly sparse stands underuse the available land area (Sievidov and Sievidov, 2020; Ayarna et al., 2021). Proper density selection can optimize light interception, improve resource-use efficiency, and increase water productivity, which is especially important in greenhouse, high-tunnel, hydroponic, and organic systems where input costs are high and production efficiency is critical (Chau and Chinh, 2021; Torres-Quezada and Gandini-Taveras, 2023). At the same time, density management also affects canopy microclimate, including shading and relative humidity, with implications for disease pressure, fruit health, and the use of plant protection inputs (Ansari et al., 2017).

The importance of density control is further reinforced by the physiological responses that tomato plants show when neighboring plants are close. Competition can begin as soon as plants detect proximity signals such as reduced light intensity, altered red:far-red balance, and leaf contact, which trigger shifts in morphology and assimilate partitioning even before severe resource depletion occurs (Karpe et al., 2024). Under dense canopies, tomato plants often express shade-avoidance traits and low-light adaptations, including stem or internode elongation, higher slenderness, thinner leaves, and increased senescence, all of which can alter plant architecture

and reproductive performance (Francesca et al., 2026). Several studies also show that higher density can increase plant height while reducing vegetative biomass per plant or modifying leaf area relationships, indicating that architectural responses are central to density adaptation rather than secondary effects (Tuan and Mao, 2015; Sievidov and Sievidov, 2020; Ayarna et al., 2021). For this reason, regulating planting density is not only a matter of fitting more plants into a field or greenhouse, but also a way of steering canopy structure, source-sink balance, and the conditions under which flowers set and fruits develop (Ansari et al., 2017; Evangelista et al., 2025).

Research on the effects of planting density on tomato growth and development shows a consistent trade-off between yield per plant and yield per unit area, although the exact optimum varies with cultivar, environment, and management system. In greenhouse tomato in northwest China, increasing density reduced fruit number per plant, mean fruit weight, and yield per plant, yet total yield increased, with an economic optimum of 3.7~4.4 plants/m². Similar responses have been reported in hydroponic and soilless systems, where raising density increased yield per square meter but often reduced average fruit weight and shifted yield toward greater fruit number per area (Ayarna et al., 2021). Studies in field and greenhouse conditions likewise show that moderate rather than extreme densities frequently maximize marketable or total yield, with reported optima near 25 974~28 571 plants/ha, 33 000~45 830 plants/ha, or about 3.5 plants/m² depending on genotype and production context (Tuan and Mao, 2015; Sievidov and Sievidov, 2020; Dinh and Dang, 2023). Even so, responses are not uniform: some studies found little effect on yield per hectare, others found cultivar-specific quadratic responses, and high-tunnel trials reported yield losses per plant of 32%~46% when density exceeded the locally suitable arrangement (Maboko and Du Plooy, 2018; Torres-Quezada and Gandini-Taveras, 2023; Evangelista et al., 2025).

Beyond total yield, density also influences fruit set characteristics, marketable yield, and quality traits that are directly relevant to commercial production. Excessively high density can hamper fruit set, reduce fruit size, lower sweetness and acidity, and increase the risk of flower abortion when assimilate supply per plant becomes limiting (Karpe et al., 2024; Francesca et al., 2026). In contrast, lower or moderate densities often improve fruit set rate, fruit number per plant, and individual fruit weight, as observed in field and greenhouse studies in Vietnam and Bangladesh (Tuan and Mao, 2015; Chau and Chinh, 2021). Density effects on reproductive traits are nevertheless context-dependent: under summer heat stress, plant density did not affect fruit set in heat-tolerant hydroponic cultivars, while in a greenhouse study blossom drop decreased as density increased to 3.5 plants/m² (Ayarna et al., 2021). Fruit quality responses are equally nuanced. Higher density often reduces fruit size and some market attributes (Haque and Sakimin, 2022), but some studies report limited change in qualitative traits across density ranges or even gains in selected compounds such as lycopene under particular light environments (Talpur et al., 2023; Evangelista et al., 2025). These mixed findings indicate that the effect of planting density on tomato performance cannot be judged from yield alone, because architecture, flower retention, fruit set, fruit growth, and quality formation respond simultaneously and sometimes in opposite directions (Caradonia et al., 2023).

This article analyzes the effects of planting density on tomato plant architecture, fruit set characteristics, and yield performance, with particular attention to the mechanisms by which density regulation influences population structure and yield formation. Previous studies have mainly focused on individual indicators, such as total yield, planting spacing, water productivity, or fruit quality, while the integrated relationships among canopy structure, reproductive processes, and final yield formation have received comparatively less attention. By synthesizing existing evidence on plant architectural traits, flower and fruit development, and yield responses, this article examines why moderate planting densities can improve yield per unit area, whereas excessive density may result in smaller fruits, reduced marketable yield, or lower productivity per plant. Because suitable planting density is jointly affected by cultivar architecture, production environment, and associated cultivation practices, the article further discusses density optimization under different production systems and the potential application of precision management technologies. The analysis provides a reference for efficient tomato cultivation, population structure optimization, and precision density management under different production conditions.

2 Effects of Planting Density on Tomato Plant Architecture

2.1 Effects on plant morphological characteristics

Planting density clearly alters tomato plant morphological characteristics, but the direction and magnitude of change depend on genotype, stage, and production system. Across several experiments, higher density generally increased plant height or internode elongation while reducing stem thickness, compactness, or vegetative mass per plant, which is consistent with a shade-avoidance response under stronger neighbor competition. In controlled-environment tomato, increasing density promoted internode elongation and higher slenderness, while basal stem diameter declined, showing that plants became less compact as canopy crowding intensified (Karpe et al., 2024). A parallel density study under combined drought and non-drought conditions likewise found taller plants, longer internodes, reduced stem diameter, and lower leaf mass per area at high density, reinforcing that these responses are robust morphological signatures of dense planting (Francesca et al., 2026).

Field and greenhouse studies broadly support the same pattern, although not every trait responds in every environment. In Vietnam, the highest density tested produced the greatest plant height, whereas a moderate density gave better fruit set and yield, indicating that taller growth under crowding does not necessarily reflect superior whole-plant performance (Tuan and Mao, 2015). In a spring film greenhouse, increasing density raised plant height but reduced vegetative mass per plant, and the best overall biometric balance was reported at 3.5 plants/m² (Sievidov and Sievidov, 2020). Other studies show that density effects can be trait-specific or weak under some conditions: one field trial found significant density effects on most agronomic traits except plant height, and another reported no significant differences among planting distances for plant height, branches, leaves, flowering age, stem diameter, or harvested fruit traits (Ariefin et al., 2024). Seedling studies add that density strongly affects specific leaf area, health index, and dry matter ratios, whereas plant height and leaf area can be driven more by facility conditions than density alone (Zhang et al., 2025), so morphological responses should be interpreted in relation to environment and developmental stage.

2.2 Effects on leaf arrangement and canopy structure

Planting density reshapes leaf arrangement and canopy structure mainly by changing leaf area deployment, leaf area index, mutual shading, and the vertical distribution of light within the stand. High density increased LAI sharply in dwarf tomato, reaching 6.7 compared with about 2.1–2.2 at lower-density treatments, while also accelerating loss of shaded basal leaves (Karpe et al., 2024). The same study showed that low density produced much greater leaf area and leaf dry weight per plant, indicating that sparse stands favor larger individual canopies, whereas dense stands favor greater canopy occupation per unit ground area rather than per-plant expansion. This canopy trade-off is central to tomato density responses because canopy coverage determines light interception, but excessive crowding worsens lower-canopy shading and leaf senescence (Jiang et al., 2017).

Several studies suggest that optimum canopy structure is achieved not by maximizing density indefinitely, but by reaching an LAI range that improves interception without excessive self-shading. For processing tomato, an LAI of about 4–5 has been identified as ideal for light interception and productivity, and densification early in the season was suggested where LAI is otherwise suboptimal (Evangelista et al., 2025). In winter single-truss tomato, the densest fixed treatment produced the tallest stems but the lowest leaf area and shoot dry weight, whereas movable or lower-density arrangements improved the lower-canopy light environment (Jiang et al., 2017). Modeling work further indicates that canopy performance depends not only on density per se but also on structural traits such as internode length and leaf dimensions, because longer internodes and optimized leaf shape can improve within-canopy light penetration and interception (Zhang et al., 2022). Recent imaging research also highlights LAI as a practical structural indicator for greenhouse tomato management, although measurement accuracy can decline when leaf density and occlusion increase (Naito et al., 2025).

2.3 Effects on photosynthetic characteristics and dry matter accumulation

Planting density affects photosynthetic characteristics primarily through its control over light interception, light distribution, and assimilate availability per plant. Greenhouse synthesis shows that total dry matter production is closely linked to intercepted light, with light interception determined largely by LAI and canopy light extinction

characteristics. In three-truss tomato, higher density increased fruit yield per area relative to lower density, consistent with improved interception at the crop level rather than greater productivity of individual plants (Higashide, 2022). Likewise, in dwarf tomato, increasing density raised efficiency in converting incident and intercepted light into red-ripe fruits, and total plant dry weight per square meter increased with density before saturating at the highest constant density. However, per-plant assimilate availability fell under constant high density, and final whole-plant dry weight per area was not higher than a dynamic 90% ground-cover treatment, suggesting diminishing returns once crowding becomes excessive (Karpe et al., 2024).

Photosynthetic responses themselves are nuanced, because dense canopies can increase canopy light capture while depressing photosynthesis in shaded leaves. In winter greenhouse tomato, leaf photosynthesis was higher in the movable-bench and lower-density treatments than in the fixed high-density treatment, and those treatments also maintained greater leaf area and shoot dry weight (Jiang et al., 2017). By contrast, a recent study found that high density unexpectedly enhanced photosynthetic rates despite activating shade-avoidance morphology, implying that moderate canopy shade can sometimes improve physiological efficiency depending on water status and environment (Francesca et al., 2026). Classic modeling work further suggests that plant density has a smaller direct effect on dry matter partitioning than on dry matter production, because partitioning is governed more strongly by sink strength and fruit load, while LAI simulation remains highly influential for crop growth prediction. Seedling and greenhouse studies also show that higher density can raise radiation or light-use efficiency even when individual plants are smaller (Xu et al., 2024; Zhang et al., 2025), so the architectural effect of density on photosynthesis is best understood as a balance between greater canopy capture and lower per-plant light availability. In sum, planting density modifies tomato architecture by coordinating morphological plasticity, canopy organization, and crop-level carbon gain, with moderate or dynamically adjusted densities often producing the most favorable balance between structural development and biomass accumulation (Higashide, 2022; Karpe et al., 2024).

3 Effects of Planting Density on Tomato Fruit Set Characteristics

3.1 Effects on inflorescence formation and flowering dynamics

Planting density influences inflorescence formation mainly by altering the balance between vegetative growth, assimilate supply, and the number of reproductive sites carried per unit area. In protected tomato, increasing density raised the number of trusses per ground area, but plants did not convert all additional flowers into fruits, indicating that reproductive structure formation can outpace the plant's capacity to sustain fruiting. In dwarf tomato pruned to a fixed flower number, high density still reduced reproductive success, showing that density effects persist even when the potential floral load is standardized (Karpe et al., 2024). Studies evaluating agronomic components also show that density significantly affects clusters per plant, flowers per cluster, distance between clusters, and blossom drop, confirming that flowering dynamics are structurally responsive to crop crowding.

The direction of response varies with production system and genotype. In Bangladesh field tomato, lower density increased flowers per cluster and supported higher fruits per cluster and fruits per plant, suggesting that wider spacing favors stronger reproductive expression per individual plant. In a spring greenhouse in Ukraine, density had little effect on the timing of developmental phases, indicating that planting density can modify reproductive intensity more than phenological schedule (Sievidov and Sievidov, 2020). Additional evidence from seedling-density work shows that higher nursery density later increased flower number and yield per plant after transplanting, likely because early restriction of vegetative growth redirected photoassimilates toward inflorescences in formation (Moreno-Pérez et al., 2021). More broadly, yield analyses across genotypes identify flowers per cluster and fruits per cluster as important positive contributors to yield, which helps explain why density effects on flowering traits propagate into final productivity (Muntaha et al., 2023; Ramana et al., 2025).

3.2 Effects on fruit set rate and fruit development

Planting density has a clear effect on fruit set rate and fruit development, but the response is not monotonic. Several studies found that moderate or lower densities improved fruit set, fruits per cluster, fruits per plant, and

individual fruit weight. In Vietnam field conditions, 25 974 plants/ha gave the best fruit set, fruit number, fruit weight, and overall yield (Tuan and Mao, 2015). In greenhouse tomato, 25 000 plants/ha produced the highest fruit setting rate at 75.35%, along with 94.84 fruits per plant and 113.24 g average fruit weight (Chau and Chinh, 2021). A similar pattern appeared in Bangladesh, where 25 000 plants/ha maximized fruits per cluster, fruits per plant, and fruit yield per plant, while 28 571 plants/ha maximized total and marketable yield.

At higher density, tomato often compensates by increasing yield per area despite weaker per-plant fruiting. In soilless greenhouse culture, raising density to 3.5 plants/m² increased yield per square meter in all cultivars, and fruit yield per square meter correlated strongly with fruit number per plant but negatively with average fruit weight. In dwarf tomato, despite lower fruit number per plant, constant high density produced 11.1 kg/m² and 72% flower fruiting success, but fruit number per plant was lower and distal flowers were preferentially aborted, consistent with assimilate limitation during fruit set (Karpe et al., 2024). Earlier protected-cultivation work reached a similar conclusion: tomato adjusts the number of set fruits by aborting excess flowers, and 6.7 plants/m² appeared to be the upper practical limit for maximizing set fruit number under the tested leaf-to-inflorescence balance. Not all systems respond identically, however. In one field study, higher density reduced fruit number and yield per plant but did not change marketable or total yield per hectare (Maboko and Du Plooy, 2018), while under combined drought and high density, yield per plant declined even though high density alone increased yield per hectare and produced larger fruits in irrigated plants (Francesca et al., 2026).

3.3 Effects on fruit quality formation

Fruit quality formation is one of the most density-sensitive outcomes, but evidence is mixed because different quality traits respond in different directions. Strong evidence shows that constant high density reduces individual fruit size and several market traits. In dwarf tomato, high density lowered fruit fresh weight, fruit size, hardness, total soluble solids, and citric acid content, and made soluble solids less uniform across fruits. That same study found that dynamic spacing maintained quality similar to low density while preserving much higher yield per area, suggesting that quality losses are tied more to sustained crowding than to temporary canopy closure (Karpe et al., 2024). In organic field tomato, higher density reduced marketable yield per plant mainly through fewer fruits, but it also reduced fruit loss from infection, showing that density can alter fruit health as well as intrinsic quality (Caradonia et al., 2023).

Other studies indicate that some quality attributes remain stable or even improve at higher density depending on environment and trait measured. In hydroponic greenhouse tomato, density affected pericarp thickness, pH, uniform ripening, and total soluble solids, but the highest density increased TSS only in one cultivar and lowered juice pH in two cultivars, indicating a genotype-dependent quality response. Under open-field high density, fruits showed lower titratable acidity but 72.75% higher lycopene, with no difference in firmness, suggesting that denser canopies can improve selected nutritional traits even when flavor chemistry shifts (Francesca et al., 2026). Broader genetic studies help interpret this variability: fruit weight, TSS, titratable acidity, pericarp thickness, and lycopene all vary widely among genotypes and are strongly tied to yield or processing quality, so density effects on fruit quality are likely filtered through cultivar-specific sink strength and biochemical capacity (Muntaha et al., 2023; Naik et al., 2025; Ramana et al., 2025).

4 Effects of Planting Density on Tomato Yield Performance

4.1 Effects on individual plant yield and population yield

Increasing planting density generally reduces yield per plant while improving land-use efficiency and often increasing yield per unit area (Maboko and Du Plooy, 2018; Haque and Sakimin, 2022). In greenhouse dwarf tomato, constant high density produced 111 g fruit fresh weight per plant but the highest harvestable yield per area, 11.1 kg/m², showing the classic trade-off between plant-scale and area-scale productivity (Karpe et al., 2024). In Bangladesh field tomato, 25 000 plants/ha gave the highest fruit yield per plant, but 28,571 plants/ha gave the highest total and marketable yield. In Vietnam field conditions, 25 974 plants/ha produced the maximum fruit yield, indicating that moderate rather than maximal density can optimize total yield when crowding starts to depress reproductive performance (Tuan and Mao, 2015).

The density that maximizes population yield varies substantially with system and genotype (Figure 1) (Dinh and Dang, 2023). In soilless greenhouse culture, increasing density to 3.5 plants/m² raised yield per square meter in all three cultivars tested. In a spring film greenhouse, the indeterminate hybrid Tobolsk F1 reached its maximum yield of 15.8 kg/m² at 3.5 plants/m² (Sievidov and Sievidov, 2020). In Brazilian processing tomato, yield responses were hybrid-specific: CVR-2909 and N-901 responded positively or quadratically to denser stands up to 40 000 plants/ha, whereas U-2006 did not respond across 20 000–40 000 plants/ha (Evangelista et al., 2025). In contrast, one field study on indeterminate tomato found that increasing density reduced marketable and total yield per plant but did not affect yield per hectare, and the lowest density without pruning tended to be most economical (Maboko and Du Plooy, 2018).



Figure 1 Relationship between sowing densities and plant parameters (Adopted from Dinh and Dang, 2023)

Image caption: a) a sowing density of 50 000 plants/ha and b) a sowing density of 33 000 plants/ha (Adopted from Dinh and Dang, 2023)

4.2 Effects on yield components

Planting density changes yield through its effects on fruit number, fruit size, and mean fruit weight, and these components usually move in opposite directions (Cardoso et al., 2018). Higher density often lowers fruit number per plant and average fruit weight while increasing fruit number per unit area (Maboko and Du Plooy, 2018; Caradonia et al., 2023; Karpe et al., 2024). In the Golestan soilless study, fruit yield per m² correlated strongly and positively with number of fruits per plant but negatively with average fruit weight, showing that total yield gains under denser stands are driven more by fruit number than by fruit enlargement. In the Ukraine greenhouse study, fruit size and the yield of standard fruits declined as plant density increased, even though total yield still increased to an optimum (Sievidov and Sievidov, 2020). The same inverse pattern appears in broader review evidence: decreasing density tends to increase fruit size, whereas increasing density raises total yield only up to a threshold (Haque and Sakimin, 2022).

Several experiments quantify these component shifts under different management contexts. In hydroponic tomato, the highest total yield, 22.61 kg/m², occurred at 11.1 plants/m² with two bunches per plant, confirming that density interacts with pruning and truss number in determining sink load (Cardoso et al., 2018). Earlier processing-tomato work showed that low densities produced the most fruits per plant, but the highest process-fruit yield, 42.5 tons/acre, occurred at 78 408 plants/acre because fruit size remained relatively uniform and the larger plant population compensated for lower plant productivity. That study also found that densities of at least 9 801 plants/acre were needed to reach 30 tons/acre and that wider spacing increased sunburn and sunscald culls because reduced canopy cover exposed more fruits. More recent open-field optimization found an optimum near 45 830 plants/ha, with no significant differences in fruit weight per plant or fruit diameter across densities, underscoring that the dominant yield component can differ by cultivar and environment (Dinh and Dang, 2023).

4.3 Mechanisms of tomato yield formation under density regulation

The main mechanisms linking density regulation to tomato yield are light interception, leaf area index, dry matter production, and the balance between source supply and sink demand (Higashide, 2022). Total dry matter production is determined by intercepted light, and planting density changes yield chiefly by altering canopy light capture per unit ground area rather than by simply changing the efficiency of individual plants. In controlled tomato canopies, higher density increased plant dry weight per area and intercepted light, but whole-plant dry weight eventually saturated under constant high density, indicating diminishing returns once assimilate availability per plant becomes limiting (Karpe et al., 2024). Modeling and review work likewise identify LAI as a key control point: light interception depends on LAI and canopy extinction, simulated growth is highly sensitive to LAI, and optimal yield requires an LAI matched to solar radiation and crop stage (Figure 2) (Higashide, 2022).

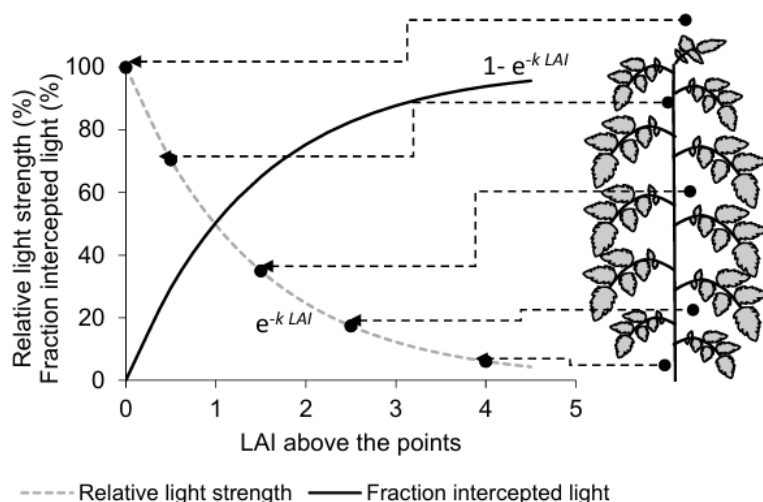


Figure 2 Relative light strength and intercepted light in a plant canopy as a function of leaf area index (LAI) at a light extinction coefficient (k) of 0.75 (Adopted from Higashide, 2022)

Density also regulates yield through dry matter partitioning and fruit sink strength, but the evidence suggests that partitioning responds more to fruit load than to density alone. Under constant high density, dry matter partitioned to fruits was slightly higher, yet fruit number per plant was lower and distal flowers were preferentially aborted, implying stronger sink demand in the remaining fruits but poorer fruit set under local assimilate shortage (Karpe et al., 2024). A classic quantitative analysis similarly found that assimilate supply altered by plant density had no direct influence on dry matter partitioning, whereas partitioning was strongly influenced by the number of fruits on the plant. Independent evidence from branching and light manipulation supports this interpretation: reduced yield can arise from smaller fruit size because of lower fruit sink strength, not necessarily because carbohydrate supply is limiting (Paponov et al., 2023). Under stress, these mechanisms shift further, since high density increased yield per hectare in the field but reduced yield per plant when combined with drought, showing that the outcome of density regulation depends on how canopy light capture interacts with water limitation (Francesca et al., 2026).

5 Optimization of Suitable Planting Density under Different Cultivation Systems

5.1 Differences in density requirements among tomato varieties

Tomato varieties differ in their density requirements because plant architecture, vigor, and sink capacity change how effectively a canopy converts added plants into added yield. In industrial processing tomato, hybrid responses were not uniform: CVR-2909 and N-901 showed quadratic or positive yield responses to increasing density, whereas U-2006 showed little response between 20 000 and 40 000 plants/ha. The weak density response of U-2006 was attributed to its smaller, more compact habit and probably lower leaf area index and light interception (Evangelista et al., 2025). In contrast, greenhouse hydroponic hybrids Dafnis, Izmono, and Hirad all produced their highest yield per square meter at 3.5 plants/m², but the size of the gain differed among cultivars, indicating shared direction but cultivar-specific magnitude.

Determinate and indeterminate tomatoes also differ in how density should be optimized across seasons and systems. For determinate cultivars in a closed hydroponic gravel-film system, spring/summer marketable yield improved at 20~25 plants/m², whereas in summer/fall 10 plants/m² was more cost-effective because higher density no longer increased yield under lower radiation. In a spring film greenhouse, the indeterminate hybrid Tobolsk F1 reached maximum yield at 3.5 plants/m², consistent with breeder recommendations centered around 2.5~3.5 plants/m² for indeterminate types under those conditions (Sievidov and Sievidov, 2020). Under summer heat in NFT hydroponics, cultivar choice also determined whether high density was useful: the heat-tolerant cultivar benefited from denser planting, while Jaguar was uneconomical because blossom end rot sharply reduced marketable yield (Ayarna et al., 2021). In organically grown hydroponic tomato under abiotic stress, grafted 'Velocity F1' at 3.5 plants/m² outperformed the denser 5.5 plants/m² treatment, showing that the optimum for vigorous indeterminate material under stress can shift downward rather than upward (Figure 3) (Dash et al., 2023).

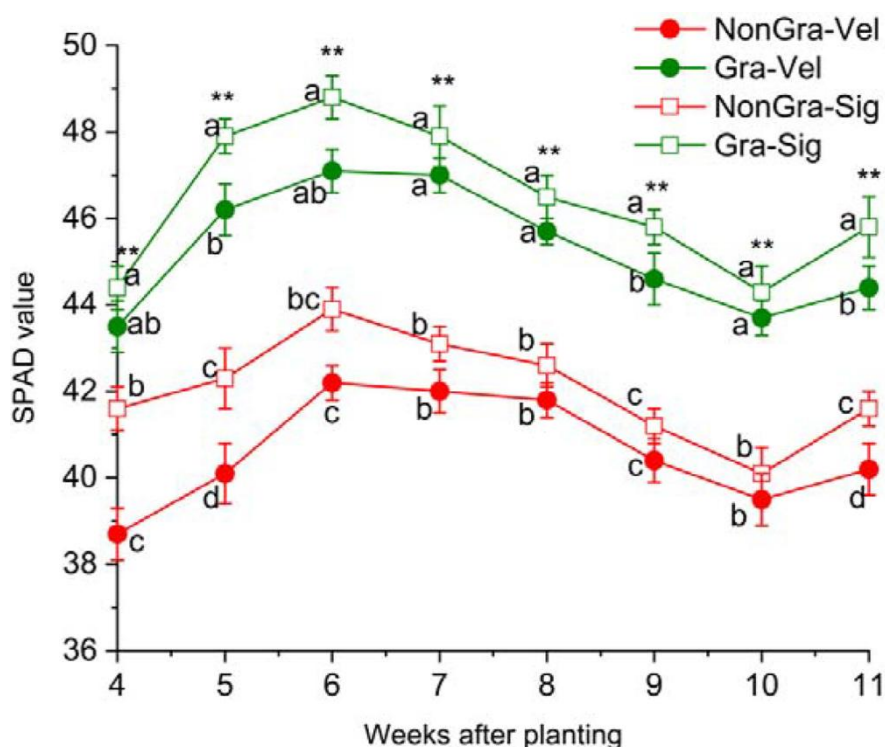


Figure 3 Effect of grafting and cultivar on the soil plant analysis development value of tomato (Adopted from Dash et al., 2023)

Image caption: Vertical bar represents the SE; Dissimilar letters on the line graph show statistical differences, the same letters show statistical similarities according to Tukey's honest significant difference test at $P < 0.05$. NonGra-Vel=nongrafted 'Velocity F1'; Gra-Vel=grafted 'Velocity F1'; NonGra-Sig=nongrafted 'Sigma F1'; Gra-Sig=grafted 'Sigma F1'; Significant at $P < 0.01$ (Adopted from Dash et al., 2023)

5.2 Density optimization strategies under protected cultivation conditions

Under protected cultivation, density optimization is best treated as a balance between maximizing yield per area and avoiding the fruit-size, quality, and stress penalties of chronic overcrowding (Caradonia et al., 2023; Karpe et al., 2024). In greenhouse soilless culture in Golestan, increasing density to 3.5 plants/m² increased yield per square meter in all three hybrids tested, supporting denser planting than the commonly used 2~2.5 plants/m² (Dash et al., 2023). In a separate hydroponic greenhouse study, the highest total yield, 22.61 kg/m², was obtained at 11.1 plants/m² with two bunches per plant, showing that optimal density in protected systems depends on pruning intensity and planned sink load as well as spacing itself (Cardoso et al., 2018). In spring film-greenhouse production, 3.5 plants/m² was likewise optimal for Tobolsk F1, while in closed hydroponic determinate tomato the best density shifted with season because high density was less beneficial under shorter days and lower radiation (Sievidov and Sievidov, 2020).

Protected systems also allow management combinations that change the effective density optimum. Dynamic spacing in controlled-environment dwarf tomato kept plants initially dense and then reduced spacing in steps to maintain 75% or 90% ground coverage, achieving much higher yield than constant low density while preserving fruit quality close to the low-density treatment (Karpe et al., 2024). Grafting can also shift the preferred density under stress: in Qatar, grafted ‘Velocity F1’ at 3.5 plants/m² improved photosynthesis, fruit set, and marketable yield relative to nongrafted plants, while in organic field production the combination of rootstock use and 2.5 plants/m² gave the better performance under suitable conditions (Caradonia et al., 2023; Dash et al., 2023). More broadly, protected soilless systems are attractive because closed-loop, electronically managed greenhouses reduce water, nutrient, and environmental burdens, making density optimization part of a larger resource-efficiency strategy rather than a stand-alone spacing decision (D’Amico et al., 2023; Ambore, 2025).

5.3 Density regulation based on precision cultivation

Precision cultivation shifts density regulation from a fixed recommendation to a responsive control problem based on canopy status, light capture, and real-time crop feedback (Wang et al., 2026). In dynamic spacing experiments, ground coverage was measured twice weekly with smartphone imaging and plants were re-spaced when coverage exceeded preset thresholds, providing a simple operational rule for maintaining productive competition without prolonged crowding (Karpe et al., 2024). Functional-structural modeling now supports more exact optimization of spacing geometry: in Chinese solar greenhouses, simulations across row patterns, path widths, and orientations identified an east-west configuration with a plant distance of 0.32 m and a density of 39 000 plants/ha as optimal for mechanized planting. For vertical farming, a dwarf tomato FSP model validated across multiple densities accurately predicted fruit dry mass, total dry mass, and leaf area index, and showed that ideotype traits affecting light distribution become density-dependent design targets (Butturini et al., 2026).

Recent sensing and autonomous-control studies show how these tools can be used in practice. Greenhouse sensor networks now monitor temperature, humidity, light, and CO₂ at multiple canopy positions and can drive predictive control models with average errors below 5%, supporting intelligent environmental regulation around the chosen plant density. IoT-based weighing and photosynthesis modeling can estimate LAI and photosynthetic LAI non-destructively with high accuracy and update biomass predictions in real time, enabling closed-loop density and canopy management (Wang et al., 2026). In autonomous dwarf-tomato greenhouse production, algorithms managed density reductions from 56 toward 42, 30, and 20 plants/m²; keeping density high for too long increased production per area but also caused stretching, canopy entanglement, thin stems, and more small fruits, confirming that precision density control must optimize morphology and operability as well as yield (Maree et al., 2025).

6 Current Research Issues and Future Development Directions

6.1 Lack of unified density standards under different ecological conditions

Planting-density standards remain difficult to unify because the reported optimum varies widely across ecological conditions, cultivation systems, and tomato growth habits. Recommended densities span about 1.1 plants/m² for open-field determinate tomato and 3.6 plants/m² for indeterminate glasshouse crops (Francesca et al., 2026). Even within protected cultivation, economic optima differ by region, including 3.7–4.4 plants/m² in northwest China, 3.5 plants/m² in a spring film greenhouse in Ukraine (Sievidov and Sievidov, 2020), and higher densities in some hydroponic systems (Cardoso et al., 2018). Open-field studies are equally inconsistent, with optima reported at 28 571 plants/ha in Bangladesh, 45 830 plants/ha in Vietnam under drip irrigation (Dinh and Dang, 2023), and 16 000 plants/ha in field-grown indeterminate tomato when costs and pruning labor were considered (Maboko and Du Plooy, 2018).

These differences reflect real biological and environmental heterogeneity rather than simple experimental noise. Hybrid-specific responses are clear in the Brazilian Savanna, where CVR-2909 and N-901 responded positively or quadratically to denser planting, but U-2006 did not respond across the tested range because its compact architecture likely limited LAI change and light interception gains (Evangelista et al., 2025). Seasonal context also matters: determinate tomato in a closed hydroponic system benefited from 25 plants/m² in spring/summer but only

10 plants/m² was cost-effective in summer/fall (Sievidov and Sievidov, 2020). Some locations show little response to spacing at all, as one recent field study found no significant effect of planting distance on measured growth and yield traits (Ariefin et al., 2024). Future work therefore needs ecology-specific density standards built around genotype, radiation regime, water availability, and production objective rather than a single universal recommendation (Francesca et al., 2026).

6.2 Insufficient research on the synergistic effects of planting density and other cultivation practices

A second major gap is the limited integration of planting density with other cultivation practices, even though existing studies show that these interactions can change the density optimum substantially. Density and fertilization interact strongly in greenhouse tomato: in Lam Dong, the combination of 25 000 plants/ha with the highest fertilizer rate produced the greatest fruit yield, marketable yield, and economic return (Chau and Chinh, 2021). Density also interacts with pruning and truss management in hydroponics, where the highest yield, 22.61 kg/m², occurred at 11.1 plants/m² with two bunches per plant (Cardoso et al., 2018). Field evidence similarly shows that plant density and stem pruning jointly affect performance, and under one indeterminate system the lowest density without pruning was the most practical recommendation (Maboko and Du Plooy, 2018).

The same pattern appears for grafting, irrigation, stress management, and pest control, but the literature remains fragmented. In organic tomato, rootstock use improved marketable yield per plant by more than 59%, while 2.5 plants/m² gave the better overall performance under suitable conditions (Caradonia et al., 2023). Under combined high density and drought, tomato responses became more complex: high density enhanced photosynthetic traits under adequate water, but high density plus drought reduced yield per plant more than either stress alone, indicating that density thresholds must be redefined under water limitation (Francesca et al., 2026). High-tunnel work in Virginia also suggests that irrigation or pollination, rather than light or nutrient competition, may explain yield losses at higher densities in that system (Torres-Quezada and Gandini-Taveras, 2023). In desert conditions, an intermediate spacing reduced some key insect pests and increased yield, showing that density can function as part of integrated pest management (Asiry et al., 2022). Future studies need more multifactor designs that test density together with fertigation, pruning, grafting, stress, and pest management in the same framework (Cardoso et al., 2018; Chau and Chinh, 2021).

6.3 Intelligent management based on canopy structure optimization as a future trend

A clear future direction is intelligent density management based on canopy structure optimization rather than static spacing rules. Recent work shows that canopy light interception, photosynthesis, and yield depend not only on plant number but on row orientation, spacing geometry, and the dynamic relationship between canopy structure and light distribution. In Chinese solar greenhouses, a 3D functional-structural model identified an east-west configuration with a plant distance of 0.32 m and a density of 39 000 plants/ha as optimal for mechanized planting. Modeling work also shows that total dry matter production is governed by intercepted light, that the optimal LAI depends on solar radiation, and that crop growth models can support management decisions for climate control, fertilization, and irrigation (Higashide, 2022).

The most promising systems now move from fixed density to dynamic canopy regulation. Dynamic plant spacing that maintained 75% or 90% ground coverage preserved fruit quality close to low-density treatments while greatly increasing yield per area, showing that density can be adjusted during growth to keep competition within a target range (Karpe et al., 2024). New digital tools make that strategy increasingly feasible: canopy photosynthesis models can separate the effects of canopy structure, light environment, and physiology across climates; plant factories provide stable, precisely controlled environments for density-dependent seedling production (Zhang et al., 2025); and recent greenhouse studies show that adjusting row spacing under current density can still improve accumulated canopy photosynthesis. The future trend is therefore density regulation by real-time canopy targets such as LAI, ground cover, and photosynthetic efficiency, supported by structural modeling and precision environmental control rather than fixed, one-size-fits-all spacing recommendations.

7 Conclusion and Prospects

Planting density regulates tomato population performance by modifying plant architecture at both the individual-plant and canopy scales. Under constant high density, tomato shows a characteristic shade-response syndrome, including internode elongation, increased slenderness, higher specific leaf area, and lower assimilate availability per plant, while total plant weight per unit area increases and then saturates. In spring greenhouse tomato, increasing density increased plant height and reduced vegetative mass per plant, with 3.5 plants/m² giving the best balance among vegetative mass, height, and leaf area. Variety-specific responses reinforce that architecture mediates density effects: in the Brazilian Savanna, the compact hybrid U-2006 showed little yield response to density, likely because its smaller habit limited changes in leaf area index and light interception, whereas other hybrids responded positively up to 40 000 plants/ha. Seedling studies also show that density changes structural quality early, with low density improving health index and dry matter ratio, while high density can increase radiation use efficiency, indicating that architectural regulation begins before transplanting.

Appropriate planting density promotes fruit set and yield efficiency by balancing reproductive sink demand with canopy resource capture. Moderate densities often maximize fruit set, fruit number per plant, fruit weight, and yield per plant, as shown by optima around 25 000 plants/ha in greenhouse Vietnam and 25 974 plants/ha in field Vietnam. In Bangladesh, 25 000 plants/ha maximized flowers per cluster, fruits per cluster, fruits per plant, and yield per plant, while 28 571 plants/ha maximized total and marketable yield, illustrating the consistent trade-off between plant-level and area-level productivity. Comparable patterns appear in protected systems: higher densities increased yield per square meter in hydroponic and soilless tomato, including 3.5 plants/m² in Golestan, 25 plants/m² for determinate closed hydroponics in spring/summer, and 3.7~4.4 plants/m² as the economic optimum in northwest China's solar greenhouses. But when density becomes excessive, fruit number per plant, average fruit weight, and yield per plant decline, and flower abortion becomes more likely, especially for distal flowers under assimilate shortage.

Precision density management is emerging as a major direction for high-efficiency tomato production because fixed spacing recommendations cannot accommodate variation among cultivars, seasons, pruning systems, and stress environments. Dynamic spacing that maintained 75% or 90% ground coverage preserved fruit quality close to low density while more than doubling harvestable yield per area relative to constant low density, showing that density can be managed as a moving canopy target rather than a static initial decision. This logic is strengthened by evidence that density optima shift with management context, including bunch number per plant in hydroponics, fertilizer regime in greenhouse production, grafting under abiotic stress, and season in determinate closed hydroponics. New functional-structural models now identify optimal canopy configurations for mechanized greenhouses and vertical farming, including an east-west layout at 39 000 plants/ha in Chinese solar greenhouses and density-responsive ideotype design for dwarf tomato indoors. Taken together, the evidence supports a shift from uniform density recommendations toward canopy-based, cultivar-specific, and dynamically adjusted density regulation to improve yield, quality, and resource-use efficiency across tomato production systems.

Conflict of Interest Disclosure

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

References

- Ambore B., Priyanga P., Pattankar V.V., Nivedita G.Y., Sunitha K., and Jyothi S., 2025, Hydroponics: innovative sustainable technologies for tomato cultivation, *Journal of Information Systems Engineering and Management*, 10(53s): 753-763.
<https://doi.org/10.52783/jisem.v10i53s.10972>
- Ansari G., Lal M., Kanwar H.S., Kanwar R., and Verma R., 2017, Effect of planting geometry and training on growth and seed yield of tomato (*Solanum lycopersicum* L.), *Journal of Applied and Natural Science*, 9(2): 1146-1150.
<https://doi.org/10.31018/jans.v9i2.1338>
- Ariefin M.N., Bahagia R.H., and Jelatu S., 2024, Application of various planting distances on growth response and yield of tomato plants (*Solanum lycopersicum* L.), *Agriculture*, 19(2): 165-174.
<https://doi.org/10.36085/agrotek.v19i2.7277>

- Asiry K.A., Huda M.N., and Mousa M.A.A., 2022, Abundance and population dynamics of the key insect pests and agronomic traits of tomato (*Solanum lycopersicon* L.) varieties under different planting densities as a sustainable pest control method, *Horticulturae*, 8(10): 976.
<https://doi.org/10.3390/horticulturae8100976>
- Ayarna A.W., Tsukagoshi S., Nkansah G.O., and Maeda K., 2021, Effect of plant density on the yield of hydroponically grown heat-tolerant tomato under summer temperature conditions, *American Journal of Plant Sciences*, 12(6): 901-913.
<https://doi.org/10.4236/ajps.2021.126060>
- Butturini M., Smoleňová K., Restina J., Stolz J., de Vries J., and Marcelis L.F.M., 2026, A functional-structural plant model for dwarf tomato ideotype identification in vertical farming, *In Silico Plants*, 8: diaf024.
<https://doi.org/10.1093/insilicoplants/diaf024>
- Caradonia F., Francia E., Alfano V., and Ronga D., 2023, Grafting and plant density influence tomato production in organic farming system, *Horticulturae*, 9(6): 669.
<https://doi.org/10.3390/horticulturae9060669>
- Cardoso F.B., Martinez H.E.P., Silva D.J.H., Milagres C.C., and Barbosa J.G., 2018, Yield and quality of tomato grown in a hydroponic system, with different planting densities and number of bunches per plant, *Pesquisa Agropecuária Tropical*, 48(4): 340-349.
<https://doi.org/10.1590/1983-40632018v4852611>
- Chau M.H., and Chinh N.X., 2021, Effect of plant density and fertilizer application rates on growth, fruit yield and quality of tomato (*Solanum lycopersicum* L.) in greenhouse condition, *Asian Plant Research Journal*, 8(3): 22-31.
<https://doi.org/10.9734/APRJ/2021/v8i330177>
- D'Amico A., De Boni A., Ottomano Palmisano G., Acciani C., and Roma R., 2023, Environmental analysis of soilless tomato production in a high-tech greenhouse, *Cleaner Environmental Systems*, 11: 100137.
<https://doi.org/10.1016/j.cesys.2023.100137>
- Dash P.K., Guo B., and Leskovic D.I., 2023, Optimizing hydroponic management practices for organically grown greenhouse tomato under abiotic stress conditions, *HortScience*, 58(10): 1129-1138.
<https://doi.org/10.21273/HORTSCI17249-23>
- Dinh K.H.T., and Dang T.A., 2023, Optimization of sowing density for improving fruit yield of tomatoes grown in open-field crop, *Indian Journal of Agricultural Research*, 57(6): 802-806.
<https://doi.org/10.18805/IJAr.AF-709>
- Evangelista A.W.P., Alves Júnior J., Bezerra R.S., and Casaroli D., 2025, Planting densities and growing times of tomato cultivars for industrial processing in the climatic conditions of the Cerrado de Goiás (*Brazilian Savanna*), *Australian Journal of Crop Science*, 19(4): 388-397.
<https://doi.org/10.21475/ajcs.25.19.04.p264>
- Francesca S., Cirillo V., Cuccurullo A., Choukri R., Pollaro N., Addonizio M., Faize M., Baghour M., and Rigano M.M., 2026, Interactive effects of high planting density and drought on physiological traits and yield in tomato, *Journal of the Science of Food and Agriculture*, 106(5): 2648-2655.
<https://doi.org/10.1002/jsfa.70368>
- Haque M.A., and Sakimin S.Z., 2022, Planting arrangement and effects of planting density on tropical fruit crops-a review, *Horticulturae*, 8(6): 485.
<https://doi.org/10.3390/horticulturae8060485>
- Higashide T., 2022, Review of dry matter production and growth modelling to improve the yield of greenhouse tomatoes, *The Horticulture Journal*, 91(3): 247-266.
<https://doi.org/10.2503/hortj.UTD-R019>
- Jiang C.Y., Johkan M., Hohjo M., Tsukagoshi S., Ebihara M., Nakaminami A., and Maruo T., 2017, Responses of leaf photosynthesis, plant growth and fruit production to periodic alteration of plant density in winter produced single-truss tomatoes, *The Horticulture Journal*, 86(4): 511-518.
<https://doi.org/10.2503/hortj.OKD-060>
- Karpe M., Marcelis L.F.M., and Heuvelink E., 2024, Dynamic plant spacing in tomato results in high yields while mitigating the reduction in fruit quality associated with high planting densities, *Frontiers in Plant Science*, 15: 1386950.
<https://doi.org/10.3389/fpls.2024.1386950>
- Maboko M.M., and Du Plooy C.P., 2018, Response of field-grown indeterminate tomato to plant density and stem pruning on yield, *International Journal of Vegetable Science*, 24(6): 612-621.
<https://doi.org/10.1080/19315260.2018.1458265>
- Marce S.C., Zhang P., van Marrewijk B.M., de Zwart F., Bijlaard M., and Hemming S., 2025, Autonomous greenhouse cultivation of dwarf tomato: performance evaluation of intelligent algorithms for multiple-sensor feedback, *Sensors*, 25(14): 4321.
<https://doi.org/10.3390/s25144321>
- Moreno-Pérez E.D.C., Sánchez-del Castillo F., Ruiz-Díaz M., and Contreras-Magaña E., 2021, Effect of population densities and paclobutrazol applications on seedling quality and yield in tomato, *Revista Chapingo Serie Horticultura*, 27(1): 5-17.
<https://doi.org/10.5154/r.chsh.2020.05.010>
- Muntaha S., Nesa N.U., and Sagor G.H.M., 2023, Genetic dissection for yield and fruit quality traits in tomato (*Lycopersicon esculentum* Mill.), *European Journal of Agriculture and Food Sciences*, 5(5): 45-53.
<https://doi.org/10.24018/ejfood.2023.5.5.734>

- Naik B.P.K., Gokul A.P., Naidu S.A., Velavan M., Praveenkumar S., and Ruban J.S., 2025, Characterization and evaluation of tomato (*Solanum lycopersicum* L.) genotypes for distinctness, uniformity, stability and yield attributes, *Journal of Advances in Biology & Biotechnology*, 28(10): 1154-1170.
<https://doi.org/10.9734/jabb/2025/v28i103134>
- Naito H., Fukatsu T., Shimomoto K., Hosoi F., and Ota T., 2025, Leaf area estimation in high-wire tomato cultivation using plant body scanning, *AgriEngineering*, 7(7): 206.
<https://doi.org/10.3390/agriengineering7070206>
- Paponov M., Verheul M.J., Dobrev P.I., and Paponov I.A., 2023, Additive effects of light and branching on fruit size and chemical fruit quality of greenhouse tomatoes, *Frontiers in Plant Science*, 14: 1221163.
<https://doi.org/10.3389/fpls.2023.1221163>
- Ramana V., Srihari D., Reddy R.V.S.K., Vani Praveena M., Sujatha M., and Bhavane M.H.V., 2025, Path coefficient analysis of yield and quality components in tomato (*Solanum lycopersicum* L.), *International Journal of Advanced Biochemistry Research*, 9(2): 576-579.
<https://doi.org/10.33545/26174693.2025.v9.i2h.3835>
- Sievidov V., and Sievidov I., 2020, Influence of plant density on the growth and productivity of an indeterminate tomato hybrid, *Scientific Reports of the National University of Life and Environmental Sciences of Ukraine*, 16(5): 5.
<https://doi.org/10.31548/dopovidi2020.05.005>
- Talpur M.M.A., Shaghaleh H., Hamad A.A.A., Chang T., Zia-ur-Rehman M., Usman M., and Hamoud Y.A., 2023, Effect of planting geometry on growth, water productivity, and fruit quality of tomatoes under different soil moisture regimes, *Sustainability*, 15(12): 9526.
<https://doi.org/10.3390/su15129526>
- Torres-Quezada E., and Gandini-Taveras R.J., 2023, Plant density recommendations and plant nutrient status for high tunnel tomatoes in Virginia, *Horticulturae*, 9(10): 1063.
<https://doi.org/10.3390/horticulturae9101063>
- Tuan N.M., and Mao N.T., 2015, Effect of plant density on growth and yield of tomato (*Solanum lycopersicum* L.) at Thai Nguyen, Vietnam, *International Journal of Plant & Soil Science*, 7(6): 357-361.
<https://doi.org/10.9734/IJPSS/2015/18573>
- Wang X., Tong X., Han B., Li Z., Li Q., Liu X., Sun Z., Sigrimis N., and Li T., 2026, Innovative photosynthesis model twinning after intelligent interpretation of complex sensor analytics, *Computers and Electronics in Agriculture*, 244: 111496.
<https://doi.org/10.1016/j.compag.2026.111496>
- Xu X., Yang F., Song J., Zhang R., and Cai W., 2024, Does the daily light integral influence the sowing density of tomato plug seedlings in a controlled environment, *Horticulturae*, 10(7): 730.
<https://doi.org/10.3390/horticulturae10070730>
- Zhang H., Miao C., Zhu C., Ding X., Yang S., Chang L., and Jiang Y., 2025, Effects of different cultivation facilities and planting densities on tomato seedling production, *HortScience*, 60(7): 1065-1074.
<https://doi.org/10.21273/HORTSCI18568-25>
- Zhang Y., Henke M., Li Y., Xu D., Liu A., Liu X., and Li T., 2022, Analyzing the impact of greenhouse planting strategy and plant architecture on tomato plant physiology and estimated dry matter, *Frontiers in Plant Science*, 13: 828252.
<https://doi.org/10.3389/fpls.2022.828252>

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Research Insight

Open Access

Effects of Canopy Management Practices on Fruit Development and Yield Stability of Fresh Table Grapes

Feixue Pan^{1,2} ✉¹ Yongjia Feixue Family Farm, Yongjia, 325100, Zhejiang, China² Zhejiang Agronomist College, Hangzhou, 310021, Zhejiang, China✉ Corresponding email: 54070795@qq.comPlant Gene and Trait, 2026, Vol.17, No.4 doi: [10.5376/pgt.2026.17.0020](https://doi.org/10.5376/pgt.2026.17.0020)

Received: 25 Jul., 2026

Accepted: 22 Aug., 2026

Published: 31 Aug., 2026

Copyright © 2026 Pan, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Pan F.X., 2026, Effects of canopy management practices on fruit development and yield stability of fresh table grapes, Plant Gene and Trait, 17(4): 277-288 (doi: [10.5376/pgt.2026.17.0020](https://doi.org/10.5376/pgt.2026.17.0020))

Abstract Canopy structure plays an important role in regulating plant growth, fruit development, and yield stability during fresh table grape production. Appropriate canopy management can improve fruit quality and production stability by regulating light distribution, microenvironmental conditions, source-sink relationships, and nutrient allocation. However, grape cultivars, cultivation systems, and ecological environments show different responses to canopy management practices, and the establishment of suitable precision management systems remains an important challenge in current production. This review used ‘Shine Muscat’ (*Vitis vinifera* ‘Shine Muscat’) as a representative case to synthesize the mechanisms by which canopy optimization management affects growth, fruit development, and yield formation in fresh table grapes. The effects of canopy structure regulation, light environment optimization, and microenvironment improvement on vegetative growth, photosynthetic efficiency, and fruit quality formation were summarized. Based on the production practice of ‘Shine Muscat’ grape, the effects of shoot control, trellis optimization, inflorescence thinning, cluster regulation, and light environment management on plant growth, berry enlargement, fruit maturation, and marketable fruit rate were analyzed. Furthermore, the regulatory roles of canopy management in source-sink balance, nutrient allocation, and yield stability under different environmental conditions were discussed. It is suggested that canopy management in fresh table grapes should shift from single-factor regulation toward an integrated management system based on cultivar characteristics, water-fertilizer supply, and crop load optimization. In addition, the integration of remote sensing, intelligent sensing, and artificial intelligence technologies will promote the development of precision canopy management. This review provides theoretical references and practical approaches for high-quality, efficient, and stable production of fresh table grapes.

Keywords Canopy management; Fresh table grapes; ‘Shine Muscat’; Fruit development; Yield stability

1 Introduction

Fresh table grape production depends on achieving high marketable yield together with stable berry size, color, firmness, soluble solids, and cluster uniformity under increasingly variable seasonal conditions. Canopy management is central to this goal because it regulates canopy microclimate, light interception, air circulation, source-sink balance, and the spatial distribution of vegetative and reproductive organs, all of which affect fruit development and productivity (Collins et al., 2020; Du et al., 2023). In grapevine, the light environment within the canopy is especially important because shade reduces yield components, delays ripening, and lowers quality, whereas improved canopy microclimate can simultaneously enhance yield and fruit composition. This importance is becoming even greater under climate change, as longer growing seasons, faster ripening, overheating stress, sunburn, and more frequent extreme events are forcing renewed attention to training systems and in-season canopy manipulation as practical adaptation tools (Del Zozzo and Poni, 2024; Lan, 2025).

In fresh table grapes, canopy management has particular significance because commercial value depends not only on total yield, but on visible and textural traits that directly determine consumer acceptance. Seasonal fluctuations in environment can alter yield and berry composition, making the maintenance of high and consistent fruit quality a continuing challenge in table grape systems (Petoumenou and Patris, 2021). Studies across grape production systems show that canopy interventions such as shoot thinning, leaf removal, pruning intensity adjustment, shoot topping, cluster thinning, and training-system selection are used to optimize light distribution and vegetative growth, thereby influencing berry growth, ripening, disease risk, and harvest quality (Poni et al., 2023;

Galar-Martínez et al., 2024; Lan, 2025). Mechanistically, greater light interception in the canopy and bud zone improves photosynthetic performance, carbohydrate status, and reproductive development. Shoot thinning increased inflorescence primordia number and size through changes in bud microclimate, shoot growth capacity, and carbohydrate content, and bud light interception was positively correlated with bud fruitfulness, indicating that canopy management can influence not only the current crop but also the following season's yield potential (Collins et al., 2020). At the berry level, contrasting high- and low-light canopy positions altered phenolic compounds, sugar-related metabolism, and transcription of genes associated with photosynthesis, carbohydrate metabolism, and photoprotection, showing that canopy light environment directly shapes fruit developmental physiology and composition (Yang et al., 2024).

Research progress over the last two decades shows that canopy management can deliver substantial agronomic value, but responses are strongly practice-, cultivar-, and climate-dependent. Reviews of summer pruning note that shoot positioning, shoot thinning, trimming, leaf removal, and cluster thinning are no longer viewed only as corrective operations, but as flexible tools for directing ripening and adapting vineyards to warming conditions. Leaf removal and shoot thinning can improve cluster exposure and hasten maturity, yet excessive exposure in warm climates can reduce the expected benefit for some quality traits and increase economic cost; in Cabernet Sauvignon, shoot thinning raised soluble solids by about 2.5 °Brix but also halved yield and increased labor cost markedly (Torres et al., 2020). Likewise, modern warm-climate viticulture increasingly applies leaf removal and shoot thinning more cautiously because clusters often need protection from overheating and sunburn (Poni et al., 2023). Training-system effects are also prominent. In North Dakota, leaf removal had no significant effect on 'Frontenac' fruit quality, whereas the Geneva Double Curtain increased cluster number and yield without reducing soluble solids or acidity (Olson et al., 2021). In a rainy region of China, the single-curtain system improved cluster-zone light, photosynthetic capacity, assimilate allocation to fruit, and reduced vegetative growth (Du et al., 2023). Canopy division has also doubled yield relative to dense vertical systems in vigorous vineyards, while open canopies increased photon flux, photosynthetic rate, soluble solids, and phenols in berries (Hernández-Ordoñez et al., 2024). In table grape cultivars, preharvest canopy-related applications improved red coloration and consumer acceptability in 'Crimson Seedless' under warming conditions, while summer pruning in 'Alphonse Lavallée' increased cluster and berry size, soluble solids, maturity index, phenolics, antioxidant activity, and berry mechanical resistance important for transportability (Petoumenou and Patris, 2021; Doğan, 2025). Yet not all interventions are consistently beneficial: in 'Sugraone', lateral-shoot formation increased yield with limited effects on standard quality traits, whereas in 'MidSouth' grapes early pruning, leaf removal, and shoot thinning often reduced yield and did not sufficiently improve fruit quality, underscoring the need for locally calibrated management (Leão and Lima, 2018; Williams et al., 2023).

This review examines the effects of canopy management practices on fruit development and yield stability in table grapes. Existing studies indicate that canopy management plays an important role in regulating the grapevine growing environment, improving fruit quality, and enhancing production stability. However, substantial differences exist among grape cultivars, training systems, ecological conditions, and combinations of management practices, and the precise matching of cultivar characteristics with canopy regulation strategies still requires further investigation. Using 'Shine Muscat' grape (*Vitis vinifera* 'Shine Muscat') as a representative case, this review synthesizes evidence on how optimized canopy management influences vine growth, fruit development, and yield formation. Particular attention will be given to the effects of different canopy regulation practices on vine growth, canopy structure, photosynthetic characteristics, fruit quality, and yield stability, while also summarizing the application effects of shoot control, training-system optimization, inflorescence thinning, cluster regulation, and light-environment management. This review provides a theoretical basis for optimizing canopy architecture in table grapes, improving the stability of fruit quality and yield performance in commercial production, and providing a reference for the precise, efficient, and sustainable development of the grape industry under climate change.

2 Mechanisms of Canopy Management Affecting Growth and Development of Fresh Table Grapes

2.1 Regulation of canopy structure and balance of vegetative growth

Canopy structure determines whether grapevines allocate resources to productive fruit growth or to excessive vegetative expansion. Foundational reviews describe canopy management as the manipulation of shoot number, shoot spacing, leaf area, fruit-zone exposure, and vigor so that the canopy is neither overly dense nor overly sparse, with the goal of maintaining an appropriate balance between shoot growth and fruit load (Lan, 2025). Dense, vigorous canopies promote long shoots, active laterals, and shading, which divert photosynthates into superfluous leaf area and create imbalance, while excessively short or thinned canopies can leave insufficient leaf area to ripen fruit adequately. In vigorous vineyards, lateral shoots often worsen crowding, humidity, and disease pressure, but in moderate-vigor systems lateral leaves can support sugar accumulation during ripening and increase starch reserves, showing that the value of vegetative growth depends on canopy context rather than on leaf area alone.

Experimental evidence shows that structural interventions affect fruit set, bunch architecture, and yield components by changing sink competition and carbohydrate partitioning. Removing active vegetative sinks at bloom increased fruit set, berries per cluster, and cluster weight in Pinot noir, whereas promoting vegetative growth during that period reduced reproductive allocation. Early canopy practices also altered berry number, berry fresh weight, and bunch compactness determinants in cultivar-dependent ways, indicating that the position and timing of leaf or shoot removal matter physiologically (Mataffo et al., 2023). In pre-flowering leaf-removal trials, intensive removal of main leaves and lateral shoots reduced yield potential by 47% on average, while even partial removal lowered yield potential and shifted must composition, supporting cautious use of severe early defoliation (Verdenal et al., 2024). Multi-season work in Montepulciano further showed that shoot thinning alone reduced canopy density without reliably improving composition, whereas shoot thinning plus pre-flowering defoliation reduced yield, lowered *Botrytis* incidence, improved fruit composition, and produced a carry-over reduction in the following year's yield (Silvestroni et al., 2019).

2.2 Optimization of canopy light environment and improvement of leaf photosynthetic efficiency

The most consistent mechanism linking canopy management to grapevine performance is the regulation of the internal light environment. Canopy architecture directly controls light quantity and quality in leaves, buds, and clusters, and light interception is repeatedly identified as the dominant microclimatic driver of canopy photosynthesis, fruitfulness, and ripening. Practices such as shoot thinning, positioning, leaf removal, and divided or alternative training systems improve light penetration and canopy porosity, but the target is balance rather than maximum openness because excessive gaps waste incident radiation and excessive exposure can cause photoinhibition or quality losses (Lan, 2025). In overhead table grape systems, modeling showed that the most productive leaf layers were those receiving intermittent shade plus sunflecks, whereas the topmost continuously exposed leaves showed some photoinhibition, indicating that moderate internal illumination can support whole-canopy carbon gain efficiently even at relatively high leaf area index.

Training-system and canopy-opening studies show how this mechanism translates into photosynthetic performance. In 'Miguang' grape, the single-curtain system increased photosynthetic photon flux density in the cluster zone, raised chlorophyll content, improved net photosynthetic capacity of basal-to-middle leaves during berry expansion and veraison, and increased assimilate allocation to fruit while reducing vegetative growth (Du et al., 2023). In a desert vineyard, open canopies increased photon flux density, daily light integral, photosynthetic rate, and leaf area during vegetative growth, while berries from open canopies had higher soluble solids and total phenols, although canopy opening also increased temperature (Hernández-Ordoñez et al., 2024). Canopy architecture also modified water-use behavior: a sprawl system in Syrah improved radiation interception efficiency and water-use efficiency relative to vertical shoot positioning under semiarid stress (De La Fuente et al., 2026). Under drought, variation in photosynthesis within canopies was mainly explained by differences in light interception, while severe stress progressively suppressed gas exchange across most canopy positions, showing that light optimization and water status interact rather than acting independently.

2.3 Regulation of canopy microenvironment and fruit quality formation

Canopy management also affects fruit development by altering the berry microenvironment, including temperature, humidity, airflow, evaporation, and solar exposure. Reviews emphasize that canopy manipulation changes not only sunlight but also temperature and humidity around clusters, thereby influencing disease incidence, berry thermal relations, and ripening conditions (Lan, 2025). This mechanism is especially important in humid or rainy regions, where vigorous shoot growth, high air humidity, and poor ventilation accelerate fungal spread and depress fruit quality (Du et al., 2023). It is also increasingly important in warm climates, where excessive cluster exposure and heat accumulation can impair color development and composition rather than improve them (Hunter et al., 2021; Petoumenou and Patris, 2021; Dou et al., 2024).

Berry-quality responses show that the effect of exposure is nonlinear. In warm-climate Cabernet Sauvignon, shoot thinning hastened maturity, increased soluble solids by about 2.5 °Brix, and reduced methoxypyrazines, but it did not improve anthocyanins at harvest and reduced yield substantially, indicating that more exposure does not necessarily improve all quality traits (Torres et al., 2020). Row-orientation work showed that morning-exposed berries with cooler afternoon profiles had slightly advanced sugar ripening and generally higher anthocyanins and phenols, whereas bunches reaching late-afternoon heat peaks had poorer composition (Hunter et al., 2021). Controlled-environment studies confirm the mechanism: high temperature and low light both impaired coloring, high temperature promoted sugar accumulation but caused softening, and high heat downregulated anthocyanin-pathway genes while reducing total anthocyanin accumulation in sensitive cultivars (Dou et al., 2024; Zha et al., 2024). At the molecular level, high-light berry microclimates increased expression of genes linked to photosynthesis, carbohydrate metabolism, photoprotection, and flavonol synthesis, supporting a direct connection between canopy-regulated microclimate and fruit metabolic composition. In table grapes specifically, improving canopy-associated preharvest conditions enhanced red color and consumer acceptability in ‘Crimson Seedless’, with Sunred® increasing anthocyanin accumulation and overall market acceptance (Petoumenou and Patris, 2021).

3 Case Background: Canopy Optimization Management Practice in ‘Shine Muscat’ Grapes

3.1 Cultivar characteristics and problems in production

A major practical problem in ‘Shine Muscat’ is that basic cultivation standards remain incompletely standardized despite fast acreage expansion. Korean studies note that growers lack cultivar-specific protocols for seedlessness induction and cluster thinning, and leaving inflorescences longer than 5 cm increases later berry-thinning labor and often produces clusters exceeding 1 000 g (Figure 1) (Shin et al., 2019). Related work showed that natural berries can be relatively small and clusters sparse, while rust spot near maturity can reduce appearance quality and commodity value.



Figure 1 Shape of ‘Shine Muscat’ clusters at harvest time following floral cluster thinning to 3 cm (A), 4 cm (B), and 5 cm (C) (Adopted from Shin et al., 2019)

Fruit-load and uniformity problems are central because heavier or less-regulated clusters tend to dilute quality. Floral cluster thinning is used to improve cluster uniformity and regulate fruit quality, and in ‘Shine Muscat’ larger cluster load is associated with poorer within-cluster consistency and lower sugar-acid balance (Shin et al.,

2019; Choi et al., 2023). Low crop load increased single-berry weight, sugar-acid ratio, phenolics, antioxidant activity, terpene and C13-norisoprenoid contents, and sensory scores, showing that this cultivar is highly responsive to source-sink regulation (Li et al., 2023).

3.2 Design of canopy optimization management practices

Canopy optimization in ‘Shine Muscat’ should be designed as a combined system rather than a single operation, integrating training architecture, shoot-vigor control, crop-load regulation, and fruit-zone management. Broader trellis research shows that training-system choice changes canopy architecture, light exposure, photosynthetic activity, yield, and berry composition, and divided or high-canopy systems often improve radiation capture or yield stability relative to dense vertical systems (Del Zozzo and Poni, 2024; Domingues Neto et al., 2024). In table grapes under protected cultivation, trellis and thinning must be coordinated because the SAYM system produced larger leaf area index (LAI) but lower light transmission and photosynthetically active radiation (PAR) than pergola, while heavy berry thinning improved total soluble solids (TSS), TSS/titratable acidity (TA), pH, color density, and skin anthocyanins (Yin et al., 2022).

For ‘Shine Muscat’ specifically, the design of canopy optimization practices should include standardized cluster-length control, precise berry thinning, and carefully dosed growth regulators to synchronize vegetative control with berry development. Thinning clusters to 3~4 cm or about 4 cm improved fruit growth and maintained a more appropriate sugar-acid ratio than 5 cm treatments, which left more berries but smaller berry size and lower ratio (Shin et al., 2019; Choi et al., 2023). PGR programs also require restraint: GA₃+TDZ and GA₃+CPPU can achieve near-complete seedlessness and increase berry size, but excessive CPPU, GA₃, EBR, or high retardant doses can lower soluble solids, increase hollowness, thicken rachises, or restrict leaf and cluster development (Cheng et al., 2025; Yang et al., 2025).

3.3 Evaluation indicators for different canopy management systems

The evaluation of different canopy management systems in ‘Shine Muscat’ should cover three dimensions: canopy structure and physiology, yield stability, and market-oriented fruit quality. Classic canopy-assessment work recommends quick field diagnosis by point quadrat analysis and canopy scoring, together with multiple numeric descriptors of canopy surface, shade, spacing, and fruit-zone exposure. Consistent with this, recent trellis studies assessed budbreak, bearing-shoot proportion, LAI, transmission coefficient, PAR, mean leaf angle, transpiration, and photosynthetic rate as core indicators of canopy performance (Yin et al., 2022).

Yield and fruit-quality indicators should then be tracked together because training systems often shift productivity and quality in different directions. Useful production indices include cluster number, cluster weight, berry weight, total yield, and leaf area-to-fruit balance, while quality indices include SSC, TA, SSC/TA ratio, firmness, peel residual feel, color density, anthocyanins, phenolics, sugars, aroma, and postharvest disease incidence (Shin et al., 2019; Olson et al., 2021; Yin et al., 2022; Yu et al., 2022; Choi et al., 2023). For ‘Shine Muscat’, this expanded indicator set is especially justified because supplementary blue light improved TSS, sugars, berry hue, and monoterpene-driven floral and fruity aroma, rootstocks altered berry weight, TSS/TA, phenolics, and volatile profiles, and rain-shelter plus root restriction reduced disease incidence and postharvest risk (Chen et al., 2024; Ren et al., 2024; Li et al., 2025).

4 Effects of Canopy Optimization on Fruit Development of ‘Shine Muscat’ Grapes

4.1 Effects on plant growth and canopy structure

‘Shine Muscat’ shows a strong tendency toward excessive vegetative growth, and this vigor is a primary reason canopy optimization is necessary in commercial production (Cheng et al., 2026). Dense canopies reduce photosynthetic efficiency, worsen the canopy microclimate, delay maturation, and can also impair flower-bud differentiation and shoot maturation (Cheng et al., 2025). In response, chemical growth-control strategies have been effective at suppressing shoot elongation in ‘Shine Muscat’, with both mepiquat chloride and chlormequat chloride reducing shoot growth, and CCC showing stronger inhibition than MC. A later study similarly found that Pro-Ca alone had limited effect at low concentrations, whereas Pro-Ca 300 mg/L+MC 300 mg/L effectively inhibited shoot elongation and improved canopy branch density. These results indicate that canopy optimization in

‘Shine Muscat’ depends not only on reducing vigor, but on reshaping canopy architecture into a more open and better-distributed structure (Collins et al., 2020).

Training and canopy-positioning studies support the same conclusion from a structural perspective. In grapevines, canopy manipulation is used to optimize canopy structure, balance vegetative and reproductive growth, and ensure more effective fruit exposure to sunlight (Collins et al., 2020). In a related table-grape system, the single-curtain training system reduced vegetative growth, shortened internodes, and redistributed leaf area toward the middle canopy, producing a more functionally efficient canopy than pergola training (Du et al., 2023). Under heat stress in rain-shelter ‘Shine Muscat’, trellis-system effects were also integrated canopy effects, simultaneously altering vigor, water relations, and canopy microclimate, with the upward-trained pendulous system maintaining the lowest canopy heat load and the least sunburn damage (Luo et al., 2026). Structural optimization is therefore best understood as a coordinated adjustment of shoot growth, branch density, leaf distribution, and cluster exposure, rather than simple canopy reduction (Zarrouk et al., 2024).

4.2 Effects on photosynthetic characteristics and dry matter accumulation

The clearest physiological effect of canopy optimization in ‘Shine Muscat’ is the improvement of the canopy light environment, especially under rain-shelter or facility cultivation where incoming light is often limited (Yuan et al., 2024; Li et al., 2025). In protected ‘Shine Muscat’, reflective ground film increased net leaf photosynthetic rate by 24.9% on 3309C and 35.2% on 5BB rootstocks, showing that light-environment optimization can substantially raise leaf carbon assimilation even without major changes in vegetative growth indices. Supplemental lighting also improved production performance in the same cultivar, although the mechanism was more complex: night lighting at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ produced the highest yield, sugar-acid ratio, and economic return, while differences in Pn, Pmax, and apparent photosynthetic efficiency among treatments were small. This suggests that canopy-light optimization can enhance whole-vine productivity not only by increasing instantaneous leaf photosynthesis, but also by extending effective light use and improving the fruit developmental environment (Yuan et al., 2025).

Evidence from related grape systems clarifies how these changes translate into dry matter accumulation. In ‘Miguang’, the single-curtain system increased cluster-zone photon flux density, chlorophyll content, net photosynthetic capacity of basal and middle leaves at berry expansion and veraison, and assimilate distribution to fruit, while also increasing shoot soluble sugar and starch content and reducing vegetative growth (Figure 2) (Du et al., 2023). In ‘Shine Muscat’, reduced light intensity had the opposite effect: shading decreased leaf photosynthetic activity, transpiration, and stomatal conductance, reduced organic matter accumulation, and then suppressed glucose, fructose, and soluble solids while increasing malic, tartaric, and citric acids in berries (Yang et al., 2024). Heat-tolerant trellis optimization also preserved stomatal aperture, chlorophyll content, chlorophyll fluorescence, and net photosynthetic rate under prolonged heat stress, especially in the U-PT system, indicating that canopy optimization protects dry matter production by maintaining photosynthetic apparatus stability under stress (Luo et al., 2026). Grafting adds a related resilience mechanism in ‘Shine Muscat’, because grafted plants under drought maintained better water status, photosynthesis, and antioxidant defense than self-rooted plants, helping sustain assimilate production under environmental stress (Jiao et al., 2023).

4.3 Effects on fruit enlargement, maturation, and quality formation

The most direct fruit response to canopy optimization in ‘Shine Muscat’ is improved berry enlargement and more favorable ripening, but the benefit depends strongly on treatment intensity and combination. Moderate shoot-control treatments such as MC 500 mg/L or CCC 100 mg/L improved berry size, soluble solids, and the sugar-acid ratio while maintaining effective shoot control, whereas high concentrations restricted leaf and cluster development (Cheng et al., 2025). The combined Pro-Ca 300 mg/L + MC 300 mg/L treatment also increased single-berry weight, berry diameter, and SSC, supporting the idea that regulating vigor can redirect growth toward fruit development (Cheng et al., 2026). Floral cluster thinning further improved fruit development in this cultivar: thinning to 4 cm promoted fruit growth and maintained an appropriate sugar-acid ratio, whereas 5 cm thinning left more berries but produced smaller berries and a lower sugar-acid ratio (Choi et al., 2023). More broadly, low crop load increased single-berry weight, sugar-acid ratio, phenolics, antioxidant activity, terpene and

C13-norisoprenoid contents, and sensory scores, showing that source-sink optimization is a major route by which canopy-related management improves ‘Shine Muscat’ quality (Li et al., 2023).

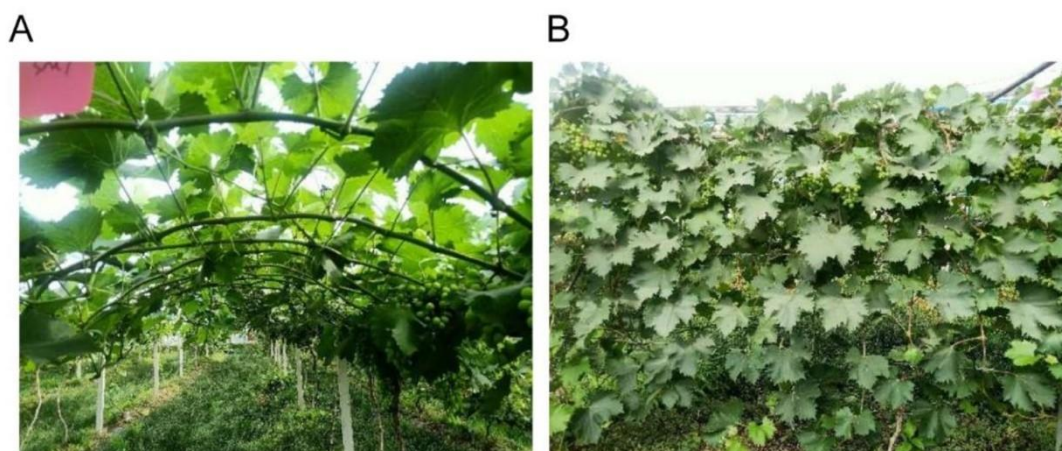


Figure 2 PER (pergola) (A) and SCT (single-curtain training system) (B) of ‘Miguang’ grape (Adopted from Du et al., 2023)

Berry-quality formation also responds to canopy-regulated light, temperature, and hormonal conditions. Supplementary light under facility cultivation reduced green hue, lowered organic acids, increased soluble solids, glucose, and fructose, and enhanced monoterpene accumulation and floral-fruity sensory quality, with blue light giving the best overall quality improvement (Li et al., 2025). Reflective ground film likewise improved sugar-acid ratio and aroma composition in protected ‘Shine Muscat’ (Yuan et al., 2024). PGR combinations produced strong but differentiated berry responses: GA₃+TDZ and GA₃+CPPU achieved nearly or fully 100% seedlessness, CPPU and TDZ increased berry weight and size through cortical expansion, GA₃ increased berry weight but also promoted rachis thickening and lowered TSS, and EBR at higher concentrations inhibited berry growth (Yang et al., 2025). At the cellular level, GA₃ promoted berry longitudinal elongation by enlarging cells and reducing cell density, whereas CPPU promoted transverse expansion by increasing both cell number and cell dimensions, explaining why different management combinations can improve berry size while also altering berry shape and commercial appearance (Chen et al., 2025).

5 Case Analysis: Effects of Canopy Optimization on Yield Stability of ‘Shine Muscat’ Grapes

5.1 Effects on yield components and marketable fruit rate

Canopy optimization changes yield stability first through its effects on the immediate components of yield, including fruit set, bunch number, bunch weight, berry number, and berry weight. In grapevine, fruit weight per node is determined by shoots per node, bunches per shoot, bunch weight, berries per bunch, and berry weight, so canopy practices can stabilize total output only if they improve several of these components together rather than enlarging one at the expense of another. In ‘Shine Muscat’, combined GA₃ and CPPU treatments significantly improved fruit set, cluster density, the percentage of seedless berries, and overall yield stability, while also increasing single-berry mass, cluster mass, soluble solids, and fruit hardness. Floral cluster thinning also changed the balance between cluster compactness and individual berry growth: a 4 cm thinning standard promoted fruit growth and maintained a better sugar-acid ratio, whereas 5 cm thinning produced more berries per cluster but smaller berries and a lower sugar-acid ratio (Figure 3) (Choi et al., 2023).

The marketable fruit rate in ‘Shine Muscat’ depends not only on total yield but also on maintaining berry size, appearance, firmness, sugar accumulation, and peel eating quality within commercial ranges. PGR treatments combining GA₃ with TDZ produced the largest cluster weight, berry weight, and berry diameter, while CPPU-based treatments better preserved fruit skin and flesh firmness and the positive residual feel of the edible peel, both of which are relevant to market acceptance (Choi et al., 2023). Yield control studies further showed that raising production to 24 000 kg/ha did not reduce fruit size, but it lowered soluble solids, worsened coloration, increased acidity and hardness, and retained more chlorophyll, whereas keeping yield at or below 21 000 kg/ha better balanced productivity and fruit quality (Kim et al., 2019). More generally, early canopy interventions can

alter fruit set, berry number per bunch, and berry fresh weight in cultivar-dependent ways, so stable marketable yield requires moderate and cultivar-specific regulation rather than severe canopy reduction (Mataffo et al., 2023).



Figure 3 Effects of different floral cluster thinning intensities on the cluster shape of ‘Shine Muscat’ grapes at harvest (Adopted from Choi et al., 2023).

Image caption: Floral cluster thinning was performed to 3 cm, 4 cm, and 5 cm, respectively, seven days before full bloom (Adopted from Choi et al., 2023)

5.2 Effects on source-sink balance and nutrient allocation

The second mechanism is the regulation of source-sink balance, because canopy optimization determines how much assimilating leaf area is available per unit fruit mass and how dry matter is partitioned among shoots, berries, and reserve organs. Grapevines are managed around the ratio of leaf area to fruit mass, and imbalance can appear as delayed ripening, fruit abortion, or alternate bearing (Martínez-Lüscher and Kurtural, 2021). Modeling work supports the same framework by showing that weather and source-sink ratio at critical stages determine bunch number, berry number, and berry fresh weight, while carbohydrate allocation must account for both sink strength and sink priority, including reserve storage (Zhu et al., 2021). In practice, this means canopy optimization in ‘Shine Muscat’ should aim to preserve enough functional leaf area to support ripening while preventing excessive vegetative demand from competing with clusters.

Evidence across grape systems shows that nutrient and assimilate allocation shifts strongly with canopy structure and crop load. In source-sink manipulation studies, moderate to high leaf or cane density increased berry weight, bunch weight, bunch volume, and yield in some cultivars, while the lowest cane density combined with the highest leaf density improved assimilate accumulation efficiency per gram of berry. By contrast, severe defoliation had major negative effects on berry size, berries per cluster, soluble solids, root starch, root mass, and ripening date, and these effects carried over into the following season as reduced leaf area, clusters per vine, berries per cluster, and yield (Martínez-Lüscher and Kurtural, 2021). Related experiments showed that under shade, vegetative development was maintained at the expense of berries, whereas under water deficit and high crop load, berry growth became the priority sink, confirming that carbon and nutrient allocation are plastic and environment-dependent (Poupard et al., 2025). For ‘Shine Muscat’, this supports using moderate vigor control, cluster thinning, and light optimization to direct assimilates toward fruit without triggering carbon starvation of the vine (Cheng et al., 2025; Lan, 2025).

5.3 Effects on yield stability under different environmental conditions

Yield stability in ‘Shine Muscat’ also depends on whether canopy optimization can buffer environmental stress, especially low light in protected cultivation and high temperature during ripening. Supplemental LED lighting under rain-shelter conditions increased ‘Shine Muscat’ yield, and the 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ night treatment raised yield by 45.1% relative to the unsupplemented control while also giving the highest economic return (Yuan et al.,

2025). Supplementary light of different wavelengths also improved soluble solids, glucose, fructose, and monoterpene accumulation, with blue light giving the best overall promotion of fruit quality under facility cultivation (Li et al., 2025). These results show that in low-radiation systems, canopy optimization includes light supplementation and not only shoot or leaf manipulation.

Under heat stress, stability depends more on avoiding excessive cluster and canopy temperatures than on maximizing exposure. In rain-shelter ‘Shine Muscat’, the upward-trained pendulous trellis maintained the lowest canopy temperatures, higher relative humidity, less sunburn, higher chlorophyll content, and better gas exchange and fluorescence performance than H-shaped trellising, and PCA identified it as the most heat-tolerant system (Luo et al., 2026). Shade-net studies reached a similar conclusion from another angle: shading cooled the canopy, improved the consistency of soluble solids and coloring, and increased berry uniformity, with green and blue nets performing best (Zha et al., 2022). Broader canopy-architecture work also found that shading through modulated shoot positioning altered berry water relations and stress responses, with effects becoming more pronounced in hotter, drier, or more climatically anomalous seasons (Zarrouk et al., 2024). At the reproductive level, canopy microclimate also matters for the next crop, because improved bud-zone light interception increases bud fruitfulness and inflorescence primordia development, supporting more stable bunch number in the following season (Collins et al., 2020).

6 Case Implications and Future Development Directions

The establishment of precision canopy management systems should be based on cultivar characteristics, as grape cultivars differ significantly in vigor, cluster compactness, fruitfulness, and responses to canopy regulation practices. Canopy management should not rely on fixed pruning or leaf-removal standards, but should consider canopy surface area, internal shading, cluster exposure, and the balance between fruit development and shoot growth. Optimizing canopy architecture according to cultivar characteristics affects not only current-season yield but also fruitfulness in the following growing season. Studies on fresh table grapes have shown that reducing canopy density combined with summer pruning improved yield, cluster weight, soluble solids content, and anthocyanin accumulation in ‘Crimson Seedless’ grapes, while T-trellis systems in muscat-flavored table grapes promoted moderate vigor, improved sugar-acid ratios, and enhanced polyphenol and monoterpene accumulation. Therefore, future research should establish cultivar-specific canopy management systems by integrating parameters such as trellis type, shoot density, leaf-area distribution, and cluster exposure thresholds to meet different production objectives.

Canopy regulation should be integrated with water-fertilizer management and crop-load control because canopy structure alone cannot fully determine grape yield and quality when water availability, nutrient status, and sink demand vary. Irrigation, canopy architecture, and production targets interact with each other. Studies have shown that reduced irrigation can decrease berry weight and yield but increase anthocyanins, tannins, and total phenolic compounds, whereas higher irrigation levels promote berry enlargement and yield formation. Fertilization management also influences canopy function and productivity; combined organic and inorganic fertilization can improve soil nutrient availability, enhance photosynthetic capacity, and increase grape yield and quality. Therefore, future fresh table grape production should develop an integrated management system based on the coordination of “canopy structure-water status-nutrient supply-fruit load”. Through comprehensive regulation, source-sink balance can be maintained, marketable yield stability can be improved, and vineyard adaptability to climate variability can be enhanced.

Digital technologies can improve the precision of grape canopy management by monitoring canopy spatial variation, physiological status, and yield changes. Currently, UAVs, proximal sensors, satellite remote sensing, and ground-based monitoring platforms have been applied to assess grapevine growth, canopy structure, leaf area index (LAI), water status, nutrient status, yield, and fruit quality. Low-cost RGB photogrammetry can estimate canopy structure, UAV-derived canopy thickness can effectively predict yield ($R^2 = 0.80$), and machine-learning models have achieved an average yield prediction accuracy of 85.95% across different years and vineyards. In the future, multimodal sensing technologies integrating hyperspectral imaging, thermal imaging, and canopy

physiological parameters may further improve the prediction of yield and quality traits. However, large-scale adoption of digital technologies is still limited by equipment costs, data-processing capacity, and technical compatibility. Therefore, future development should focus on sensor integration, Internet of Things (IoT)-based monitoring, and intelligent decision-support platforms to promote precision pruning, irrigation, fertilization, and harvesting management.

Acknowledgments

The author would like to thank all individuals who provided support and assistance during the preparation of this manuscript.

Conflict of Interest Disclosure

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

References

- Chen H., Li C., Li Y., Wang X., and Xi Z., 2024, Effects of cultivars as rootstocks on the expression of aroma components and related genes in ‘Shine Muscat’ grape, *European Food Research and Technology*, 250(4): 1043-1059.
<https://doi.org/10.1007/s00217-023-04444-1>
- Chen J., Guo Y., Hu H., Fang C., Wang L., Hu L., Lin Z.F., Zhang D., Yang Z., and Wu Y., 2025, Regulation of cell metabolism and changes in berry shape of Shine Muscat grapevines under the influence of different treatments with the plant growth regulators gibberellin A3 and N-(2-chloro-4-pyridyl)-N’-phenylurea, *Horticulturae*, 11(10): 1160.
<https://doi.org/10.3390/horticulturae11101160>
- Cheng D., He S., Li L., Tong X., Gu H., Sun X., Li M., and Chen J., 2025, Effects of mepiquat chloride and chlormequat chloride on the growth and fruit quality of ‘Shine Muscat’ grapevines, *Agriculture*, 15(12): 1267.
<https://doi.org/10.3390/agriculture15121267>
- Cheng D., He S., Li L., Tong X., Gu H., Sun X., Li M., and Chen J., 2026, Impact of prohexadione calcium and mepiquat chloride on vegetative growth and fruit quality in ‘Shine Muscat’ grapevines, *Horticulturae*, 12(4): 418.
<https://doi.org/10.3390/horticulturae12040418>
- Choi S., Ban S., and Choi C., 2023, The impact of plant growth regulators and floral cluster thinning on the fruit quality of ‘Shine Muscat’ grape, *Horticulturae*, 9(3): 392.
<https://doi.org/10.3390/horticulturae9030392>
- Collins C., Wang X., Lesefko S., De Bei R., and Fuentes S., 2020, Effects of canopy management practices on grapevine bud fruitfulness, *OENO One*, 54(2): 313-325.
<https://doi.org/10.20870/oeno-one.2020.54.2.3016>
- De La Fuente M., Linares R., Lissarrague J.R., Sánchez-Élez S., and Baeza P., 2026, Influence of canopy vineyard management on physiological behaviour and radiation interception efficiency in Syrah, *Horticulturae*, 12(2): 242.
<https://doi.org/10.3390/horticulturae12020242>
- Del Zozzo F., and Poni S., 2024, Climate change affects choice and management of training systems in the grapevine, *Australian Journal of Grape and Wine Research*, 2024: 7834357.
<https://doi.org/10.1155/2024/7834357>
- Doğan O., 2025, Determination of effects of some summer pruning applications on yield and quality characteristics of Alphonse Lavallée (*Vitis vinifera* L.) grape variety, *Horticulturae*, 11(4): 445.
<https://doi.org/10.3390/horticulturae11040445>
- Domingues Neto F.J., Tecchio M.A., Borges C.V., Rodrigues J.D., Ono E.O., Lima G.P.P., Moura M.F., Hernandes J.L., Silva M.S., and Leonel M., 2024, Yield performance and quality assessment of Brazilian hybrid grapes influenced by rootstocks and training systems, *Horticulturae*, 10(9): 909.
<https://doi.org/10.3390/horticulturae10090909>
- Dou F., Phillip F.O., and Liu H., 2024, Combined metabolome and transcriptome analysis revealed the accumulation of anthocyanins in grape berry (*Vitis vinifera* L.) under high-temperature stress, *Plants*, 13(17): 2394.
<https://doi.org/10.3390/plants13172394>
- Du W., Li S., Du T., Huang W.C., Zhang Y., Kang H., Yao Y., Gao Z., and Du Y.P., 2023, ‘Miguang’ grape response to pergola and single-curtain training systems, *Horticulturae*, 9(1): 113.
<https://doi.org/10.3390/horticulturae9010113>
- Galar-Martínez M., Torres N., Sebastián B., Palacios J., Arzoz I., Juanena N., Villa-Llop A., Loidi M., Dewasme C., Roby J.P., and Santesteban L.G., 2024, Respectful pruning improves grapevine development: a case study in young vineyards, *Australian Journal of Grape and Wine Research*, 2024: 8448405.
<https://doi.org/10.1155/2024/8448405>
- Hernández-Ordoñez E., Cruz-Álvarez O., Orozco-Avitia J.A., Hernández-Rodríguez O.A., Alonso-Villegas R., Jacobo-Cuéllar J.L., Gardea-Bejar A., and Ojeda-Barrios D., 2024, Physiological responses of cabernet sauvignon to dividing canopies in the chihuahuan desert, *Agriculture*, 14(12): 2101.
<https://doi.org/10.3390/agriculture14122101>

- Hunter J.J., Volschenk C.G., Mania E., Castro A., Booyse M., Guidoni S., Pisciotto A., Lorenzo R., Novello V., and Zorer R., 2021, Grapevine row orientation mediated temporal and cumulative microclimatic effects on grape berry temperature and composition, *Agricultural and Forest Meteorology*, 310: 108660.
<https://doi.org/10.1016/j.agrformet.2021.108660>
- Jiao S., Zeng F., Huang Y., Zhang L., Mao J., and Chen B., 2023, Physiological, biochemical and molecular responses associated with drought tolerance in grafted grapevine, *BMC Plant Biology*, 23(1): 110.
<https://doi.org/10.1186/s12870-023-04109-x>
- Kim J.H., Jung M.H., Park Y.S., Lee B.H.N., and Park H.S., 2019, Suitable yields and establishment of harvesting standard in ‘Shine Muscat’ grape, *Horticultural Science and Technology*, 37(2): 178-189.
<https://doi.org/10.12972/kjhst.20190018>
- Lan H.F., 2025, The role of canopy management in optimizing grapevine yield and quality, *International Journal of Horticulture*, 15(3): 133-142.
<https://doi.org/10.5376/ijh.2025.15.0015>
- Leão P.C.S., and Lima M.A.C., 2018, Canopy management of table grapes cultivar in tropical conditions, *Journal of Agricultural Science and Technology B*, 8(4): 228-233.
<https://doi.org/10.17265/2161-6264/2018.04.004>
- Li J., Ma T., Bao S., Yin D., Ge Q., Li C., Fang Y., and Sun X., 2023, Suitable crop loading: an effective method to improve ‘Shine Muscat’ grape quality, *Food Chemistry*, 424: 136451.
<https://doi.org/10.1016/j.foodchem.2023.136451>
- Li W., Zheng T., Zhang J., Li W., Chen K., Zhang K., and Fang Y., 2025, Supplementary light with different wavelengths improved the monoterpenes aroma and quality traits of ‘Shine Muscat’ grape berries under facility cultivation, *Food Chemistry*, 474: 143255.
<https://doi.org/10.1016/j.foodchem.2025.143255>
- Luo L., Liu X.Y., Lyu X., Zhong Q., Ma Y.J., Li R., and Liu W., 2026, Trellis systems ameliorate heat damage by regulating canopy temperature, photosynthetic efficiency and leaf microstructure of grapevine, *Frontiers in Plant Science*, 16: 1648999.
<https://doi.org/10.3389/fpls.2025.1648999>
- Martínez-Lüscher J., and Kurtural S.K., 2021, Same season and carry-over effects of source-sink adjustments on grapevine yields and non-structural carbohydrates, *Frontiers in Plant Science*, 12: 695319.
<https://doi.org/10.3389/fpls.2021.695319>
- Mataffo A., Scognamiglio P., Molinaro C., Corrado G., and Basile B., 2023, Early canopy management practices differentially modulate fruit set, fruit yield, and berry composition at harvest depending on the grapevine cultivar, *Plants*, 12(4): 733.
<https://doi.org/10.3390/plants12040733>
- Olson B.K., Brooke M., Wang Z., Syvante K., Stenger J., and Hatterman-Valenti H., 2021, ‘Frontenac’ grape response to canopy management in North Dakota, *Horticulturae*, 7(9): 288.
<https://doi.org/10.3390/horticulturae7090288>
- Petoumenou D.G., and Patris V.E., 2021, Effects of several preharvest canopy applications on yield and quality of table grapes (*Vitis vinifera* L.) cv. Crimson Seedless, *Plants*, 10(5): 906.
<https://doi.org/10.3390/plants10050906>
- Poni S., Frioni T., and Gatti M., 2023, Summer pruning in Mediterranean vineyards: is climate change affecting its perception, modalities, and effects, *Frontiers in Plant Science*, 14: 1227628.
<https://doi.org/10.3389/fpls.2023.1227628>
- Poupard M., Gallo A., Boulard R., Guillem P., Rolland G., Simonneau T., Christophe A., and Pallas B., 2025, Source-sink manipulations through shading, crop load and water deficit affect plant morphogenesis and carbon sink priorities leading to contrasted plant carbon status in grapevine, *Annals of Botany*, 136(1): 49-66.
<https://doi.org/10.1093/aob/mcae203>
- Ren W., Sun C., Wang L., Zhu C., Ren D., Wang T., Wang L., Cai Y., Wang Y., Zhu P., and Xu L., 2024, Postharvest disease, latent infection, and preharvest control of ‘Shine-Muscat’ grapes, *Postharvest Biology and Technology*, 214: 112989.
<https://doi.org/10.1016/j.postharvbio.2024.112989>
- Shin H.W., Kim G.H., and Choi C., 2019, Effects of plant growth regulators and floral cluster thinning on fruit quality of ‘Shine Muscat’ grape, *Horticultural Science and Technology*, 37(6): 678-686.
<https://doi.org/10.7235/HORT.20190068>
- Silvestroni O., Lanari V., Lattanzi T., Palliotti A., VanderWeide J., and Sabbatini P., 2019, Canopy management strategies to control yield and grape composition of Montepulciano grapevines, *Australian Journal of Grape and Wine Research*, 25(1): 30-42.
<https://doi.org/10.1111/ajgw.12367>
- Torres N., Martínez-Lüscher J., Porte E., and Kurtural S.K., 2020, Optimal ranges and thresholds of grape berry solar radiation for flavonoid biosynthesis in warm climates, *Frontiers in Plant Science*, 11: 931.
<https://doi.org/10.3389/fpls.2020.00931>
- Verdenal T., Zufferey V., Dienes-Nagy Á., Bieri S., Bourdin G., Reynard J.S., and Spring J.L., 2024, Exploring grapevine canopy management: effects of removing main leaves or lateral shoots before flowering, *OENO One*, 58(4): 8175.
<https://doi.org/10.20870/oeno-one.2024.58.4.8175>

- Williams H.N., Stafne E.T., Zhang Y., and Chang S., 2023, Evaluating the effects of early pruning, leaf removal, and shoot thinning on 'MidSouth' grapes over two consecutive vintages in South Mississippi, *Agronomy*, 13(2): 368.
<https://doi.org/10.3390/agronomy13020368>
- Yang P., Wu Z.W., Liu B., Wang L., and Wang S., 2025, Synergistic effects of gibberellic acid, forchlorfenuron, thidiazuron, and brassinosteroid combinations on seedless berry development and quality enhancement in 'Shine Muscat' and 'Red Muscat of Alexandria' grapes, *Biology*, 14(9): 1270.
<https://doi.org/10.3390/biology14091270>
- Yang Z., Shen L., Hu L., Cai Y., Zheng Q., and Wu Y., 2024, The *PEPCK* and *FBP* genes regulate gluconeogenesis metabolism in grape berries in response to light intensity, *Horticulturae*, 10(12): 1270.
<https://doi.org/10.3390/horticulturae10121270>
- Yin Y., Li M., Jia N., Sun Y., Han B., Liu C., Liu S., Zhao S., and Guo Z., 2022, Effects of trellis system and berry thinning intensity on vine performance and quality composition of two table grape cultivars under protected cultivation in northern China, *Scientia Horticulturae*, 299: 111045.
<https://doi.org/10.1016/j.scienta.2022.111045>
- Yu R., Torres N., Tanner J.D., Kacur S.M., Marigliano L.E., Zumkeller M., Gilmer J.C., Gambetta G.A., and Kurtural S.K., 2022, Adapting wine grape production to climate change through canopy architecture manipulation and irrigation in warm climates, *Frontiers in Plant Science*, 13: 1015574.
<https://doi.org/10.3389/fpls.2022.1015574>
- Yuan Y., Liu S., Xie Y., Nie J., Yang X., and Huang R., 2025, The effects of light duration and intensity with supplemental light-emitting diode lights on grape photosynthesis, yield, and fruit quality, *Agronomy*, 15(3): 518.
<https://doi.org/10.3390/agronomy15030518>
- Yuan Y., Xie Y., Li B., Wei X., Huang R., Liu S., and Ma L., 2024, To improve grape photosynthesis, yield and fruit quality by covering reflective film on the ground of a protected facility, *Scientia Horticulturae*, 327: 112792.
<https://doi.org/10.1016/j.scienta.2023.112792>
- Zarrouk O., Pinto C., Alarcón M.V., Flores-Roco A., Santos L., David T.S., Amâncio S., Lopes C., and Carvalho L.C., 2024, Canopy architecture and sun exposure influence berry cluster-water relations in the grapevine variety Muscat of Alexandria, *Plants*, 13(11): 1500.
<https://doi.org/10.3390/plants13111500>
- Zha Q., Wu J., Xi X., He Y., Yin X., and Jiang A., 2022, Effects of colored shade nets on grapes and leaves of 'Shine Muscat' grown under greenhouse conditions, *American Journal of Enology and Viticulture*, 73(1): 39-47.
<https://doi.org/10.5344/ajev.2021.21022>
- Zha Q., Zhong H., Tang M., Yin X., Sun P., Jiang A., Xi X., and Wu J., 2024, Effects of temperature and light during the veraison period on grape berry growth, *Plant Stress*, 14: 100642.
<https://doi.org/10.1016/j.stress.2024.100642>
- Zhu J., Parker A., Gou F., Agnew R., Yang L., Greven M., Raw V., Neal S., Martin D., Trought M.C.T., Huth N., and Brown H.E., 2021, Developing perennial fruit crop models in APSIM next generation using grapevine as an example, *In Silico Plants*, 3(2): diab021.
<https://doi.org/10.1093/insilicoplants/diab021>

Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Reasons to publish in GenBreed Publisher *An Online Publishing Platform*

- ★ Peer review quickly and professionally
- ☆ Publish online immediately upon acceptance
- ★ Deposit permanently and track easily
- ☆ Access free and open around the world
- ★ Disseminate multilingual available

Submit your manuscript at: <http://genbreedpublisher.com/>

