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## Review Article

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# Variation in Quality Traits Among Different Tea Cultivars Used for Longjing Tea

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**Abstract** This study investigates different tea plant cultivars used for Longjing tea processing, focusing on their quality trait differences and underlying formation mechanisms. First, the typical quality characteristics of Longjing tea are summarized from aspects such as appearance, aroma, taste, liquor color, and infused leaves, and the synergistic effects of cultivar, environment, and processing techniques on quality formation are clarified. Furthermore, differences among cultivars in key chemical components, including amino acids, tea polyphenols, caffeine, and volatile aroma compounds, are compared to reveal their contributions to freshness, bitterness-astringency balance, and aroma profiles. The results indicate that cultivars determine the flavor type and quality level of Longjing tea by regulating metabolite composition and processing response pathways. In addition, this study discusses differences in processing suitability and quality stability among cultivars, and highlights recent advances in molecular biology and multi-omics technologies for elucidating quality traits and breeding new cultivars. In response to current limitations such as incomplete evaluation systems and insufficient multi-factor studies, it proposes strengthening multidimensional evaluation and integrated research on cultivar-environment-processing interactions, providing references for the selection of high-quality cultivars and the development of the Longjing tea industry.

**Keywords** Longjing tea; Tea plant cultivars; Quality traits; Chemical composition; Processing suitability

## 1 Introduction

Longjing tea, one of the most representative pan-fired flat green teas in China, is produced in Hangzhou, Zhejiang Province. It is renowned both domestically and internationally for its typical quality characteristics of “green color, rich aroma, mellow taste, and beautiful shape,” and has been granted geographical indication protection (Shen et al., 2024). Its distinctive sensory quality and profound cultural heritage place it at the core of China’s premium green tea system, while its limited early-spring yield and well-established grading system confer significant economic value (Yu et al., 2023; Zhao et al., 2024). In recent years, with the shift toward premium and health-oriented consumption, demand for high-quality green tea—particularly Longjing tea with strong geographical identity—has continued to increase, promoting industrial expansion and making it a key pillar of the tea industry in Zhejiang and across China (Huang et al., 2024; Teng et al., 2024).

Against this background, the formation mechanism and stability of Longjing tea quality have become important research focuses. Previous studies have shown that Longjing tea quality depends not only on processing techniques but also on the combined effects of cultivar, growing environment, and harvesting period (Yu et al., 2023). With the advancement of metabolomics, sensory science, and genomics, researchers are now able to systematically elucidate, at the molecular level, the dynamic changes of amino acids, catechins, phenolic acids, and volatile compounds during processing, as well as their contributions to key quality attributes such as freshness, bitterness-astringency balance, and chestnut-like aroma (Huang et al., 2024; Teng et al., 2024; Zeng et al., 2024). Meanwhile, techniques such as stable isotope analysis, near-infrared spectroscopy, and chemometric modeling have been applied to authenticity identification and quality grading, reflecting increasing industry demands for quality stability and traceability (Zhao et al., 2024; Wu et al., 2025).

Among the various influencing factors, tea plant cultivars are considered one of the core determinants of quality differences in Longjing tea. Significant variations exist among cultivars in genetic background, physiological



traits, and metabolic profiles, leading to distinct accumulation patterns of flavonoids, amino acids, alkaloids, and aroma precursors even under similar cultivation and processing conditions (Yu et al., 2023; Bassiony et al., 2024). These differences directly affect the freshness, bitterness, and overall flavor balance of the tea infusion. For example, “Longjing 43” and local population varieties differ markedly in chlorophyll composition, amino acid content, and responses to environmental factors, thereby influencing the color and taste of the final product (Teng et al., 2024), while variations in volatile compounds determine characteristic aroma types such as bean-like and chestnut-like notes (Yan et al., 2025). With advances in breeding and molecular biology, several improved cultivars suitable for Longjing tea processing (e.g., Longjing 43, Wuniuzao, and Zhenong series) have been developed and widely adopted. However, differences in processing suitability and quality stability among cultivars remain evident (Teng et al., 2024). Meanwhile, genomic tools such as QTL mapping and molecular markers have provided new insights into the genetic basis of quality traits (Gao et al., 2023a; Ao et al., 2025), yet systematic comparisons among specialized Longjing cultivars are still lacking, highlighting the need for comprehensive multi-dimensional studies (Huang et al., 2024).

This study focuses on different tea plant cultivars used for Longjing tea processing, aiming to analyze their differences in appearance, sensory characteristics, and chemical composition. Special attention is given to the roles of non-volatile and volatile metabolites in quality formation, as well as processing suitability and its molecular regulation mechanisms. Furthermore, by integrating advances in metabolomics and genetics, this study evaluates the potential applications of cultivar differences in quality grading, authenticity identification, and the breeding of high-quality specialized cultivars. The findings are expected to provide a theoretical basis for cultivar selection and precise matching between cultivars and processing techniques, thereby promoting the high-quality development of the Longjing tea industry.

## **2 Basis of Longjing Tea Quality Formation**

### **2.1 Typical quality characteristics of Longjing tea**

Longjing tea, as a typical representative of flat green tea in China, exhibits its quality characteristics mainly in appearance, aroma, taste, liquor color, and infused leaves, forming a stable and highly recognizable style. High-quality Longjing tea is characterized by flat, smooth, straight, and uniform dry leaves, with a tender green or bright green color; the brewed liquor appears bright yellow-green and clear, while the infused leaves are tender, uniform, soft, and well-expanded (Bassiony et al., 2024; Zeng et al., 2024). This distinctive “flat, smooth, straight” appearance results not only from the tenderness and uniformity of fresh leaves but also from key processing steps such as flattening and shaping, serving as an important feature distinguishing it from other green teas. Generally, fresh leaves consisting of one bud with one or two young leaves are more suitable for producing high-quality appearance. Some studies have shown that the appearance quality of Longjing tea can be quantitatively evaluated using colorimetric parameters, where L, a, b values and chlorophyll content are significantly correlated with sensory evaluation. Moderate brightness and yellow-green coloration are favorable for high-quality appearance, whereas excessive chlorophyll may lead to darker color and reduced visual quality (Shan et al., 2023a; Bassiony et al., 2024; Zhang et al., 2024). In addition, higher-grade samples often exhibit lighter and brighter liquor, reflecting more tender raw materials and more precise processing control (Shan et al., 2025).

Aroma and taste are the core dimensions in evaluating Longjing tea quality. Longjing tea is typically characterized by a fresh aroma, with high-quality samples exhibiting prominent bean-like and chestnut-like notes, often accompanied by floral or sweet nuances, resulting in a delicate, persistent, and layered aroma profile (Teng et al., 2024). Its aroma is mainly derived from volatile compounds such as linalool, geraniol, hexanal, and various aldehydes, ketones, and pyrazines, whose combinations can effectively reproduce the characteristic Longjing aroma (Bassiony et al., 2024). Aroma formation depends on both precursor compounds in fresh leaves and transformations during processing, with the initial pan-firing stage playing a critical role, while subsequent steps modulate aroma composition (Zeng et al., 2024). In terms of taste, Longjing tea is characterized by freshness, mellow sweetness, moderate bitterness and astringency, and a lasting aftertaste (Zhang et al., 2024). Its flavor is

determined by the balance among amino acids, catechins, caffeine, and other compounds, where amino acids contribute to freshness, while polyphenols and caffeine form the structural basis of taste. Bitterness and astringency are mainly associated with catechins (e.g., EGCG) and related flavonoids and are strongly influenced by processing conditions (Shan et al., 2023a; Shan et al., 2025). Therefore, the taste of Longjing tea is essentially the result of the synergistic interaction of multiple compounds.

## **2.2 Main factors affecting quality formation**

### **2.2.1 Cultivar factors**

Tea plant cultivars determine the genetic background and metabolic characteristics of fresh leaves and are the fundamental source of quality differences in Longjing tea. Significant variations exist among cultivars in the composition of amino acids, catechins, flavonoids, alkaloids, and aroma precursors, leading to distinct sensory profiles even under identical cultivation and processing conditions (Shan et al., 2023; Zeng et al., 2024; Ao et al., 2025). For example, commonly used materials such as “Longjing 43,” “Baie No.1,” and local population varieties differ markedly in metabolic profiles and quality expression. Longjing 43 generally contains higher levels of flavonoids and chlorophyll b, contributing to its typical color and style, whereas Baie No.1 often exhibits higher glutamic acid and glutamine levels along with different caffeine/theobromine ratios, influencing freshness enhancement and bitterness expression (Teng et al., 2024; Zhang et al., 2024). Thus, differences in freshness, chestnut-like aroma intensity, body, and briskness among cultivars fundamentally reflect variations in metabolic composition and processing responses.

### **2.2.2 Environmental factors**

Environmental conditions constitute an important external basis for Longjing tea quality formation. Suitable temperature, light, precipitation, soil properties, and ecological conditions promote tea plant growth and metabolite accumulation, thereby improving raw material quality. Recent studies have shown that altitude, habitat, and cultivation environment can significantly regulate key metabolites such as amino acids, flavonoids, sugars, and aroma precursors (Bassiony et al., 2024). For instance, higher altitudes generally favor the accumulation of flavonoids, amino acids, and soluble sugars, enhancing sweetness and freshness, while regional climatic conditions further shape the characteristic flavor profiles of Longjing tea. Therefore, the quality potential of Longjing tea is not determined solely by cultivar but arises from genotype  $\times$  environment interactions, which establish the metabolic basis later expressed through processing (Ao et al., 2025).

### **2.2.3 Processing factors**

Processing is the key external factor determining Longjing tea quality and the core step in transforming raw material potential into final product quality. The typical process includes withering, fixation (kill-green), shaping/pan-firing, further frying, and drying or aroma enhancement, each contributing differently to the formation of appearance, aroma, and taste (Zeng et al., 2024; Zhang et al., 2024). Withering significantly influences non-volatile compounds such as amino acids, catechin dimers, organic acids, and phenolic acids, thereby affecting taste and liquor color. Studies indicate that optimal sensory quality is achieved when leaf moisture content is about 70% at the end of withering (Shan et al., 2023). Fixation temperature affects enzyme inactivation and thermal reactions; for example, around 215 °C can reduce bitterness while preserving beneficial amino acids and phenolic acids, leading to improved taste balance (Figure 1) (Shan et al., 2025).

Processing is also crucial for aroma development. Metabolomic studies show that flavonoids, amino acids, alkaloids, lipids, and carbohydrates undergo significant changes during processing. While different cultivars exhibit similar trends, the magnitude of change varies. The initial frying stage is critical for the rapid formation of volatile compounds, whereas subsequent steps adjust the balance among fresh, chestnut-like, sweet, and floral aromas (Zeng et al., 2024; Zhang et al., 2024). Brewing conditions also affect quality expression; for instance, lower temperatures (70°C - 80°C) favor amino acid extraction while slowing the release of bitter compounds, enhancing freshness and reducing astringency (Teng et al., 2024; Deng et al., 2025).

## 2.3 Quality evaluation indicators and methods

### 2.3.1 Sensory evaluation

Sensory evaluation is the core basis for assessing Longjing tea quality. According to national and industry standards, a 100-point scoring system is typically used, evaluating appearance, liquor color, aroma, taste, and infused leaves, with aroma and taste often assigned higher weights (Shan et al., 2023; Bassiony et al., 2024; Zeng et al., 2024; Zhang et al., 2024). Trained panelists assess tea samples through visual inspection, aroma perception, tasting, and leaf observation. This method effectively captures key sensory attributes such as freshness, chestnut-like aroma, tenderness, mellowness, and sweetness.



Figure 1 Different stages in the production process of Longjing tea

To improve interpretability, quantitative descriptive analysis (QDA) is increasingly used to break down flavor attributes into subcategories such as umami, sweetness, bitterness, astringency, freshness, chestnut aroma, floral aroma, and grassy notes (Shan et al., 2025; Zeng et al., 2024). The CATA method has also been applied to link descriptive terms with consumer preferences. Studies show that enhanced umami, sweetness, and pleasant aromas increase consumer acceptance, whereas excessive bitterness and grassy notes reduce it (Deng et al., 2025).

### 2.3.2 Physicochemical indicators and instrumental analysis

To overcome subjectivity in sensory evaluation, physicochemical measurements are widely applied. Common indicators include amino acids, tea polyphenols, caffeine, water extractives, catechins, phenolic acids, organic acids, and flavonol glycosides, which are closely related to taste attributes (Shan et al., 2025). Non-volatile compounds mainly determine taste, while volatile compounds govern aroma. Techniques such as GC–MS, GC–IMS, and LC–MS are widely used to analyze these components (Shan et al., 2023; Zhang et al., 2024).



Comprehensive chemical analysis has advanced quality evaluation from simple composition measurement to biomarker identification. By correlating key volatile compounds (e.g., linalool, geraniol, aldehydes, pyrazines) and non-volatile compounds (e.g., theanine, EGCG, flavonol glycosides) with sensory scores, quantitative relationships can be established (Shan et al., 2023; Bassiony et al., 2024; Zhang et al., 2024; Shan et al., 2025).

### 2.3.3 Chemometrics, intelligent sensing, and rapid detection

In recent years, multivariate analysis, machine learning, and intelligent sensing technologies have been increasingly applied in Longjing tea evaluation. Methods such as PCA, logistic regression, PLS-DA, and neural networks are used to identify key quality markers and predict taste, aroma, and overall quality (Bassiony et al., 2024). Indicators such as total amino acids, theanine, EGCG, and specific flavonol glycosides show strong discriminative ability (Shan et al., 2025).

Meanwhile, technologies such as electronic noses, electronic tongues, and near-infrared spectroscopy enable rapid and non-destructive quality assessment. For example, electronic noses can differentiate tea grades and brands (Moreira et al., 2024), while NIR combined with machine learning can predict sensory scores and chemical composition. Integrated multi-scale analytical frameworks combining metabolomics, colorimetry, intelligent sensing, and sensory evaluation are increasingly used to systematically reveal how processing and brewing influence final tea quality (Shan et al., 2023; Teng et al., 2024; Zhang et al., 2024; Deng et al., 2025).

## 3 Major Types of Tea Cultivars Used for Processing

### 3.1 Traditional and main cultivars

Traditional Longjing tea processing has long relied on local population-type tea germplasm, among which the Longjing population variety is the most representative. Population varieties are genetically heterogeneous groups that gradually formed through long-term farmer selection, natural adaptation, and local cultivation practices, and are characterized by broad genetic backgrounds, strong ecological adaptability, and diverse flavor types. These materials show considerable individual variation in bud and leaf size, sprouting time, leaf structure, and metabolite composition. However, it is precisely this within-population variation that provides an important material basis for the formation of the classic Longjing tea style in the core West Lake production area (Yu et al., 2023). From a quality perspective, fresh leaves of population varieties are generally rich in internal compounds, especially with advantages in aroma performance. The teas produced from them often exhibit more complex volatile profiles and stronger aroma layering, forming typical bean-like and chestnut-like notes, and sometimes even certain floral and fruity characteristics (Figure 2) (Ao et al., 2025; Yan et al., 2025). Therefore, population varieties have long been regarded as important raw materials for producing high-quality Longjing tea with a traditional style.

However, the advantages of population varieties coexist with limitations. Due to their large genetic variation within the population, different individual plants vary significantly in sprouting uniformity, bud plumpness, yield potential, and metabolite accumulation. As a result, under modern standardized and large-scale production systems, they often face problems such as uneven sprouting, inconsistent harvesting periods, and large batch-to-batch quality fluctuations (Figure 3) (Ao et al., 2025). Comparative metabolomic studies under uniform cultivation and processing conditions have shown that, between Longjing population varieties and Longjing 43, flavonoid metabolites often contribute the most to quality differences, and this cultivar effect may even exceed some effects of production area and storage time (Yu et al., 2023). This indicates that although population varieties possess advantages in traditional flavor, their insufficient stability in quality expression limits their application in large-scale mechanized production systems.

Compared with population varieties, Longjing 43 (LJ43) is currently one of the most widely used elite clonal cultivars in Longjing tea production and is also the dominant cultivar in the modern standardized production system. Longjing 43 was selected from superior local germplasm and has advantages such as early sprouting, uniform bud emergence, relatively strong cold resistance, wide adaptability, and stable yield, making it suitable for premium green tea processing as well as mechanized harvesting and standardized processing (Gao et al., 2023a). In terms of quality, Longjing 43 generally has relatively high amino acid levels, a well-balanced taste



foundation, and a stable chestnut-like aroma style. At the same time, its relatively high contents of flavonoids, flavonols, and free fatty acids provide a metabolic basis for aroma formation and mouthfeel expression (Zeng et al., 2024). Therefore, teas made from Longjing 43 usually exhibit fresh, balanced, and stable overall quality characteristics. Although in some cases its aroma complexity is slightly simpler than that of traditional population varieties, its industrial adaptability and commercial consistency are stronger. Notably, Longjing 43 is not only a major production cultivar but has also become an important model material in tea plant basic research. Its high-quality chromosome-level genome assembly has shown that gene loci related to flavor formation, metabolic regulation, and disease resistance underwent strong selection during tea domestication (Gao et al., 2023a). The establishment of this genomic resource has not only enhanced the understanding of the mechanisms underlying the superior traits of Longjing 43, but has also provided a theoretical basis for subsequent marker-assisted breeding, target metabolite-oriented improvement, and the breeding of specialized cultivars for Longjing-type tea processing.

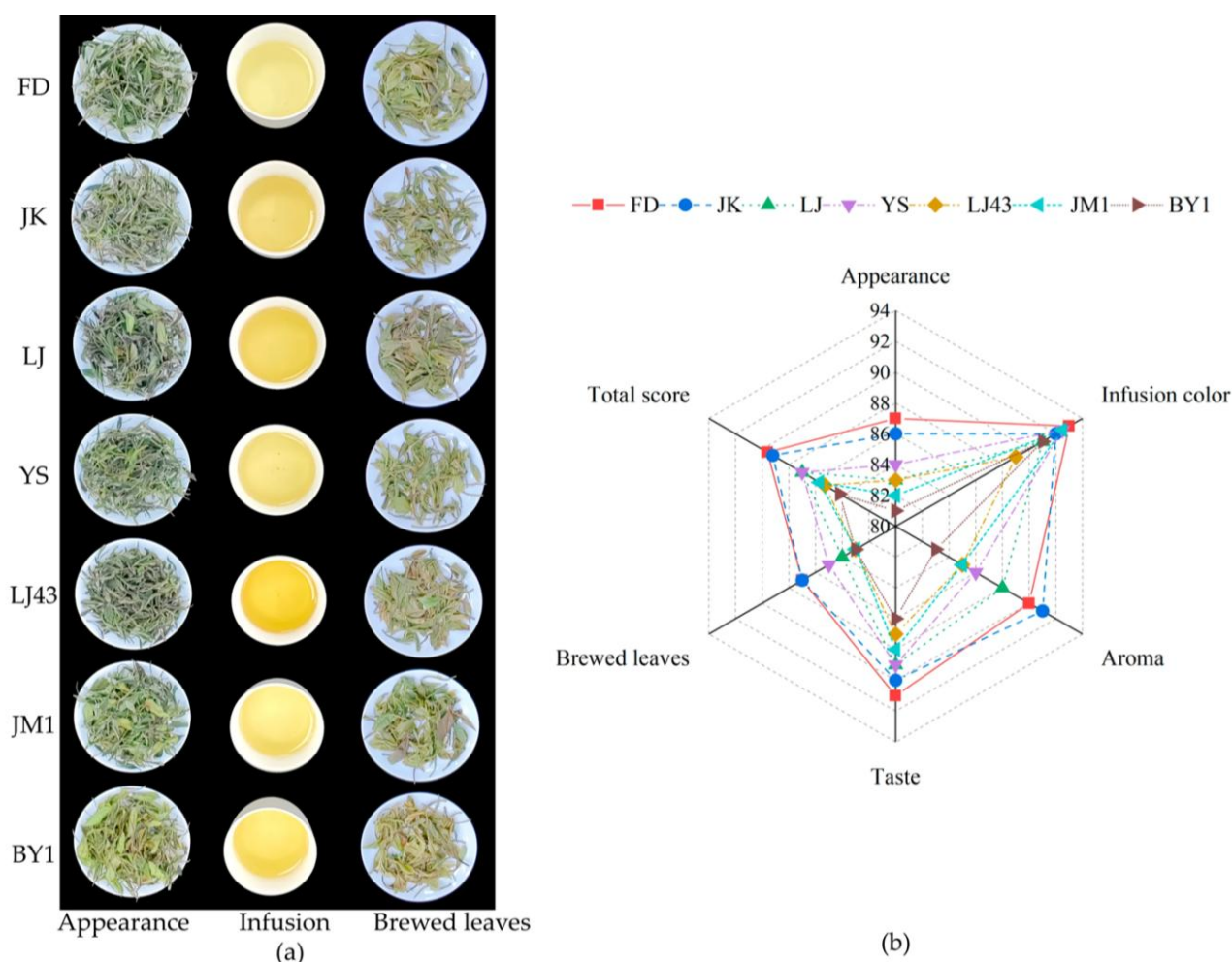


Figure 2 The sensory qualities of HGW (Adopted from Ao et al., 2025)

Image caption: (a) The photos of tea samples, infusions, and brewed tea leaves. (b) Evaluation of each quality factor and calculation of the total score (Adopted from Ao et al., 2025)

### 3.2 Promoted cultivars

With the expansion of the Longjing tea industry and increasing market demand for early harvesting, high yield, strong processing suitability, and cross-regional adaptability, a group of promoted cultivars has gradually been applied in Longjing tea production. Among them, Wuniuzao is a typical extremely early-sprouting cultivar. Because of its early spring bud break and significantly advanced market entry, it has high economic value, especially for capturing the early-spring premium tea market. The fresh leaves of Wuniuzao are relatively tender and show good potential for appearance formation, producing fairly uniform flat green tea under proper harvesting

and processing conditions. At the same time, its strong sprouting capacity also helps increase the supply of fresh leaves in early spring. However, in terms of flavor expression for high-end Longjing tea, some studies have shown that Wuniuzao is slightly inferior to traditional population varieties or Longjing 43 in aroma layering and taste body, especially when developing products with a high-end traditional style, where a trade-off often needs to be made between “earlier market entry” and “depth of quality.”



Figure 3 Morphological characteristics of Longjing 43 under different conditions

In addition to Wuniuzao, cultivars in the Zhenong series (such as Zhenong 117) have also become important clonal materials gradually promoted in some Longjing-producing areas in recent years. These cultivars usually possess strong adaptability, high yield potential, and good bud uniformity, and they show relatively stable growth vigor and processing suitability under multiple ecological conditions. In non-traditional Longjing-producing regions such as western Sichuan, materials such as Wuniuzao, Changye Longjing, and Zhenong 117 have all performed well in bud-leaf traits, biochemical composition, and suitability for premium green tea processing. Among them, Wuniuzao and Changye Longjing have relatively high total catechin and amino acid contents and moderate tea polyphenol levels, giving them better overall quality, while Zhenong 117 maintains similar quality but yields more than local control cultivars, making it suitable for medium-scale promotion. These results indicate that, under proper cultivation and processing conditions, promoted cultivars can reproduce the key quality characteristics of the Longjing style to a certain extent.

From the perspective of aroma metabolite profiles, there are obvious differences among promoted cultivars. Comparative studies have found that after being processed into Longjing tea, Wuniuzao differs from Longjing 43 and population varieties in the relative contents of esters, aldehydes, heterocyclic compounds, alcohols, and acids, suggesting some specificity in its aroma expression pathway. However, core aroma compounds such as linalool, D-limonene,  $\beta$ -ionone, jasmone, and (Z)-hexenyl esters still dominate across different materials, indicating that the basic aroma framework of Longjing tea can still be maintained (Ao et al., 2025). In general, teas made from Longjing 43 and population varieties tend to have relatively higher ester and aldehyde contents, whereas some introduced materials may accumulate more heterocyclic compounds or organic acids, thereby altering the balance among chestnut-like, fresh, and sweet aromas to some extent (Ao et al., 2025). In terms of non-volatile components, these promoted cultivars usually combine relatively high amino acid contents with moderate catechin levels, which is favorable for forming a good freshness foundation while maintaining a balance between

astringency and body. Therefore, such cultivars are particularly suitable as important supplementary raw materials outside the core traditional production areas, meeting the needs for early harvesting and yield, while also providing more options for developing Longjing-type products with different market positions.

### **3.3 Newly bred cultivars and their biological characteristics**

In recent years, as tea breeding objectives have shifted from simply pursuing high yield toward high quality, functional flavor, and precise processing suitability, a number of newly bred cultivars and special germplasm suitable for Longjing tea processing have gradually attracted attention. During the breeding process, these new materials place greater emphasis on targeted improvement, such as high amino acid content, high aroma potential, low bitterness and astringency, and strong environmental responsiveness, thereby providing a new resource base for the premiumization and diversification of Longjing tea. Among them, albino or color-variant materials are currently one of the most actively studied groups. Represented by cultivars such as “Baie No.1,” their spring tender shoots are jade white or pale yellow and are characterized by high amino acid content and relatively low catechin levels, making them more likely to produce tea with fresh, sweet, and mild taste and lower bitterness and astringency (Li et al., 2025; Yan et al., 2025). Metabolomic studies have shown that these materials are rich in various amino acids and sugars, whereas bitterness-related components are significantly reduced, resulting in a fresher and sweeter flavor profile in the final tea (Bassiony et al., 2024).

From the perspective of genetics and metabolic mechanisms, newly bred cultivars not only exhibit significant sensory differences but also have analyzable molecular bases. In population studies constructed using Longjing 43 and albino materials, key QTL regions controlling the accumulation of theanine and multiple free amino acids have been identified, providing clear targets for breeding high-umami cultivars (Yan et al., 2025). In terms of processing response, the metabolic pathways also differ among cultivars. For example, Baie No.1 shows obvious dynamic changes in volatile compounds during processing, with floral and fresh aroma compounds dominating in the early stage and chestnut-like aroma-related compounds gradually accumulating in the later stage, showing a distinct aroma formation trajectory compared with traditional cultivars (Li et al., 2025). At the same time, under the same processing conditions, different cultivars show significant differences in non-volatile metabolite composition, reflecting different quality formation patterns.

In addition, newly bred cultivars also show important potential in environmental adaptability. For example, Longjing 43 exhibits specific flavonoid synthesis and light-response regulation characteristics under shading conditions, providing a basis for screening cultivars with stable quality under different ecological conditions (Li et al., 2025; Cui et al., 2026). However, these new varieties still face challenges in their promotion and application, including insufficient regional adaptability verification and limited evidence for long-term quality stability. Some special cultivars may show outstanding freshness or aroma, but whether they conform to the traditional Longjing style and market perception still requires further evaluation. Therefore, future studies should combine multi-location and multi-year trials, metabolomic analysis, and sensory evaluation to systematically verify the processing suitability and quality stability of new cultivars, so as to support their scientific promotion and application.

## **4 Differences in Quality Traits Among Cultivars**

### **4.1 Differences in appearance quality**

The inherent differences in bud–leaf morphology among tea cultivars are an important basis affecting the appearance quality of Longjing tea. Longjing tea has high requirements for raw material morphology, and fresh leaves with tender buds and leaves, moderate length, soft texture, and balanced thickness are generally more conducive to forming the typical “flat, smooth, straight, and even” appearance. Studies have shown significant differences among germplasm resources in bud length, leaf size, leaf thickness, and hundred-bud weight, which gives some cultivars greater shaping potential, whereas cultivars with thicker leaves or coarser buds are more likely to show insufficient flatness or reduced uniformity during processing (Li et al., 2025). For example, Longjing 43 has relatively short buds and high uniformity, making it easier to form a smooth and straight appearance, whereas population varieties, due to their strong genetic heterogeneity, exhibit greater variation in



bud and leaf traits and thus relatively lower appearance consistency in the finished tea (Yu et al., 2023; Yan et al., 2025). In addition, technologies such as hyperspectral imaging can quantitatively identify differences in fresh leaf morphology and texture among cultivars, further indicating that appearance quality has a clear genetic basis (Figure 4) (Zhao et al., 2024).

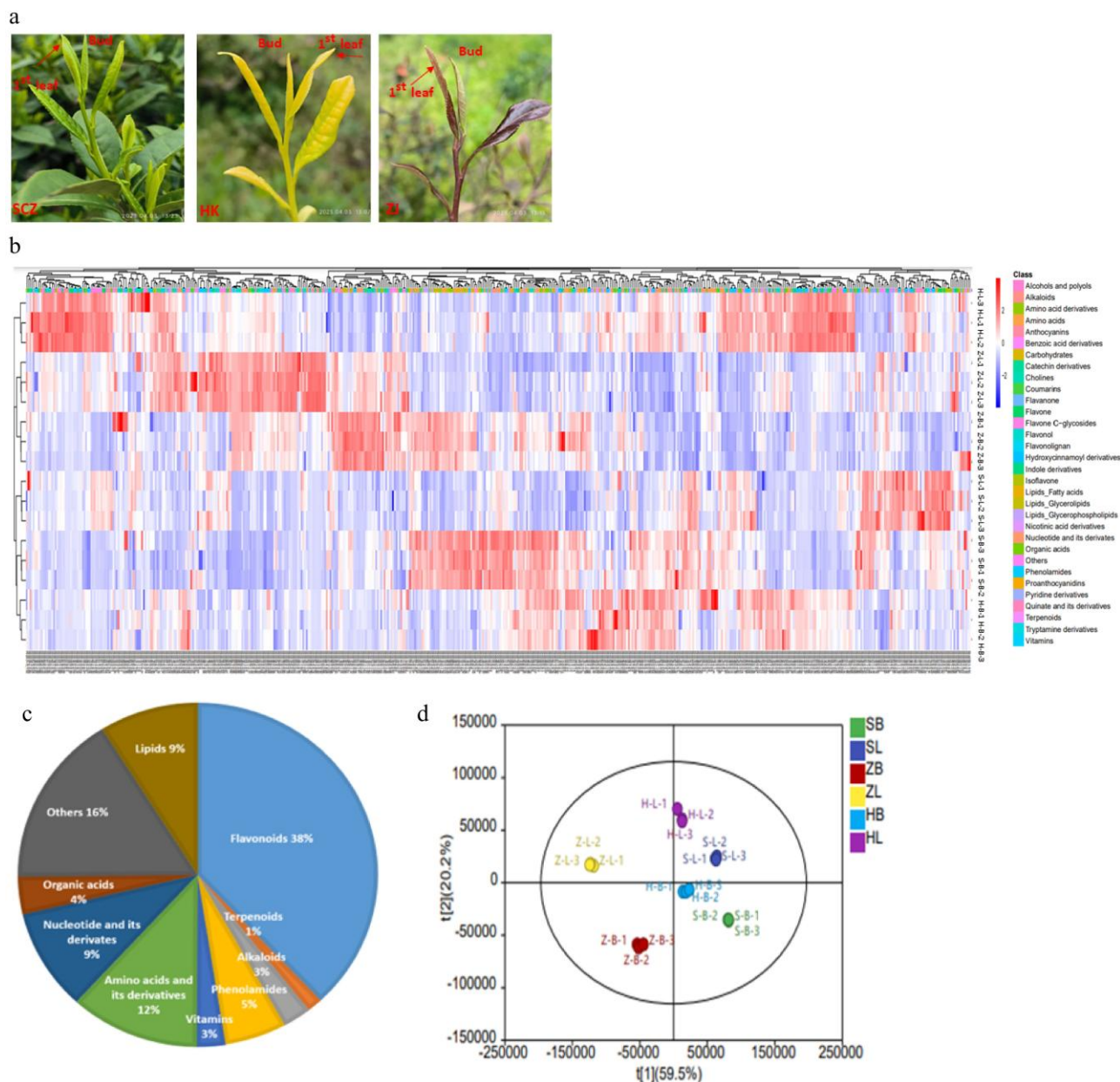


Figure 4 Detection and identification of specialized metabolites (Adopted from Zhao et al., 2024)

Image caption: (a) The phenotypes of two tissues of the three cultivars. 'Shuchazao' (SCZ), 'Huangkui' (HK) and 'Zijuan' (ZJ). (b) Clustering heatmap tree of total metabolites of two tissues of the three cultivars. Z-scores normalize the value. Red indicates a high abundance, and blue indicates a low relative abundance of metabolites. (c) Composition and proportion of different metabolites in different tea cultivars. (d) PCA of the metabolites in different tissues of tea plants. SB: SCZ-bud; ZB: ZJ-bud; HB: HK-bud; SL: SCZ-leaf; ZL: ZJ-leaf; HL: HK-leaf (Adopted from Zhao et al., 2024)

Color is another key indicator of the appearance quality of Longjing tea. Differences among cultivars in chlorophyll, carotenoids, and anthocyanin contents lead to variations in the overall color of dry tea, liquor, and infused leaves. High-quality Longjing tea usually appears tender green or bright green with luster, while different cultivars may show light green, yellow-green, or composite hues. Studies have shown that the relatively high chlorophyll b content in Longjing 43 contributes to the formation of a typical overall color (Teng et al., 2024). In



contrast, albino or color-variant cultivars such as “Baie No.1”, “Huangjinya”, and “Zijuan” often display lighter, bright yellow, or darker tones due to differences in pigment composition (Shan et al., 2023; Zeng et al., 2024). Among them, albino cultivars show lighter and brighter color because of reduced chlorophyll, whereas purple cultivars may exhibit darker overall color and some degree of bitterness and astringency due to anthocyanin accumulation (Zeng et al., 2024).

Uniformity reflects sprouting consistency and processing adaptability and is an important component of appearance quality. Clonal elite cultivars such as Longjing 43 and some promoted cultivars, due to their high genetic consistency and uniform sprouting, are conducive to standardized harvesting and raw material grading, thereby improving the uniformity of the finished tea. By contrast, population varieties and some highly heterogeneous materials tend to produce greater raw material variation because of inconsistent sprouting, which affects the final visual quality (Yu et al., 2023). Therefore, cultivar selection plays a fundamental role in the formation of Longjing tea appearance quality, influencing the entire process from fresh leaf development to harvest grading and final processing.

#### **4.2 Differences in sensory quality**

Aroma and taste are the most critical sensory dimensions for distinguishing different Longjing tea cultivars. Because cultivars differ in volatile precursors, non-volatile taste compounds, and processing response patterns, the finished teas show different aroma types, freshness, bitterness–astringency intensity, and aftertaste characteristics (Yu et al., 2023; Teng et al., 2024). In general, traditional population varieties, with their more complex metabolic background, tend to produce richer bean-like and chestnut-like aromas with some floral nuances, resulting in more variable and regionally distinctive aroma styles. In contrast, Longjing 43 is mainly characterized by a more balanced fresh–chestnut aroma, a more elegant aroma profile, and better stability, giving it a strong advantage in standardized processing (Yan et al., 2025). Studies on different aroma styles of Longjing tea have shown that when classified into tender-aroma, fresh-aroma, or high-aroma types, their volatile profiles differ markedly, with systematic changes in the types and contents of alcohols, aldehydes, terpenes, and heterocyclic compounds. For example, in bean-aroma and fresh-aroma Longjing teas, geraniol and (E,E)-2,4-heptadienal are important contributors to bean-like aroma, whereas hexanal-d and heptanal-d are more associated with fresh green notes (Ao et al., 2025). This indicates that aroma differences among cultivars are reflected not merely in intensity but more importantly in characteristic aroma combinations and relative proportions.

Among special cultivars, the albino cultivar “Baie No.1” exhibits a different aroma formation pathway from ordinary green-leaf cultivars. Studies have shown that during the early stages of processing, it tends to accumulate more fresh and floral volatile compounds, while during the later frying and aroma-enhancing stages, it gradually develops an aroma framework dominated by pyrazines associated with chestnut-like notes (Teng et al., 2024; Yan et al., 2025). Therefore, even when processed into Longjing tea, different cultivars may express different aroma styles, such as “floral-dominant,” “bean-aroma prominent,” or “chestnut-aroma pronounced,” which directly affects product style classification and market positioning. Taste differences are likewise clearly cultivar-dependent. Variations among cultivars in amino acids, flavonoids, alkaloids, lipids, and peptides systematically influence freshness, bitterness–astringency, mellowness, and aftertaste potential of the tea liquor (Yu et al., 2023; Yan et al., 2025). Cultivars with higher amino acid content usually exhibit stronger freshness and lower stimulation, making them suitable for producing a fresh and balanced taste profile, whereas cultivars with higher levels of tea polyphenols, complex catechins, and flavonol glycosides often show stronger taste, more obvious astringency, but also a more defined body and longer aftertaste (Yu et al., 2023; Li et al., 2025).

Taking Longjing 43 as an example, it usually contains higher levels of theanine and glutamine, along with greater flavonoid accumulation, and therefore often produces tea with better freshness and balance. By contrast, albino or special cultivars such as Baie No.1 generally accumulate more glutamic acid and glutamine but relatively lower levels of bitterness-related alkaloids such as caffeine and theobromine, resulting in a sweeter, fresher, milder, and less stimulating taste (Teng et al., 2024). In addition, Longjing 43 and population varieties differ not only in small-molecule metabolites but also in peptide composition. Studies have shown that population varieties contain

more water-soluble peptides, whereas Longjing 43 has higher theanine and glutamine contents, and these jointly affect umami, kokumi, and mellowness formation (Yan et al., 2025). Research on differently colored cultivars also indicates that green and purple cultivars generally exhibit stronger bitterness and astringency because of higher flavan-3-ol and anthocyanin levels, while yellow or albino cultivars usually have a milder flavor due to higher free amino acid contents (Zeng et al., 2024). Therefore, cultivar differences do not simply determine a single flavor attribute, but rather shape distinct sensory styles by altering the balance among freshness, sweetness, astringency, body, and aftertaste. For this reason, aroma and taste are regarded as the core indicators for distinguishing different Longjing tea cultivars and their product types (Yu et al., 2023; Ao et al., 2025).

#### **4.3 Differences in liquor color and infused leaf performance**

Liquor color and infused leaves are important components of the visual quality of Longjing tea and are also the result of the combined effects of cultivar traits and processing suitability. High-quality Longjing tea usually has a tender bright green or yellow-green, clear liquor with high transparency, while the infused leaves are soft, uniform, and consistent in color. Due to differences in soluble substances, tea polyphenol and catechin composition, pigment background, and leaf structure, cultivars vary in liquor brightness, overall hue, and the unfolding state of infused leaves (Teng et al., 2024). Studies have shown that cultivars with higher water extract and tea polyphenol contents tend to have deeper-colored liquor with a stronger sense of concentration, whereas cultivars with lower internal compounds produce lighter and brighter liquor with a thinner mouthfeel (Zhang et al., 2024), indicating that liquor color not only reflects processing outcomes but also the chemical basis of the cultivar.

Further studies have found that the overall color of tea liquor is closely related to various metabolites, such as catechin dimers, phenolic acids, organic acids, and galloyl glucose, which play important roles in liquor brightness and yellow-green balance (Teng et al., 2024). Because the accumulation of these compounds varies among cultivars, even under the same processing and brewing conditions, significant differences may still be observed in liquor brightness and overall tone. For example, albino and low-chlorophyll cultivars tend to produce brighter, more yellow-green or pale-yellow liquor, whereas purple cultivars rich in anthocyanins may present darker or mixed hues (Shan et al., 2023; Zeng et al., 2024).

The performance of infused leaves reflects leaf structural characteristics and processing response. Differences among cultivars in bud-leaf tenderness, leaf thickness, and cell structure affect the unfolding, softness, and integrity of leaves after brewing. High-quality cultivars usually have tender leaves with relatively uniform structure, resulting in soft, bright, and even infused leaves. In contrast, cultivars with thicker leaves or higher maturity are more likely to show rough, broken, or unevenly colored infused leaves (Li et al., 2025). In addition, clonal cultivars such as Longjing 43 generally show better consistency in infused leaves because of their uniform buds and leaves, whereas population varieties often show greater variation (Yan et al., 2025). Overall, liquor color and infused leaf performance are important comprehensive manifestations of cultivar differences and the degree of match between cultivar and processing method (Zeng et al., 2024; Zhang et al., 2024).

### **5 Differences in Chemical Components and Their Roles**

#### **5.1 Differences in major quality components**

Amino acids, tea polyphenols, and caffeine are the core chemical bases determining the taste characteristics of Longjing tea. Significant differences in their contents and proportions among cultivars directly affect freshness, bitterness–astringency, and overall taste balance (Zeng et al., 2024). Among these, amino acid differences are particularly prominent. Studies have shown that “Baie No.1” is rich in L-glutamic acid and L-glutamine, whereas “Longjing 43” contains higher levels of flavonoids (Shan et al., 2023). Comparative analyses between Longjing 43 and population varieties indicate that the former has higher theanine and glutamine contents, while total catechin levels are similar, suggesting that differences in freshness mainly arise from amino acids and related peptides (Huang et al., 2024). Therefore, high amino acid accumulation is a key basis for the formation of a fresh and mellow taste.

Tea polyphenols, especially catechins, are the main contributors to bitterness, astringency, and the structural backbone of taste. Cultivars with higher polyphenol content generally exhibit stronger body and aftertaste

potential, although imbalanced proportions may lead to excessive bitterness (Shan et al., 2025). Studies indicate that flavan-3-ols are the most abundant compounds in Longjing tea and constitute the main chemical basis of bitterness and intensity. Differences among cultivars in polyphenols and their derivatives further result in the differentiation of “fresh-type” and “mellow-type” flavor styles (Huang et al., 2024). Caffeine also plays a regulatory role in bitterness perception and taste balance; for example, the lower caffeine content in “Baie No.1” is consistent with its milder bitterness (Shan et al., 2023).

In addition, processing and environmental conditions further regulate the dynamic changes of these components. Studies have shown that with increasing withering degree, amino acids and certain catechin dimers increase, while organic acids and phenolic acids decrease, thereby affecting taste and liquor color (Shan et al., 2025). Multi-cultivar studies also demonstrate that tea polyphenols, catechins, and amino acids exhibit significant cultivar-dependent differences (Zeng et al., 2024). Overall, the proportional relationships among these three major components are more explanatory than individual component levels: a high amino acid/low polyphenol combination favors a fresh style, whereas higher polyphenols enhance body and aftertaste.

## **5.2 Differences in volatile aroma composition**

Volatile aroma compounds are fundamental determinants of the aroma type and complexity of Longjing tea, and their composition varies significantly among cultivars. The aroma of Longjing tea mainly consists of alcohols, aldehydes, esters, ketones, and heterocyclic compounds, which originate from precursor substances in fresh leaves and are gradually formed through enzymatic and thermal reactions during processing (Gao et al., 2023b; Zhang et al., 2024). Therefore, cultivar differences are first reflected in the composition of aroma precursors.

The aroma profiles of different cultivars exhibit clear specificity. Studies have identified 97 key aroma-active compounds across multiple cultivars, among which aldehydes, ketones, and heterocyclic compounds play important roles in aroma formation (Zeng et al., 2024). Core aroma compounds such as linalool, geraniol, hexanal, and  $\beta$ -ionone are commonly present in Longjing tea, but their relative contents differ significantly and are closely related to quality evaluation (Zhang et al., 2024). This indicates that aroma differences are mainly derived from variations in the proportions of multiple compounds rather than the presence or absence of a single compound.

Differences among aroma types further highlight the role of cultivars. For example, in bean-aroma Longjing tea, geraniol and (E,E)-2,4-heptadienal contribute significantly, whereas fresh-aroma types are more associated with hexanal and heptanal (Bassiony et al., 2024). During processing of Baie No.1, volatile compounds change dynamically, with floral and fresh aromas dominating in the early stage and chestnut-like aromas forming in the later stage (Gao et al., 2023b). Thus, cultivars determine aroma style by influencing precursor metabolism and transformation pathways during processing (Li et al., 2024).

## **5.3 Correlation between chemical components and quality traits**

There is a clear correlation between tea chemical composition and sensory quality, which provides an important basis for explaining quality differences among cultivars. In general, amino acids are positively correlated with freshness, tea polyphenols and caffeine with bitterness, astringency, and intensity, while volatile compounds determine aroma types (Huang et al., 2024). Studies on different withering degrees show that compounds such as theaflavins, thearubigins, organic acids, and amino acid derivatives are significantly correlated with taste and liquor color, indicating that quality formation depends on the synergistic effects of multiple components (Shan et al., 2025).

Large-scale sample analyses have identified EGCG, caffeine, theanine, and organic acids as key quality markers, which can be used to achieve high-accuracy predictions through statistical models. For example, specific flavonoid derivatives and amino acids can effectively distinguish different taste types, with model accuracy reaching 97.6%. This demonstrates that quantitative relationships between chemical composition and quality traits can be established.

Further cultivar-focused studies show that different combinations of amino acids and catechins correspond to distinct taste characteristics. Certain amino acids are associated with a mellow taste, whereas gallic acid and theobromine tend to enhance astringency (Guo et al., 2023). At the same time, variations in volatile compound proportions directly influence aroma style (Zhang et al., 2024). Environmental factors also regulate quality expression by altering metabolite accumulation; for instance, high-altitude conditions are conducive to enhancing sweet and mellow flavors (Bassiony et al., 2024). Overall, quality traits are the result of multi-component interactions dominated by cultivar and modulated by the environment.

## **6 Processing Suitability and Cultivar Response**

### **6.1 Adaptability of different cultivars to processing techniques**

The processing suitability of tea cultivars in Longjing tea production is mainly reflected in the responses of their biochemical composition and physical structure to various processing steps. Longjing tea processing involves key stages such as withering, fixation, shaping, and pan-firing. Due to differences in bud–leaf structure, moisture content, and internal composition, cultivars exhibit distinct behaviors during heat treatment and moisture loss, thereby affecting appearance, aroma, and taste (Li et al., 2023a; Shan et al., 2023; Teng et al., 2024). Overall, cultivar differences determine the range of processing adaptability and the potential for quality expression.

From a general processing perspective, some cultivars exhibit strong adaptability. For example, Longjing 43 can produce markedly different metabolic profiles under various tea processing methods and thermal treatments, indicating its broad adaptability across multiple processing conditions (Chen et al., 2024). In addition, its relatively high chlorophyll b content contributes to the formation of the typical dry tea color, further demonstrating its suitability for the Longjing processing pathway (Zeng et al., 2024). In contrast, different cultivars show significant variation in both volatile and non-volatile components during thermal processing, reflecting differences in flavor formation pathways.

At specific processing stages, bud–leaf structure and moisture status are critical for shaping. Leaves that are soft and of moderate thickness are more likely to form a flat and smooth appearance, whereas thicker or unevenly tender leaves tend to break or fail to achieve sufficient flatness (Yu et al., 2023). Studies indicate that when leaf moisture content is within 30%–50%, plasticity is optimal, facilitating stable shaping and reducing breakage (Li et al., 2023a). Furthermore, cultivars differ in their responses to fixation and withering; for example, cultivars with high amino acid content require careful temperature control to preserve freshness, whereas those with high polyphenol content are more prone to increased bitterness and astringency if improperly processed (Shan et al., 2023).

### **6.2 Stability and consistency of finished tea quality**

The stability and consistency of finished tea quality are key indicators for evaluating cultivar suitability. Stability refers not only to the reproducibility of quality under the same processing conditions but also to the ability to maintain consistent quality across different years or environmental fluctuations. Generally, clonal cultivars with uniform genetic backgrounds exhibit more stable fresh leaf traits and metabolic profiles, making them more likely to produce consistent finished tea quality.

Studies have shown that under identical processing conditions, cultivar effects on flavonoid and other metabolites are greater than those of production region or storage factors, indicating that cultivars play a dominant and stable role in quality formation. This means that major cultivars can maintain their characteristic flavor profiles within a certain range of environmental variation, thereby supporting standardized production. Further research indicates that although different cultivars follow similar metabolic trends during processing, differences in concentration levels lead to distinct and stable quality expressions (Zeng et al., 2024).

However, environmental conditions and processing parameters still influence quality consistency. For instance, Longjing 43 can maintain relatively high catechin levels under shading conditions, demonstrating strong metabolic stability (Li et al., 2023b). In processing, controlling key parameters—such as maintaining leaf moisture at around 70% after withering—can significantly improve taste and liquor color (Shan et al., 2023).



Additionally, leaf mechanical properties vary with moisture content, with the 30%-50% range being optimal for stable shaping, indicating that quality consistency results from the combined effects of cultivar, environment, and process control.

### **6.3 Evaluation indicators and methods for processing suitability**

The evaluation of processing suitability of tea cultivars requires a comprehensive approach integrating sensory, physicochemical, and physical performance indicators. Traditional sensory evaluation, based on scoring appearance, aroma, and taste, provides a direct reflection of cultivar performance under different processing conditions. For example, in studies on Baie No.1, subdividing aroma and taste attributes has been effective in identifying optimal processing schemes (Teng et al., 2024). When combined with electronic tongue analysis, sensory results can be linked to changes in chemical composition (Shan et al., 2023).

Physicochemical indicators provide an objective basis for evaluating suitability, including amino acids, tea polyphenols, caffeine, and volatile compounds (Chen et al., 2024; Zeng et al., 2024). At the same time, physical parameters such as leaf thickness, moisture content, and mechanical properties reflect shaping ability and resistance to damage during processing (Li et al., 2023b). Together, these indicators form the foundation of suitability evaluation.

In recent years, multidimensional evaluation methods have been increasingly developed. Near-infrared spectroscopy combined with models such as PLSR and SVR enables rapid prediction of quality indicators (Chen et al., 2024), while technologies such as electronic noses and machine vision provide objective assessments of aroma and appearance. In addition, texture analysis and mechanical modeling can quantify leaf processing behavior and provide parameter support for process optimization (Li et al., 2023b). These approaches are promoting a shift in suitability evaluation from experience-based judgment to data-driven analysis.

## **7 Molecular Mechanisms and Advances in Breeding Research**

### **7.1 Genes and regulatory mechanisms related to quality traits**

The formation of quality traits in Longjing tea—such as freshness, bitterness – astringency, aroma type, and leaf color—is essentially driven by complex genetic regulatory networks involving the coordinated regulation of multiple metabolic pathways, including those of amino acids, tea polyphenols, alkaloids, and volatile compounds. In recent years, studies based on the reference genome of Longjing 43 (LJ43) and population resequencing have shown that, during the domestication of *Camellia sinensis* var. *sinensis*, genes related to flavor formation and stress resistance have undergone strong selection pressure, indicating that quality-related metabolic pathways have long been key targets of artificial selection (Gao et al., 2023b). For non-volatile components, amino acid and polyphenol metabolic pathways are central to taste formation. Genes involved in theanine biosynthesis (e.g., CsTS, CsGS) regulate amino acid accumulation and directly affect freshness, while key structural genes in flavonoid/catechin biosynthesis (e.g., CHS, F3H, DFR) control polyphenol production, thereby influencing bitterness and aftertaste. In addition, caffeine biosynthesis is regulated by N-methyltransferase genes, and differences in their expression among cultivars form an important molecular basis for taste variation.

In terms of pigment formation and bitterness regulation, multi-omics studies have revealed that chlorophyll and carotenoid biosynthesis/degradation pathways, anthocyanin biosynthesis, and transport systems jointly determine leaf color and associated quality traits. For example, in albino materials, chlorophyll synthesis is inhibited while degradation is enhanced, whereas in purple-leaf materials, anthocyanin biosynthesis and transport genes are upregulated. These changes not only affect appearance but also influence amino acid and polyphenol accumulation through altered carbon allocation (Li et al., 2023b). Under environmental regulation, key genes such as CsANS and CsANR respond to changes in light and temperature, modulating catechin and flavonoid levels and leading to differences in quality stability among cultivars under shading or elevated temperature conditions (Wu et al., 2025).

Regarding aroma formation, lipid oxidation (LOX pathway), amino acid degradation, and terpenoid biosynthesis pathways jointly contribute to the production of volatile compounds. LOX and downstream enzymes are involved

in the formation of green-leaf volatiles, while terpene synthases (TPS) regulate the accumulation of floral and fruity compounds such as linalool and geraniol. Transcription factors, including MYB, bHLH, ERF, and MYC, play central regulatory roles in these pathways. For example, CsMYB1, CsERF2, and bHLH13 form regulatory networks that influence bitterness and temperature adaptability by modulating flavonoid synthesis and carbon allocation (Shen et al., 2024). In addition, pan-genome studies have shown that LTR transposon expansion can lead to gene copy number variation, resulting in functional diversity affecting leaf color, sprouting time, and flavor metabolism. This indicates that quality differences in Longjing tea arise not only from gene expression regulation but also from structural genetic variation.

## **7.2 Application of multi-omics technologies in quality research**

Multi-omics technologies—including genomics, transcriptomics, metabolomics, and proteomics—have become essential tools for elucidating the mechanisms of Longjing tea quality formation, enabling systematic analysis from genes to metabolites to phenotypes. At the genomic level, the LJ43 reference genome and population resequencing have revealed the evolutionary history of tea plants and selection signals in quality-related genes. Pan-genome studies further integrate structural variation information across multiple cultivars, allowing the detection of presence/absence variation (PAV) and copy number variation (CNV), which can then be associated with flavor and leaf color traits (Chen et al., 2023).

In integrated transcriptomic and metabolomic analyses, thousands of differentially expressed genes have been identified among cultivars, mainly enriched in pathways such as amino acid metabolism, flavonoid biosynthesis, lipid metabolism, and carbon metabolism. The expression patterns of these genes can directly explain differences in catechin, theanine, and caffeine contents (Wen et al., 2023). Through weighted gene co-expression network analysis (WGCNA), key hub gene modules regulating flavonoid and aroma biosynthesis can be identified, enabling the pinpointing of core regulatory nodes of quality traits (Yu et al., 2025). At the metabolomic level, analytical techniques such as LC-MS, GC-MS, and NMR are widely used to compare metabolic differences among cultivars, production regions, and processing methods, and to identify quality markers. For example, the dynamic changes of polyphenols and amino acids during processing can be tracked to elucidate the regulatory pathways of quality formation.

Notably, multi-omics research has evolved from single-layer analysis to multi-scale integration, including genome×transcriptome×metabolome integration, as well as epigenetics × environmental factors × quality phenotypes. These integrative analyses reveal that environmental factors such as shading and temperature influence quality formation in a cultivar-dependent manner by regulating gene expression and metabolic networks (Shen et al., 2024; Wu et al., 2025). Therefore, multi-omics approaches not only deepen the understanding of quality formation mechanisms but also provide molecular targets for precision breeding.

## **7.3 Marker-assisted breeding and development of new cultivars**

With the advancement of molecular technologies, the breeding of cultivars suitable for Longjing tea processing is shifting from traditional empirical selection to molecular design breeding. Molecular marker-assisted selection (MAS), QTL mapping, and genome-wide association studies (GWAS) have provided powerful tools for the precise improvement of quality traits. For example, in QTL mapping studies based on a genetic population derived from Longjing 43 and albino cultivars, high-density SNP maps (average spacing of 0.69 cM) have successfully identified multiple QTLs controlling free amino acids such as theanine and glutamic acid, explaining approximately 11.8%-23.7% of phenotypic variation (Chen et al., 2023). These findings provide clear genetic targets for breeding high-umami Longjing tea cultivars. At the genome-wide level, GWAS has identified multiple loci associated with catechins, caffeine, leaf color, and stress resistance (Gao et al., 2023a). Meanwhile, SNP resources based on the LJ43 reference genome facilitate the development of molecular markers, enabling early-stage prediction and selection of quality traits.

In terms of marker types, ILP (intron length polymorphism) markers, due to their high polymorphism and cross-species applicability, are widely used in cultivar identification and genetic analysis (Liu, 2024). In addition, graph-based pan-genome technologies allow structural variations to be incorporated into breeding systems,

providing new approaches for improving complex traits. Future trends in molecular breeding are expected to include multi-trait improvement (quality, stress resistance, and processing suitability), multi-omics-driven precision breeding, and the integration of high-throughput phenotyping with artificial intelligence models. Nevertheless, as tea plants are perennial crops with long breeding cycles, new cultivars still require long-term multi-regional trials to verify quality stability and processing adaptability. Therefore, the deep integration of molecular technologies with traditional breeding methods will remain the key pathway for improving Longjing tea cultivars.

## 8 Existing Issues and Future Perspectives

The current evaluation system for tea cultivars used in Longjing tea processing remains inadequate, mainly manifested in limited indicators, inconsistent standards, and a lack of systematic approaches. Existing studies often focus on sensory quality or partial physicochemical parameters, lacking a unified multi-dimensional evaluation system that integrates appearance, aroma, taste, and chemical composition, resulting in poor comparability among studies. In addition, differences in cultivar selection and quality evaluation standards across production regions have hindered the establishment of a standardized system specifically for Longjing tea cultivars. The strong subjectivity in evaluation, coupled with insufficient objective and quantitative indicators, further limits the scientific basis for cultivar selection and promotion. Therefore, it is necessary to develop a comprehensive evaluation system integrating sensory assessment and physicochemical analysis, while promoting the standardization and unification of evaluation criteria.

The formation of Longjing tea quality is the result of interactions among cultivar, environment, and processing techniques; however, systematic research on these interactions remains insufficient. Most studies focus on single factors, such as cultivar differences or process optimization, while comprehensive analyses of cultivar performance under varying ecological conditions and their responses to processing are relatively scarce. In practice, the same cultivar may exhibit significant differences in chemical composition and quality traits under different climates, soils, and altitudes, and the optimal processing parameters may also vary accordingly. The lack of integrated multi-factor studies limits a deeper understanding of the mechanisms underlying quality formation. Future research should emphasize multi-location and multi-year experiments and establish integrated “cultivar-environment-processing” interaction models to support precision production.

With the transformation of the Longjing tea industry toward high-quality development, the integration of specialized cultivar breeding and intelligent processing technologies will become a key direction. On the one hand, breeding efforts should target high aroma intensity, strong freshness, and low bitterness–astringency, while also considering yield and stress resistance to achieve a balance between quality and productivity. On the other hand, with the advancement of intelligent manufacturing technologies, automated and digital processing equipment is increasingly being applied in tea production, enabling precise control of processing conditions through temperature regulation, time management, and real-time monitoring. However, given that different cultivars respond differently to processing parameters, future research should focus on optimizing the compatibility between cultivars and intelligent processing systems. Promoting the coordinated development of “improved cultivars + optimized techniques + intelligent equipment” will be essential for enhancing quality stability and industrial competitiveness of Longjing tea.

## Conflict of Interest Disclosure

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

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## Research Insight

## Open Access

# Variation in Fruit Quality Traits of Peach (*Prunus persica*) Under Different Cultivation Conditions and Its Evaluation Methods

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**Abstract** This study summarizes the composition, variation patterns, and evaluation methods of fruit quality traits in peach (*Prunus persica*) under different cultivation conditions. Peach fruit quality is multidimensional, encompassing external, internal, and nutritional attributes, among which sugar-acid composition, texture, and aroma are key determinants of eating quality. Environmental factors (light, temperature, and water) and cultivation practices (fertilization, pruning, crop load regulation, etc.) significantly regulate fruit quality by influencing metabolic processes and interacting with genotype. In terms of evaluation methods, traditional physicochemical and sensory assessments remain fundamental, while modern chromatographic, spectroscopic, and non-destructive techniques (e.g., Vis/NIR and hyperspectral imaging) enable rapid and accurate quality evaluation. Meanwhile, multi-index comprehensive evaluation models (such as PCA and AHP) improve the scientific robustness and practical applicability of quality assessment. Future research should focus on integrating multi-omics and intelligent detection technologies, promoting standardized evaluation systems and precision regulation to achieve stable improvement of peach fruit quality.

**Keywords** *Prunus persica*; Fruit quality; Cultivation conditions; Non-destructive detection; Comprehensive evaluation

## 1 Introduction

Peach (*Prunus persica*) is one of the most widely cultivated temperate fruit trees worldwide, characterized by early ripening, desirable flavor, rich nutritional value, and high economic importance. It plays a significant role in both fresh consumption and processing markets. In China, the peach industry contributes substantially to agricultural structural optimization, regional brand development, and farmers' income growth. With rising living standards and shifts in consumption patterns, market demand has gradually transitioned from a focus on yield to a model emphasizing "high quality, safety, and distinctiveness." However, in some high-yield regions, per capita consumption has declined, mainly due to unstable eating quality and generally low fruit quality, such as insufficient sweetness, weak flavor, and suboptimal ripening characteristics. Therefore, improving and stabilizing peach fruit quality under diverse environments and production systems has become a key issue for industry development (Mosie et al., 2025).

Peach fruit quality is multidimensional and integrative, typically encompassing external, internal, and nutritional attributes. External quality mainly includes fruit shape, size, color, and uniformity, which directly influence consumer purchasing decisions. Internal quality involves flesh texture, firmness, soluble solids content (SSC), titratable acidity (TA), sugar-acid ratio, and volatile aroma compounds, which are the core determinants of taste and flavor; among these, SSC, TA, and their ratio are key indicators of sweetness-acidity balance. Nutritional quality is reflected by the content of functional components such as vitamin C, polyphenols, carotenoids, and mineral elements, which are associated with antioxidant capacity and overall health benefits (Mosie et al., 2025). In addition, with the advancement of evaluation systems, attributes such as storability, resistance to internal disorders, and transport tolerance have gradually been incorporated into quality assessment frameworks.

The formation of peach fruit quality is jointly regulated by genetic factors and environmental conditions, among which cultivation conditions represent important controllable factors. Environmental variables such as light, temperature, water availability, soil properties, and nutrient status influence photosynthesis and metabolic

processes, thereby regulating the accumulation of sugars, organic acids, and aroma compounds (Shin et al., 2023; Zhen et al., 2025). Meanwhile, management practices—including cultivar selection, pruning methods, crop load regulation, irrigation and fertilization, and protected cultivation—also significantly affect fruit quality. However, complex interactions among genotype, environment, and management (“G × E × M”) result in substantial variation in quality expression under different conditions, while existing studies largely focus on single factors, lacking systematic investigation. At the same time, quality evaluation methods are evolving from traditional physicochemical indices toward multi-index integration and non-destructive detection. Technologies such as visible–near infrared (Vis/NIR) spectroscopy and multivariate models provide new tools for rapid quality assessment (Mosie et al., 2025), supporting the development of standardized evaluation systems and high-quality production.

This study focuses on peach fruit quality traits under different cultivation conditions, aiming to elucidate their components and variation patterns, with particular emphasis on the mechanisms by which environmental factors and horticultural practices influence quality formation. Furthermore, it summarizes current methods for evaluating fruit quality and maturity, and explores the application potential of multi-index comprehensive evaluation and non-destructive detection technologies in peach quality research, production regulation, and postharvest grading. By integrating agronomic, physiological, and analytical perspectives, this study seeks to provide a theoretical basis and technical support for optimizing peach cultivation, improving quality stability, and promoting the high-quality development of the peach industry.

## 2 Types of Peach Fruit Quality Traits

### 2.1 External quality

External quality is the primary basis for consumers to evaluate the commercial value of peaches, directly influencing market acceptance, grading outcomes, and price. For fresh peaches, attributes such as fruit size, shape, color, surface integrity, and firmness at purchase are the first perceived quality cues and are therefore key indicators in commercial grading and distribution. Fruit shape is an important component of external quality, commonly including round, flat-round, oblong, and flat (donut) types. Significant differences in shape index (length/width ratio) are observed among cultivars and cultivation conditions (Figure 1). Studies have shown that different peach types, such as peaches, nectarines, and flat peaches, vary greatly in morphological traits including length, width, thickness, and geometric mean diameter. These differences affect not only visual uniformity and packaging suitability but also their suitability for fresh consumption or processing (Wang et al., 2023). Generally, fruits with regular shape, balanced development, and high uniformity are considered high-quality products, whereas irregular or inconsistent fruits reduce commercial grade and market value (Petrucelli et al., 2023).

Fruit color is another key external attribute affecting consumer preference. Peach skin and flesh colors typically range from white and yellow to varying degrees of red blush, mainly determined by the accumulation of anthocyanins, carotenoids, and other pigments. In recent years, CIELAB color parameters such as  $L^*$ ,  $a^*$ ,  $b^*$ , hue angle ( $h^\circ$ ), and chroma ( $C$ ) have been widely used to quantify color characteristics (Masuda et al., 2023; Petrucelli et al., 2023). Anthocyanins are closely associated with red skin coverage, while carotenoids contribute to yellow flesh and background color. Light conditions play a critical role in color development, with sufficient light promoting anthocyanin synthesis and uniform coloration. Conversely, practices such as fruit bagging alter light exposure and significantly affect color expression. It is important to note that although a high proportion of red coloration enhances visual appeal, its correlation with eating quality or internal flavor is not always significant, indicating limitations in evaluating quality based solely on appearance (Masuda et al., 2023).

Fruit size is another important indicator of commercial value, typically expressed as fruit weight, diameter, or volume. It is influenced by both genetic traits and cultivation factors such as crop load, water and nutrient supply, and tree resource allocation. Studies have shown that reducing crop load can significantly increase fruit weight, size, and coloration, but may reduce firmness at harvest, reflecting a trade-off between improved appearance and texture retention (Wang et al., 2023). Therefore, production should not focus solely on large fruit size but instead balance shape uniformity, coloration, firmness, and internal quality. Although firmness is often classified as an

internal quality trait, it is also an important visual cue during purchase. Mechanical firmness measurements are now commonly included in external quality evaluation to distinguish fruit maturity stages such as “ready to buy” and “ready to eat” (Masuda et al., 2023).



Figure 1 External appearance and visual quality traits of peach fruit

## 2.2 Internal quality

Internal quality is the core determinant of peach eating quality and consumer satisfaction. Compared with external traits, it more directly determines whether the fruit is perceived as palatable and is a key factor influencing repeat purchases. Sugar-acid composition forms the chemical basis of peach flavor. Soluble sugars in peaches mainly include sucrose, glucose, fructose, and sorbitol, with sucrose typically accounting for 75%-88% of total sugars. Organic acids are dominated by malic acid, with contributions from other acids such as citric acid varying among cultivars (Wang et al., 2023). Soluble solids content (SSC) is commonly used as an indicator of sweetness, while titratable acidity (TA) reflects sourness; their ratio provides a more comprehensive measure of flavor balance (Petrucelli et al., 2023). Studies indicate that reducing crop load can increase SSC, total sugar, and sugar-acid ratio, thereby enhancing sweetness and overall flavor intensity (Zhang et al., 2020). Thus, the sugar-acid ratio is often a better predictor of consumer preference than sugar or acid alone.

Texture is another critical component of internal quality, including firmness, juiciness, crispness, mealiness, fibrousness, and melting/non-melting characteristics. Texture development is closely related to cell wall structure, pectin metabolism, and fruit softening during ripening. As fruit matures, cell walls degrade and pectin solubilization increases, leading to reduced firmness and changes in texture. Research indicates that firmness is not only a physical parameter but also closely associated with sensory perceptions such as sourness, green notes, and overripe flavors, making it an important indicator of maturity and overall quality (Masuda et al., 2023). Cultivation factors such as water supply, harvest timing, and crop load significantly influence texture; for example, moderate water stress helps maintain firmness, whereas excessive irrigation can lead to soft flesh and reduced storability.



Flavor quality results from the combined effects of sugar-acid balance, texture, and volatile aroma compounds. Peaches contain a wide range of volatile organic compounds (VOCs), including lactones, aldehydes, esters, and alcohols. Key compounds such as hexyl hexanoate and  $\gamma$ -decalactone contribute to characteristic fruity, floral, and sweet aromas. These aroma compounds, together with sugar and acid composition, shape the overall flavor profile. Sensory studies have shown that fruits with moderate size, higher SSC/TA ratio, strong aroma, and balanced texture are generally rated higher in eating quality than larger but bland fruits (Petrucelli et al., 2023). Therefore, evaluation of internal quality should integrate sugar-acid balance, texture, and aroma rather than relying on a single indicator.

### 2.3 Nutritional and functional quality

With increasing consumer awareness of health, the nutritional and functional quality of peaches has gained growing attention. In addition to carbohydrates, water, and minerals, peaches are rich in vitamins, polyphenols, carotenoids, flavonoids, and anthocyanins, which contribute to antioxidant, anti-inflammatory, and health-promoting properties (Wang et al., 2023; Qi et al., 2024). Vitamins are key components of nutritional quality, with vitamin C being particularly important due to its antioxidant activity. Other fat-soluble vitamins and pigment-related bioactive compounds also enhance the health value of peaches (Vuković et al., 2025). The accumulation of these nutrients is influenced by cultivar, maturity stage, and environmental conditions, leading to significant variation even within the same cultivar.

Polyphenols are among the most important functional compounds in peaches, including phenolic acids, flavonoids, flavonols, catechins, and anthocyanins. These compounds not only contribute to fruit coloration but also provide antioxidant, antimicrobial, and anti-inflammatory benefits (Qi et al., 2024). Studies have shown significant variation among cultivars in total phenolics ( $\approx 9$ -578 mg GAE/100 g), total flavonoids ( $\approx 1$ -95 mg CAE/100 g), and antioxidant capacity ( $\approx 136$ -462 mg TE/100 g), with higher concentrations typically found in the peel than in the flesh (Wang et al., 2023). Yellow-fleshed peaches generally contain higher levels of carotenoids and total polyphenols, whereas white-fleshed varieties may exhibit higher average antioxidant activity.

Antioxidant capacity is an important integrative indicator of functional quality, commonly assessed using methods such as DPPH, ABTS, and FRAP. It results from the synergistic effects of vitamin C, polyphenols, carotenoids, and other bioactive compounds (Qi et al., 2024). Significant variation in antioxidant capacity exists among cultivars and is strongly influenced by maturity and environmental conditions, indicating both genetic dependence and environmental sensitivity (Vuković et al., 2025). Increasingly, peaches are being considered as potential functional foods rather than merely fresh fruits. This suggests that breeding and cultivation strategies should not only focus on yield, appearance, and flavor, but also target enhanced levels of bioactive compounds and antioxidant capacity to improve overall nutritional and health value (Wang et al., 2023).

## 3 Effects of Cultivation Conditions on Peach Fruit Quality

### 3.1 Environmental factors

Environmental factors are fundamental external conditions influencing the formation of peach fruit quality, among which light, temperature, and water availability play central roles during fruit development. These factors determine photosynthetic production and metabolic activity, and regulate the accumulation of sugars, organic acids, pigments, and secondary metabolites, thereby shaping fruit appearance, flavor, and nutritional quality. Light is one of the most critical environmental factors affecting quality potential. Adequate and well-distributed light enhances photosynthesis, increases carbon supply, promotes fruit enlargement, and improves soluble solids content (SSC), dry matter content (DMC), and anthocyanin accumulation, leading to better red coloration. Studies have shown that training systems such as open-center and fruiting-wall structures, which improve light interception and canopy light distribution, generally result in higher fruit weight, a greater proportion of large fruits, and improved coloration (Figure 2) (Anthony and Minas, 2021). Within a single tree, fruits in the upper and outer canopy typically exhibit higher SSC, better color, and superior flavor compared to those in shaded inner or lower positions (Anthony and Minas, 2022).

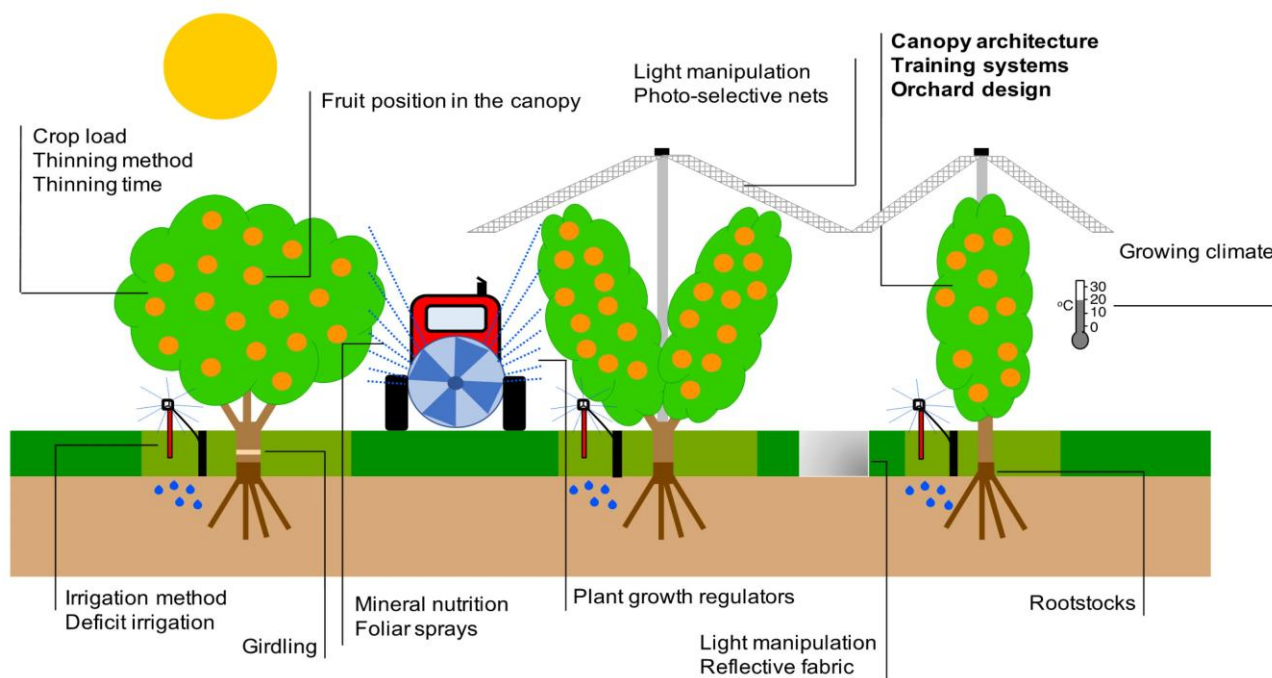


Figure 2 Overview of key orchard factors that influence preharvest peach tree and fruit physiology and affect harvest quality (Adapted from Anthony and Minas, 2021)

Temperature is another key factor regulating fruit growth and metabolic processes. Suitable temperatures and appropriate diurnal temperature variation favor sugar accumulation, acid balance, and aroma formation, thereby improving flavor quality. In general, a larger day-night temperature difference enhances the sugar-acid ratio and results in a more balanced taste. However, both extreme heat and insufficient heat accumulation can negatively affect quality (Shin et al., 2023). Controlled-environment studies indicate that high temperatures (e.g., 30 °C) accelerate early fruit growth and shorten the development period, advancing harvest by 2-3 weeks, but may reduce final fruit size and SSC, despite improving red skin coloration (Shin et al., 2023). In contrast, insufficient winter chilling can impair dormancy release, reduce fruit set and yield, and indirectly affect fruit quality (Babintseva, 2024).

Water conditions also have a profound impact on peach quality. Adequate water supply supports cell turgor, fruit expansion, and external quality, whereas excessive irrigation can dilute SSC, reduce firmness, weaken flavor, and increase the risk of cracking, diseases, and physiological disorders (Zhen et al., 2025). In contrast, moderate deficit irrigation strategies, such as deficit irrigation (DI) or partial root-zone drying (PRD), can increase DMC, firmness, SSC, glucose, and polyphenol content while reducing certain organic acids, thereby enhancing flavor intensity and antioxidant capacity. However, excessive water stress can limit fruit growth, reduce yield, and negatively affect the accumulation of some nutrients such as carotenoids. Therefore, irrigation management should be optimized according to developmental stages and regional conditions to balance yield and quality.

### 3.2 Cultivation practices

Cultivation practices serve as key regulatory tools linking environmental conditions to fruit quality formation. They influence tree nutritional status, canopy structure, light distribution, and source-sink relationships, thereby affecting external, internal, and nutritional quality traits (Figure 3). Fertilization management, particularly nitrogen (N), phosphorus (P), and potassium (K), plays a crucial role. Appropriate NPK application can improve yield, fruit size, SSC, total sugar, sugar-acid ratio, firmness, and vitamin C content while reducing titratable acidity (Babintseva, 2024). However, excessive nitrogen promotes vegetative growth, leading to poor coloration, lower SSC, and reduced flavor intensity. In contrast, potassium enhances sugar transport and coloration, whereas imbalanced phosphorus supply may negatively affect sugar accumulation. Since peach trees are perennial and

capable of recycling nitrogen, excessive fertilization does not consistently improve yield or quality, highlighting the importance of precision nutrient management.



Figure 3 Cultivation and management of peach trees

Pruning primarily affects fruit quality by regulating canopy structure and light conditions. Proper pruning improves light penetration and distribution, increases the proportion of well-exposed fruiting zones, and promotes uniform coloration and sugar accumulation. Conversely, dense canopies lead to shading, poor coloration, lower SSC, and uneven quality. Planting density also plays an important role. Appropriate density improves land use efficiency and yield per unit area while maintaining good light distribution when combined with proper pruning. However, excessive density and uncontrolled vigor increase competition and shading, resulting in poorer fruit quality. Modern high-density systems with small canopies, such as spindle or bush-type training, can achieve both high yield and good quality when light conditions are well managed.

Protected cultivation, including greenhouses and net systems, modifies environmental factors such as temperature, humidity, light, and wind, thereby influencing fruit development and quality formation. These systems often promote earlier maturity, extend the photosynthetic period, and improve external quality (Maatallah et al., 2024). However, insufficient light or excessive temperatures under protected conditions may reduce coloration, aroma, and overall flavor. Therefore, the effectiveness of protected cultivation depends on precise control of environmental and management factors to achieve optimal quality and yield.

### 3.3 Regulation techniques

In addition to environmental and conventional management practices, fine-tuning techniques such as thinning, plant growth regulator (PGR) application, and harvest timing are essential for improving fruit quality. These practices directly influence source–sink balance, fruit development, and maturation processes. Thinning is one of the most effective methods for regulating crop load and improving fruit quality. By reducing fruit number,



nutrient allocation per fruit increases, resulting in higher fruit weight, size, SSC, total sugar, sugar-acid ratio, and improved coloration (Wang et al., 2023). Studies show that retaining 25%-75% of initial fruit set can increase fruit weight by 20%-50% and SSC by up to 50% (Mazzoni et al., 2022). However, excessive thinning reduces total yield, so optimal thinning intensity must be determined based on cultivar characteristics, tree vigor, and market goals. Early thinning during bloom or early fruit development is generally more effective in improving quality and resource allocation.

Plant growth regulators (PGRs) are widely used to regulate fruit enlargement, maturity, and quality attributes such as firmness, coloration, and storability. Compounds such as gibberellins, cytokinins, calcium treatments, and biostimulants can improve fruit size, surface quality, and postharvest performance (Zhen et al., 2025). However, their effectiveness depends strongly on cultivar, dosage, timing, and environmental conditions. Improper use may lead to soft texture, poor sugar accumulation, or uneven ripening. Therefore, PGRs should be used as supplementary tools rather than substitutes for proper orchard management.

Harvest timing is a critical factor determining final fruit quality (Figure 4). Since postharvest handling can only maintain rather than improve quality, the maturity stage at harvest directly affects eating quality, storability, and consumer satisfaction. Early-harvested fruits are firmer and more suitable for storage and transport but often have lower SSC and weaker aroma. In contrast, delayed harvest improves sweetness and flavor but reduces shelf life and increases the risk of physiological disorders (Shin et al., 2023). In recent years, non-destructive indicators such as color indices, firmness, SSC, IAD, and DMC have been widely used to determine optimal harvest timing more accurately. This reflects a shift from experience-based decisions to data-driven, multi-index evaluation in harvest management.



Figure 4 Harvesting stage and maturity management of peach fruit



## 4 Mechanisms of Variation in Quality Traits

### 4.1 Physiological and biochemical mechanisms

The formation of peach fruit quality traits depends on a series of complex and coordinated physiological and biochemical processes. As a typical climacteric fruit, peach undergoes increased respiration and ethylene production during ripening, which further triggers a range of physiological changes, including carbohydrate and organic acid metabolism, cell wall remodeling, pigment reconfiguration, and volatile compound synthesis. These processes drive the transition of the fruit from a “growth stage” to a “ripening stage” quality state. Sugar and acid metabolism is the core basis determining peach flavor quality. During fruit development, photosynthetic products are transported to the fruit through the phloem and gradually converted into and accumulated as soluble sugars such as sucrose, glucose, fructose, and sugar alcohols, while organic acids such as malic acid and citric acid change dynamically at different developmental stages. In general, soluble sugars continue to accumulate and organic acids gradually decline during ripening, leading to an increase in the sugar-acid ratio and resulting in enhanced sweetness and reduced sourness. Metabolomic studies have shown that, in cultivars such as ‘Huangjin’, the color-change stage is a critical period characterized by significant accumulation of sugars and sugar alcohols and a marked decline in organic and phenolic acids, indicating that this stage is an important physiological turning point in peach flavor formation (Minas et al., 2018). Meanwhile, these primary metabolic changes also interact with cell wall degradation, causing fruit softening and texture changes, which in turn affect eating quality and postharvest storability.

Pigment synthesis and transformation are important physiological bases for external fruit quality. During peach ripening, chlorophyll gradually degrades, while anthocyanins and carotenoids accumulate, jointly driving the peel and flesh color from green to red, yellow, or mixed hues (Figure 5). Anthocyanin accumulation is usually closely related to red peel coloration, whereas carotenoids are more involved in the formation of yellow flesh and peel background color. Studies have shown that, during the color-change stage, key enzyme genes in the flavonoid pathway, such as CHS, F3'H, DFR, and A3GT, are upregulated, thereby promoting anthocyanin biosynthesis and intensifying red or mixed coloration in the fruit (Serrie et al., 2025). In addition to determining yellow coloration, carotenoids can also generate certain norisoprenoid volatiles through the carotenoid cleavage dioxygenase (CCD) pathway, thereby linking pigment metabolism with aroma formation.



Figure 5 Maturation process of peach fruit

Aroma formation further enriches peach flavor quality. The characteristic aroma of peach is composed of volatile organic compounds such as lactones, esters, aldehydes, alcohols, and terpenes. These compounds are mainly derived from the fatty acid  $\beta$ -oxidation pathway, the lipoxygenase (LOX) pathway, amino acid metabolism, and terpene and carotenoid cleavage pathways. For example, lactones usually contribute to the typical sweet and ripe-fruit aroma of peach, esters are associated with floral and fruity notes, while aldehydes and alcohols contribute to freshness (Li et al., 2023). Studies have shown that these volatile compounds change dynamically during fruit development and storage. Different cultivation conditions, such as light, temperature, and exogenous treatments, can alter the types and proportions of aroma compounds by regulating enzyme activities and the intensity of metabolic pathways, thereby leading to differences in fruit flavor among regions and years (Cao et al., 2024).

#### 4.2 Molecular genetic mechanisms

Differences in peach fruit quality traits are fundamentally controlled by genetic factors. In recent years, with the development of genomics, transcriptomics, and multi-omics integration, a large number of key genes and regulatory networks related to sugar and acid accumulation, fruit coloration, texture formation, and aroma biosynthesis have been gradually elucidated, providing important support for understanding the molecular basis of quality traits. In terms of sugar and acid metabolism, QTL mapping and genome-wide association studies (GWAS) have identified multiple genomic regions associated with soluble solids content (SSC), titratable acidity (TA), and sugar-acid balance. For example, major QTLs associated with SSC and TA have been identified on linkage group 5, and epistatic interactions among acidity-related loci can further regulate sugar-acid balance. At the candidate gene level, the malate transport-related gene *PpALMT1* and the sugar transporter gene *PpERDL16* have been confirmed to be closely associated with malate and fructose accumulation, thereby contributing to flavor differences among cultivars (Yao et al., 2025). This indicates that peach internal quality is not determined by a single metabolic enzyme but is coordinately controlled by transport, synthesis, degradation, and compartmentation processes.

In fruit coloration, structural genes and regulatory genes in the anthocyanin pathway together constitute a complex molecular regulatory network. Studies have shown that structural genes such as *CHS*, *DFR*, and *UFGT* control key steps in anthocyanin biosynthesis, while transcription factors such as MYB and bHLH act as upstream regulators that respond to environmental signals and coordinate downstream gene expression (García-Gómez et al., 2020; Da Silva Linge et al., 2021). In addition, some NAC family transcription factors are also involved in regulating flesh or peel coloration. For example, *PpBL* can affect red flesh pigmentation by regulating *PpNAC1*, and is also associated with the formation of certain aroma compounds such as linalool and (Z)-3-hexenyl acetate, reflecting a cross-link between color and aroma metabolism (Rawandoozi et al., 2020a). Aroma biosynthesis is likewise under the coordinated regulation of multiple genes. Studies have reported that terpene synthase genes, lipoxygenase-related genes, and carotenoid cleavage dioxygenase genes are all closely associated with the formation of volatile aroma compounds in peach (Li et al., 2023). *PpCCD4* and other CCD family members are closely related to the production of norisoprenoid aroma compounds, while GWAS has also identified terpene synthase genes associated with linalool synthesis. Meanwhile, different haplotypes of the *PpAAT* gene cluster can lead to variation in ester content, thereby influencing fruit aroma intensity and flavor style among cultivars. This suggests that peach aroma quality is essentially controlled by multiple gene modules and different metabolic branches (Feng et al., 2024).

In recent years, multi-omics technologies have further advanced the systematic dissection of peach quality regulatory networks. Transcriptomic studies have shown that hundreds to thousands of genes change expression during fruit ripening, involving sugar and acid metabolism, cell wall remodeling, ethylene signaling, stress response, and flavor compound formation (Veerappan et al., 2021). By integrating transcriptomic and metabolomic data, gene expression changes can be linked to the levels of sugars, organic acids, anthocyanins, and volatile compounds, thereby enabling the construction of “gene-metabolite-quality trait” regulatory network models. These studies indicate that peach quality traits are influenced not only by a few key structural genes, but also by complex transcription factor networks, coupled metabolic pathways, and polygenic control (Cao et al., 2024; Feng et al., 2024).

### 4.3 Genotype×environment interaction effects

The formation of peach fruit quality traits is not determined by genotype alone. Genotype × environment interaction (G×E) is an important cause of variation and stability differences in quality traits. In actual production, different cultivars may exhibit different quality under the same environment, while the same cultivar may show significantly different quality performance across regions, years, and management conditions. This phenomenon is a direct manifestation of G×E interaction. Multi-environment trials have shown that traits such as fruit weight, fruit size, coloration, and SSC usually display significant G×E effects. In contrast, traits such as titratable acidity and ripening date often have relatively high heritability and lower G×E effects, whereas fruit weight and shape are more environmentally sensitive and require region-specific selection and management (Rawandoozi et al., 2020b). This indicates that not all quality traits respond to the environment in the same way: some are relatively stable and suitable for wide adaptation, whereas others are highly environment-dependent and require precise matching between cultivar and region.

At the molecular level, multi-environment genomic prediction models show that the G×E effect on SSC mainly originates from the polygenic background, whereas some major QTLs and dominance effects remain relatively stable across environments. This means that peach quality traits are controlled both by stable major genes and by numerous minor-effect genes and environmental signals. Environmental factors such as light, temperature, water, canopy microclimate, and exogenous treatments interact with cultivar-specific regulatory networks by affecting sugar and acid metabolism, pigment accumulation, and volatile compound formation, ultimately leading to different quality outcomes (Cao et al., 2024). For example, in ‘Huangjin’ peach, the color-change stage is a key period of transcriptomic and metabolomic change, and the timing and intensity of this stage are strongly regulated by temperature and light. When exogenous treatments such as glutamic acid, sucrose, or brassinolide are applied, different cultivars show markedly different responses in fruit weight, firmness, SSC, anthocyanin accumulation, and the expression of key genes (e.g., *PpPAL*, *PpF3H*, *PpDFR*, *PpUFGT*, *PpGST1*, and *PpMYB10.1*), indicating that the effects of environmental or management signals are strongly genotype-dependent (Figure 6) (Kou et al., 2023). This suggests that the same management practice does not necessarily produce the same effect across cultivars, and quality regulation must be based on an understanding of cultivar-specific responses.

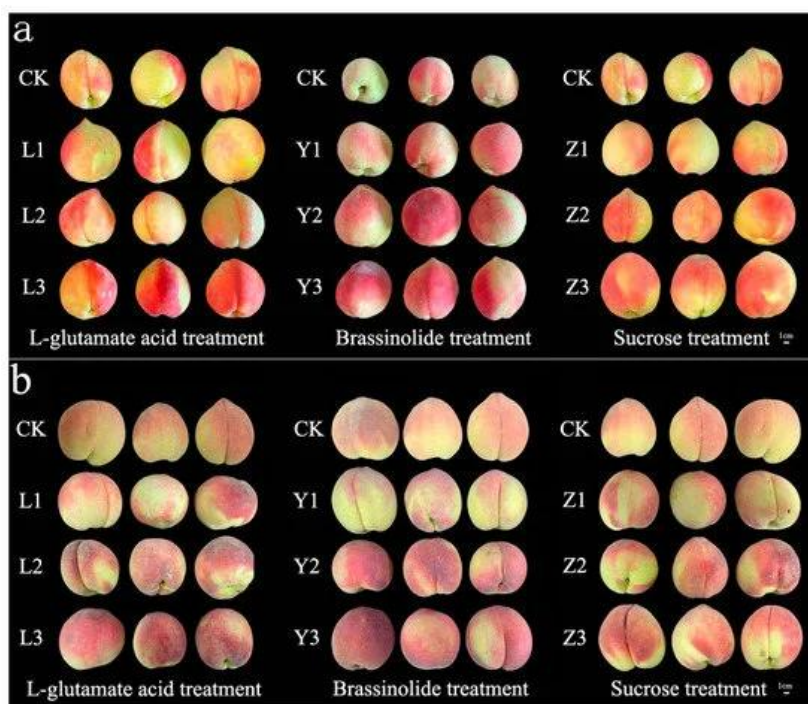


Figure 6 The ripening stage of the fruits of ‘Baifeng’ and ‘Weiduanmihong’ after treated with exogenous substances (Adopted from Kou et al., 2023)

Image caption: (a) is ‘Baifeng’; (b) is ‘Weiduanmihong’ (Adopted from Kou et al., 2023)

In addition, multi-environment GWAS studies in stone fruits have enabled researchers to distinguish between environment-shared QTLs and environment-specific QTLs, and have shown that some loci may have antagonistic effects across environments (Serrie et al., 2025). These results further demonstrate that G×E interactions are not only common but may profoundly influence quality breeding and the development of region-specific cultivation strategies. Incorporating G×E into QTL analysis, GWAS, and genomic prediction models can help identify stable trait loci and screen superior cultivars and management schemes suitable for different ecological regions. Therefore, a deeper understanding of G×E interaction mechanisms is of great importance for achieving precise matching between cultivars and environments, improving quality stability, and optimizing cultivation management. Future peach quality research needs to shift from “single-environment, single-trait” analysis toward a collaborative framework of “multi-environment, multi-omics, and multi-model” analysis in order to more comprehensively reveal the true sources of quality variation.

## **5 Methods for Evaluating Peach Fruit Quality**

### **5.1 Physicochemical and sensory evaluation methods**

Traditional methods for evaluating peach fruit quality mainly include physicochemical measurements and sensory evaluation. Physicochemical indicators are important for characterizing both internal and external quality and commonly include fruit size and weight, shape, density, peel and flesh color, firmness, soluble solids content (SSC, °Brix), titratable acidity (TA), pH, and sugar-acid ratio. These indicators are usually measured on harvested fruit. For example, calipers or image analysis are used to obtain fruit dimensions, shape index, and diameter; colorimeters are used to measure CIELAB color parameters; penetrometers or texture analyzers are used to determine firmness; refractometers are used to measure SSC; and titration is used to determine TA and pH. SSC is often regarded as an approximate indicator of sweetness, while TA and pH are used to characterize acidity. Firmness reflects not only texture status but is also closely related to harvest maturity and postharvest performance. Studies have shown that these physicochemical traits often vary significantly among cultivars or maturity stages. For example, late-ripening cultivars may have larger fruits and brighter coloration, but not necessarily the highest SSC or perceived sweetness (Farina et al., 2019).

To improve the interpretability of quality assessment, some studies have developed derived indices based on physicochemical measurements, such as sweetness index, total sweetness index, maturity index, and sugar-acid balance index, to integrate complex physicochemical composition into more interpretable quality scores (Popova et al., 2021). These approaches help move traditional physicochemical data from “single-trait measurement” toward “comprehensive quality characterization,” making them valuable for cultivar comparison and maturity evaluation. However, whether a fruit is ultimately accepted by consumers still depends on actual sensory experience. Therefore, sensory evaluation serves as an important bridge linking physicochemical indicators with eating quality. Sensory evaluation is usually performed by trained panels or consumer panels, which quantitatively score attributes such as aroma, sweetness, sourness, bitterness, astringency, juiciness, texture characteristics (e.g., firmness, crispness, fibrousness, mealiness), and overall acceptability, commonly using 9-point or 15-point scales (Table 1) (Felts et al., 2019; Sun et al., 2023). Studies have shown that SSC and TA are good predictors of sweetness and sourness perception, but more complex sensory attributes—such as fruity aroma, flavor intensity, and flavor harmony, still require direct sensory evaluation. For example, higher firmness is often associated with sourness and unripe flavor, while larger fruit tends to be perceived as juicier or more overripe (Felts et al., 2019).

In recent years, with the development of comprehensive quality evaluation concepts, researchers have increasingly tended to integrate physicochemical and sensory data. Through principal component analysis (PCA), cluster analysis, or comprehensive scoring methods, it is possible to identify cultivar types that exhibit “good appearance but average flavor” or “ordinary appearance but outstanding internal flavor,” thereby providing more refined criteria for breeding and cultivation management (Muto et al., 2022). Therefore, physicochemical measurements and sensory evaluation are not mutually substitutive but together form the basic framework for peach fruit quality assessment.



Table 1 Descriptive sensory exterior appearance attributes of fresh-market peach and nectarine genotypes evaluated on a 15-point scale (Adopted from Felts et al., 2019)

Genotype	Uniformity of color	Color-yellowness	Color-redness	Amount of bruises	Separation of pit	Pit size
A-827	10.1 cd2	9.8 bc	4.4 ab	2.1 abc	10.8 ab	8.7 bc
A-850	13.1 a	13.0 a	1.6 d	1.9 abcd	6.9 c	9.5 ab
A-865	10.8 bc	9.6 c	3.4 bc	1.1 bcde	11.9 ab	7.9 bc
Amoore Sweet	13.2 a	13.5 a	1.0 d	0.4 e	13.9 a	8.3 bc
Bowden	13.3 a	13.2 a	0.9 d	0.8 cde	13.1 a	8.1 bc
Effie	12.7 ab	12.2 ab	1.9 cd	0.6 de	13.6 a	9.4 ab
Loring	10.0 cd	10.1 bc	4.2 ab	2.5 a	8.6 bc	10.9 a
Souvenirs	9.9 cd	9.8 bc	4.4 ab	1.0 cde	11.8 ab	7.3 c
White River	8.5 d	7.9 c	5.9 a	2.3 ab	9.5 bc	11.0 a
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table caption: 0= less of the attribute; 15 = more of the attribute in terms of intensity; Genotypes were evaluated in duplicate by trained panelists; Means with different letter(s) for each attribute are significantly different ( $P<0.05$ ) using Tukey's honestly significant difference test (Adopted from Felts et al., 2019)

## 5.2 Modern analytical techniques

With the advancement of analytical technology, modern instrumental methods have been increasingly applied in peach quality research and have gradually become important tools for analyzing fruit flavor, nutritional components, and functional compounds. Compared with traditional physicochemical methods, modern analytical techniques can reveal the chemical basis of peach quality at higher resolution and greater depth, especially in the analysis of volatile aroma compounds, trace metabolites, and complex compositional networks. Chromatographic techniques are among the most mature methods currently used in peach quality research. High-performance liquid chromatography (HPLC) is mainly used to analyze non-volatile compounds such as sugars, organic acids, polyphenols, and vitamins, allowing accurate quantification of glucose, fructose, sucrose, malic acid, citric acid, and related compounds (Sun et al., 2023). These data are important for understanding the formation of sweet-sour flavor, nutritional quality differences, and metabolic characteristics among cultivars. Meanwhile, gas chromatography-mass spectrometry (GC-MS) is widely used to identify and quantify volatile aroma compounds in peach. Gas chromatography-ion mobility spectrometry (GC-IMS), due to its rapid analysis and high sensitivity to volatile compounds, has increasingly been used for aroma fingerprinting of peach fruit. Studies have shown that the combined use of GC-IMS and GC-MS can identify key aroma compounds and thereby distinguish aroma styles among cultivars (Sun et al., 2022).

When combined with sensory evaluation, chromatographic techniques can further identify key flavor markers affecting consumer preference. For example, by integrating sugar-acid data obtained by HPLC, volatile compound data identified by GC-MS, and sensory evaluation results, researchers can more systematically elucidate the chemical basis of sensory attributes such as "sweetness," "fruity aroma," "ripe aroma," or "green notes" in peach fruit (Sun et al., 2023). Such studies are of great significance for germplasm screening, elite cultivar breeding, and flavor-oriented cultivation management. In addition to chromatography, spectroscopic techniques have rapidly expanded in peach quality evaluation because of their speed, high throughput, and potential for non-destructive analysis. Visible/near-infrared spectroscopy (Vis/NIR) estimates internal quality traits such as SSC, dry matter content (DMC), firmness, polyphenols, and pigments by measuring the interaction between light and fruit tissues. Studies have shown that high-accuracy prediction of SSC and DMC can be achieved using models such as partial least squares regression (PLS), multiple linear regression (MLR), and least-squares support vector machine (LS-SVM), often with coefficients of determination ( $R^2$ ) above 0.94 and RMSEP values around 0.3%-0.6% (Minas et al., 2020). Hyperspectral imaging further integrates spatial and spectral information, allowing not only estimation of SSC and firmness but also visualization of the spatial distribution of these quality parameters within the fruit, as well as prediction of fruit size and weight (Xuan et al., 2022).

In addition, fluorescence spectroscopy, electrical property detection, and electronic nose and tongue technologies have also expanded the methodological toolbox for peach quality detection (Qi et al., 2024). These methods show considerable potential for maturity recognition, internal defect detection, and flavor evaluation, and are especially suitable for breeding and grading scenarios requiring rapid, large-scale assessment. The introduction of modern analytical techniques has gradually shifted peach quality evaluation from traditional single-indicator measurement toward multidimensional, molecular-level, and high-throughput analysis.

### 5.3 Non-destructive detection and comprehensive evaluation models

Non-destructive detection technology has become an important direction in peach quality evaluation in recent years. Its core objective is to achieve rapid, objective, and highly repeatable detection of internal quality without damaging fruit structure, thereby compensating for the limitations of destructive analysis and subjective sensory evaluation (Qi et al., 2024). Such technologies are particularly suitable for large-scale phenotyping, online grading of commercial fruit, and precision harvest decisions. At present, Vis/NIR and hyperspectral systems are the most widely used. With a single scan, they can rapidly predict SSC, DMC, firmness, and maturity indices (such as IAD), while maintaining high accuracy across different developmental stages, crop loads, and cultivars (Anthony et al., 2023). Studies have shown that by fully accounting for sources of variation such as genotype, canopy position, and management practices during model construction, the stability and generalization ability of predictive models can be significantly improved. This also helps reveal the influence of preharvest factors on fruit quality formation (Minas et al., 2023).

In addition to spectroscopic methods, a range of intelligent detection techniques has gradually been incorporated into non-destructive peach quality evaluation systems (Qi et al., 2024). Machine vision can be used to identify fruit shape, color distribution, and surface defects; hyperspectral imaging can simultaneously capture both external and internal quality information; acoustic vibration and electrical property detection show potential for firmness and internal defect recognition; and electronic noses and tongues enable rapid characterization of aroma and taste features. The integration of these technologies has promoted a shift in peach quality evaluation from traditional “static, destructive measurement” toward “dynamic, online, and intelligent monitoring.”

On this basis, the construction of comprehensive evaluation models has become increasingly important for transforming multi-source data into practical applications. Through principal component analysis (PCA), cluster analysis, and machine-learning approaches, multiple indicators such as shape, mass, firmness, color, SSC, TA, and electrical parameters can be integrated to achieve quality grading and to demonstrate that single appearance indicators cannot fully reflect overall fruit quality. In addition, the analytic hierarchy process (AHP) and fuzzy comprehensive evaluation methods can combine physicochemical indicators with sensory evaluation, weighting attributes such as sweetness, juiciness, and overall preference (Baviera-Puig et al., 2023; Sun et al., 2023). Overall, modern peach quality evaluation is shifting from reliance on single-indicator detection toward multi-source data integration, gradually establishing more comprehensive evaluation systems that better reflect actual consumer eating experience.

## 6 Construction of Quality Evaluation Systems

### 6.1 Multi-index comprehensive evaluation methods

Peach fruit quality is inherently multidimensional, and a single indicator cannot fully reflect its overall quality level. Therefore, multi-index comprehensive evaluation has become an important direction in current peach quality research and grading applications. Comprehensive evaluation systems usually integrate external quality (such as fruit shape, color, and size), physical quality (such as fruit weight, density, and firmness), internal quality (such as SSC, TA, sugar-acid ratio, texture, and flavor), and, when necessary, nutritional and functional quality (such as polyphenols and antioxidant capacity), as well as even electrical or spectral parameters, into a unified framework to achieve systematic evaluation of fruit quality (Farina et al., 2019). This approach effectively overcomes the limitations of single indicators and more objectively characterizes the comprehensive performance of fruit quality among different cultivars, maturity stages, and cultivation conditions.

Existing studies have shown that multi-index comprehensive evaluation is applicable not only to fresh peaches but also to processed products. For example, in fresh peach studies, an evaluation system based on 11 indicators—including shape index, volume, weight, density, firmness, color, impedance, phase angle, SSC, TA, and sugar-acid ratio—was able to classify fruits into different quality grades and revealed the important fact that the proportion of red peel color is only weakly correlated with internal eating quality (Zhang et al., 2020). This indicates that external traits intuitively preferred by consumers do not necessarily represent the true comprehensive quality of the fruit. Similarly, in freeze-dried peach powder studies, researchers integrated 14 indicators related to physicochemical properties, nutrition, and processing performance to evaluate samples of different cultivars and ripening stages, and found that a smaller number of core indicators could be selected without losing discriminatory power, suggesting that comprehensive evaluation systems also have potential for indicator compression and optimization (Liu et al., 2017).

From the perspective of evaluation logic, the advantages of a multi-index system are mainly reflected in three aspects. First, it can simultaneously take into account appearance, flavor, and nutritional value, thereby better meeting the actual needs of consumers and industry. Second, it helps compare materials for different purposes, such as distinguishing “high-quality fruit for fresh consumption” from “raw materials suitable for processing.” Third, it provides quantitative support for cultivar selection and optimization of cultivation practices, rather than relying solely on empirical judgment. In practice, multi-index comprehensive evaluation usually requires standardization of different indicators first to eliminate the influence of dimensional differences. Common methods include range standardization and Z-score normalization, which place all indicators on a comparable scale. Subsequently, weighted summation, comprehensive scoring functions, or multivariate models can be used to integrate multiple indicators into a single comprehensive quality score, enabling comparison among different treatments, cultivars, or regional materials (Zhang et al., 2020). At the same time, these methods are often combined with correlation and regression analyses to reveal internal relationships among different quality traits, such as sugar-acid ratio versus sensory sweetness, firmness versus maturity, and overall color parameters versus consumer preference, thereby providing a basis for selecting key indicators and improving evaluation efficiency.

## 6.2 Weight determination and model construction

After establishing a multi-index evaluation system, how to scientifically determine the weight of each indicator and construct a comprehensive evaluation model becomes the key step in achieving quantitative peach quality assessment. Because different quality indicators contribute unequally to overall quality, it is necessary to adopt reasonable weighting methods and model-construction strategies to transform raw data into interpretable comprehensive scores. Principal component analysis (PCA) is one of the most commonly used objective weighting and dimensionality-reduction methods in fruit quality evaluation studies (Farina et al., 2019; Zhang et al., 2020). Its core function is to deal with multicollinearity among multiple indicators, extract information components that explain the main variation from the original variables, and thus reduce redundancy while improving model simplicity. For example, in fresh peach studies, PCA based on 11 indicators extracted five principal components explaining about 85% of the total variation, and further combined with K-means clustering to classify fruits into five quality grades (Zhang et al., 2020). Similarly, in freeze-dried peach powder evaluation, PCA extracted five principal components from 14 variables, with a cumulative contribution rate of 84.46%, effectively distinguishing among cultivars and ripening stages. Thus, PCA not only increases the information density of evaluation models but also helps identify the dominant factors underlying comprehensive quality.

The analytic hierarchy process (AHP), by contrast, is a subjective weighting method that places greater emphasis on consumer preference or expert experience in evaluation systems. Its basic principle is to construct a judgment matrix and compare indicators pairwise to determine their relative importance. The advantage of AHP lies in its ability to reflect production goals and market demand. For example, in the evaluation of fresh peaches, consumers are often more concerned with sweetness, juiciness, and aroma than with firmness or external appearance alone. Studies have shown that, when AHP is combined with sensory analysis in peach and nectarine quality evaluation, the gustatory phase emerges as the most critical in overall quality judgment, with sweetness and juiciness usually

being the major positive contributors, whereas bitterness, sourness, and astringency have greater effects on negative evaluations (Baviera-Puig et al., 2023). Therefore, AHP has a unique advantage in building consumer-oriented evaluation systems.

However, AHP depends on expert experience and thus contains a certain degree of subjectivity, whereas PCA, although objective, lacks a direct reflection of consumer preference. For this reason, recent studies increasingly tend to adopt combined objective-subjective weighting methods, such as integrating PCA with AHP, or further combining entropy weighting, grey relational analysis, TOPSIS, and other multi-criteria decision-making methods (Tian et al., 2025; Zhou et al., 2025). These approaches can introduce preference information while preserving statistical objectivity, making weight allocation more consistent with real application needs. In other words, PCA mainly provides “importance from the data-structure perspective,” whereas AHP and related methods provide “importance from the decision-making perspective.” Their combination helps establish evaluation models that are both scientific and practical. On this basis, by constructing comprehensive quality functions, classification models, or predictive models, it becomes possible to quantitatively evaluate samples under different cultivation conditions, cultivars, or regions, and to provide support for cultivation decisions, cultivar recommendation, and commercial grading. Therefore, weight determination and model construction are not merely statistical issues, but crucial steps in transforming multidimensional quality information into actionable decision-making tools.

### **6.3 Regionalized and standardized evaluation systems**

The relative importance of peach quality traits varies with ecological conditions, production systems, major cultivars, and target markets across regions. Therefore, when constructing a quality evaluation system, both standardization and regional adaptability must be considered. In other words, an ideal system should combine a “standardized framework + regional calibration” rather than relying on a single uniform model. From the perspective of standardization, unified evaluation indicators, measurement methods, and reference systems are the basis for ensuring comparability of results across studies, regions, and experimental sites. For example, the large collaborative project represented by the EUFRIN Peach and Apricot Working Group proposed about 40 standardized indicators for new cultivar evaluation, covering phenological stages (such as flowering time and harvest date), yield, external quality, internal quality, and susceptibility to diseases, and achieved consistency in multi-environment trial results through unified measurement protocols and reference cultivars (Giovannini et al., 2021). This framework not only provides a common technical language for breeders, growers, and the industry chain, but also lays a methodological foundation for interregional quality comparison and cultivar promotion.

At the same time, peach fruit quality shows clear regional characteristics. Different ecological regions differ in light, temperature, water availability, soil conditions, and cultivation systems, so the importance of certain quality indicators also differs among regions. For example, in areas with large diurnal temperature differences and abundant light, sugar accumulation and coloration are usually more emphasized; whereas in humid regions or under protected cultivation, texture stability, flavor harmony, and disease resistance may be of greater evaluative value. This means that although the comprehensive evaluation system requires a unified basic framework, its indicator weights and application priorities should be recalibrated according to regional realities.

Studies have shown that comprehensive evaluation systems constructed using variance analysis, correlation analysis, PCA, cluster analysis, and AHP can recalculate principal components and weights by incorporating local cultivar resources, regional environmental data, and consumer preferences, thereby achieving regionalized evaluation (Mihaylova et al., 2021). On the one hand, such regional adjustments improve the suitability of the evaluation system to local production realities; on the other hand, they also provide a scientific basis for regional branding and the positioning of specialty cultivars. In addition, the recent development of non-destructive detection technologies has provided a new technical basis for integrating regionalized and standardized evaluation systems. Studies have shown that methods such as Vis/NIRS and hyperspectral imaging, after localized calibration under region-specific rootstocks, crop load levels, canopy positions, and light environments, can stably acquire



key indicators such as DMC, SSC, and maturity, and are expected to be embedded into standardized grading systems, thereby realizing an evaluation mode of “unified methods but adjustable models” across different regions (Minas et al., 2023).

## 7 Existing Problems and Development Trends

### 7.1 Current limitations

Although significant progress has been made in peach fruit quality research across multiple disciplines, the lack of unified evaluation systems remains a major bottleneck limiting result comparability and practical application. Differences in indicator selection, sampling stages, maturity criteria, and measurement methods are common among studies. Even when the same indicators (e.g., SSC, acidity, firmness) are used, inconsistencies in scales and standards reduce comparability and reproducibility. At the same time, research-oriented evaluation systems tend to be complex, whereas industry practices still rely mainly on appearance or a few simple indicators. This disconnect between research and industry affects quality stability and consumer experience (Mosie et al., 2025). In terms of mechanism studies, current research still focuses largely on phenotypic and physicochemical traits, with limited understanding of the molecular regulation underlying flavor harmony, aroma formation, and texture changes. Although GWAS and QTL studies have identified numerous loci associated with quality traits, many causal genes and regulatory pathways remain unresolved (Fan et al., 2025; Hayat et al., 2025). In addition, studies on multi-factor interactions are still insufficient. In practice, fruit quality is jointly influenced by genotype × environment × management, yet most existing research focuses on single-factor analysis, limiting systematic understanding of quality formation mechanisms and stability.

### 7.2 Application of emerging technologies

The development of multi-omics technologies has greatly enhanced the ability to elucidate the mechanisms underlying peach fruit quality. At the genomic level, high-density SNP arrays, resequencing, and GWAS approaches have enabled the identification of key genomic regions associated with quality traits, providing a foundation for molecular breeding. Meanwhile, integrated metabolomic and transcriptomic analyses have revealed key pathways involved in the formation of sugars, acids, and aroma compounds, and have identified molecular markers related to flavor and antioxidant capacity (Feng et al., 2024). Research on aroma improvement is increasingly integrating metabolite profiles, gene regulatory networks, and consumer preferences, providing theoretical support for flavor-oriented breeding (Cao et al., 2024). On the phenotyping side, intelligent detection technologies are developing rapidly. Techniques such as Vis/NIR spectroscopy, hyperspectral imaging, electrical property sensing, and electronic noses have been applied for rapid assessment of fruit quality and maturity (Qi et al., 2024), while deep-learning-based machine vision enables simultaneous prediction of multiple traits and shows strong potential for automated sorting (Masuda et al., 2023). Compared with traditional methods, these technologies offer advantages in high throughput and objectivity, making them more suitable for modern fruit production systems. Moreover, a convergence trend is emerging between multi-omics and intelligent detection technologies: the former provides molecular-level explanations, while the latter enables rapid field-level assessment. Their integration is expected to establish predictive systems linking “molecular mechanisms-field phenotypes-market quality,” thereby promoting a more systematic and dynamic approach to quality research (Fan et al., 2025; Hayat et al., 2025).

### 7.3 Climate change and precision cultivation strategies

Climate change has profound impacts on peach fruit quality. Rising temperatures, altered precipitation patterns, and more frequent extreme weather events influence phenology, metabolism, and pigment formation, thereby affecting fruit flavor and quality. For example, high temperatures may inhibit anthocyanin accumulation and accelerate ripening, while abnormal rainfall can dilute SSC and increase disease risk. These effects vary by region and cultivar, making it difficult for traditional cultivation systems to maintain stable quality (Deori et al., 2024). Therefore, precision cultivation has become an important strategy to address climate change. By regulating canopy structure, crop load, rootstock-scion combinations, and planting density, it is possible to optimize light utilization and carbon allocation, thereby improving quality stability. Studies indicate that favorable environmental conditions support optimal metabolic regulation and high-quality fruit formation, whereas adverse

conditions often lead to reduced flavor quality, suggesting that quality management should be shifted upstream to orchard-level control (Bacelar et al., 2024). Future development should integrate environmental monitoring, non-destructive detection, and decision-support models to enable real-time regulation of fruit quality and risk (Masuda et al., 2023; Qi et al., 2024). At the breeding level, combining multi-omics approaches with genomic selection will facilitate the development of new cultivars that possess both stress resistance and high quality (Fan et al., 2025; Hayat et al., 2025).

## 8 Concluding Remarks

Cultivation conditions are key determinants of peach fruit quality, mainly acting through their effects on canopy microclimate, tree carbon allocation, and fruit development. Preharvest factors such as cultivar-rootstock combinations, crop load, training systems, irrigation regimes, nitrogen supply, and temperature during fruit development can individually or interactively regulate key quality traits, including dry matter content, soluble solids concentration (SSC), acidity, firmness, color, and nutritional-functional components. The light environment within the canopy, regulated by tree architecture and pruning, significantly influences fruit size, coloration, and sugar-acid balance. Open canopies and upper canopy positions typically exhibit higher light interception, resulting in increased SSC, dry matter content, and improved color. In addition, moderate deficit irrigation and optimized fertilization can enhance SSC, firmness, polyphenol, and mineral content, whereas excessive vegetative growth or high temperatures often reduce fruit sweetness and size, despite accelerating ripening. These findings indicate that fruit quality is not a fixed varietal attribute but a highly plastic phenotype jointly shaped by environmental conditions and cultivation practices. Achieving stable, high-quality production therefore requires regionally adapted and integrated cultivation strategies.

Under varying cultivation conditions, the complexity and plasticity of peach fruit quality traits make multidimensional evaluation systems indispensable. Reliance on single external indicators, such as peel color or fruit size, is insufficient to ensure consumer satisfaction and has contributed to declining peach consumption in some markets. Modern research suggests that robust evaluation systems should integrate physical, chemical, functional, and sensory dimensions, including dry matter, SSC, titratable acidity, sugar-acid ratio, firmness, color metrics, bioactive compounds, and, where appropriate, microbial stability and storage characteristics. Multi-index evaluation frameworks, combined with multivariate statistical analysis, sensory evaluation, and advanced non-destructive technologies such as Vis/NIR and hyperspectral imaging, enable consistent characterization of fruit quality across different cultivation systems, climatic conditions, and postharvest treatments. At both breeding and production levels, such integrated systems facilitate the identification of superior genotype-management combinations, support marker-assisted and genomic selection, and provide a unified technical standard for producers, processors, and regulators. Establishing standardized, multidimensional quality evaluation systems is therefore essential for enhancing industry credibility and meeting consumer expectations.

Future progress in regulating peach fruit quality under diverse cultivation conditions will depend on deeper mechanistic understanding and the integration of emerging technologies. Multi-omics approaches—including genomics, transcriptomics, metabolomics, volatilomics, and phenomics—are increasingly revealing how sugars, acids, pigments, and secondary metabolites respond to crop load, light, water status, temperature, and postharvest stresses. Integrating these molecular insights with high-throughput, non-destructive phenotyping platforms (such as NIRS, Vis/NIR, imaging technologies, and electronic noses), along with environmental and management data, will enable predictive models of quality formation, more precise genomic selection, and improved decision support for harvest and storage. At the same time, climate change and the demand for sustainable production require that quality-focused research be embedded within adaptive training systems, deficit irrigation strategies, nutrient management, and disease control frameworks, ensuring both yield and eating quality under complex conditions. The development of integrated databases combining multi-environment trials, multi-omics data, sensor information, and sensory evaluation, along with intelligent decision-support tools for breeders and growers, will be crucial for advancing high-quality, consumer-oriented peach production systems.

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## Conflict of Interest Disclosure

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

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## Case Study

## Open Access

## Variation in Flower Color and Morphological Traits of *Phalaenopsis* and Its Application in Commercial Horticulture

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**Abstract** *Phalaenopsis* is an important ornamental crop, and its flower color and morphological traits are key determinants of ornamental value and commercial application. This study systematically analyzes the variation characteristics of flower color (including solid, bicolor, and patterned types) and morphological traits (flower form, inflorescence, and plant architecture) in *Phalaenopsis*, and further elucidates their underlying mechanisms from genetic, environmental, and cultivation management perspectives. The results indicate that variation in flower color is primarily regulated by anthocyanin metabolism and its associated regulatory genes, whereas morphological traits are governed by complex polygenic interactions. Environmental factors such as light, temperature, and nutrient conditions significantly influence trait expression by modulating physiological processes and gene expression. Based on representative cultivar case studies, the study further demonstrates how trait combinations affect ornamental value and market positioning, and discusses their practical applications in cultivar selection and production management. In response to current challenges such as cultivar homogenization and insufficient trait stability, strategies emphasizing germplasm innovation and precise regulation are proposed. This study provides a theoretical basis for trait optimization and the advancement of commercial horticulture applications in *Phalaenopsis*.

**Keywords** *Phalaenopsis*; Flower color variation; Morphological traits; Commercial horticulture; Market positioning

### 1 Introduction

*Phalaenopsis* is one of the most important ornamental plants in the Orchidaceae and occupies a central position in the global floriculture industry, having long dominated the international orchid market (Badriah et al., 2024). Owing to its elegant floral form, extended blooming period, diverse coloration, and strong adaptability, it is widely used in both potted plant and cut-flower production systems, contributing substantial economic value to the floriculture industries of Asia, Europe, and North America (Bidarnamani et al., 2024). With the advancement of protected horticulture technologies and the refinement of tissue culture propagation systems, *Phalaenopsis* has achieved large-scale commercial production and has become a key commodity in greenhouse flower trade (Sevilleno et al., 2023). In China, the industry has developed rapidly in recent years, gradually expanding from festival-oriented consumption to applications in home gardening and landscape decoration.

The commercial value of *Phalaenopsis* is primarily determined by the combined effects of flower color and morphological traits, among which color, pattern, and floral form directly influence visual appeal and market positioning (Gawenda et al., 2012). Flower coloration exhibits a continuous spectrum ranging from white and cream to yellow, pink, and deep purple, often accompanied by complex patterns such as stripes, spots, and multicolored combinations, greatly enhancing product diversity (Badriah et al., 2024). Meanwhile, morphological traits, including flower diameter, floral shape, labellum structure, inflorescence arrangement, and plant architecture, not only determine ornamental quality but also directly affect product grading and application scenarios. For example, large-flowered cultivars with well-organized inflorescences are more suitable for high-end markets, whereas compact and multi-branching types are better adapted to home gardening. In addition, traits such as spike number, inflorescence orientation, and stem strength are closely associated with transport performance and display quality (Pramanik et al., 2022).

At the genetic level, flower color and morphological traits in *Phalaenopsis* are governed by complex molecular regulatory networks. Flower coloration is mainly controlled by the anthocyanin biosynthesis pathway and its regulatory genes, such as MYB and bHLH transcription factors, while floral organ development and inflorescence architecture involve coordinated action of multiple genes (Lou et al., 2023; Wen et al., 2025). In recent years, advances in genome-wide association studies (GWAS) and transcriptomic analyses have progressively elucidated the genetic basis of these traits, providing important support for molecular breeding (Hsu et al., 2022; Iiyama et al., 2024; Mursyidin and Hidayat, 2025). However, existing studies have largely focused on individual traits or molecular mechanisms, and systematic understanding of the interactions between flower color and morphological traits, as well as their integrated phenotypic effects, remains limited.

This study aims to systematically analyze phenotypic variation in *Phalaenopsis* from the perspective of multi-trait integration and coordinated expression. Focusing on variation in flower color and morphological traits, this work explores how different trait combinations influence commercial value and market segmentation, with the objective of revealing the relationships among key traits and their functional roles in cultivar selection and commercialization strategies. In practical production systems, trait expression is jointly influenced by genetic background, environmental conditions, and cultivation practices. Environmental factors such as light, temperature, and nutrient availability can significantly regulate pigment accumulation and floral development, leading to substantial phenotypic variation within the same genotype. Moreover, with increasing diversification of consumer preferences, demand for bicolored flowers, novel plant architectures, and integrated trait performance continues to rise, rendering traditional single-trait evaluation and breeding approaches insufficient for modern ornamental horticulture.

## 2 Types of Flower Color and Morphological Traits in *Phalaenopsis*

### 2.1 Flower color types and their characteristics

Flower color is one of the most visually striking and attractive ornamental traits in *Phalaenopsis* and serves as a key phenotypic basis for product differentiation and consumer preference. In general, *Phalaenopsis* exhibits a wide spectrum of flower colors, including white, pink, purple, yellow, and intermediate hues, which can further develop into complex patterns such as bicolored, gradient, spotted, veined, and harlequin types (Figure 1). Based on color composition and spatial distribution, flower color can be broadly classified into three categories: monochromatic, bicolored, and patterned types. Monochromatic flowers exhibit relatively uniform coloration across petals and sepals, such as pure white, pink, purple, or yellow. This type of coloration is simple, stable, and visually consistent, making it highly suitable for standardized commercial production and widely used in high-end gifts, wedding decoration, and large-scale potted plant production. Phenotypic surveys indicate that most commercial hybrids still exhibit relatively uniform color distribution, reflecting high product consistency (Indraloka and Rahayu, 2022). Genetic studies further suggest that flower color traits can be partially independent from quantitative traits such as flower size, and are controlled by relatively distinct genetic mechanisms; genome-wide association studies have identified multiple QTLs associated with anthocyanin biosynthesis, providing a genetic basis for the stable breeding of monochromatic cultivars (Hsu et al., 2022).

Bicolored flower types refer to flowers that display two or more colors within a single bloom, such as edge coloration, central shading, and gradient transitions. Compared with monochromatic types, bicolored flowers exhibit stronger visual layering and impact, better meeting the growing market demand for novelty and personalization, and are therefore increasingly represented in modern commercial cultivars. Their formation is primarily associated with differential accumulation of pigments across petals, sepals, and the labellum, with the labellum often displaying a dominant contrasting color and serving as the visual focal point (Indraloka and Rahayu, 2022). At the molecular level, the expression intensity and spatial distribution of structural and regulatory genes in the anthocyanin pathway directly determine the formation of bicolored and gradient patterns. Overexpression of PhCHS5 and PhF3'5'H can significantly intensify flower coloration, particularly in the labellum, indicating that variation in pigment biosynthesis pathway activity is a key molecular basis for bicolored traits.



Figure 1 Different gene expressions result in diverse flower colors in *Phalaenopsis* orchids

Patterned flower types represent the highest level of complexity in the *Phalaenopsis* color system and include stripes, spots, veins, blotches, and harlequin patterns. These highly distinctive color forms are often used in specialty cultivar development and high-end markets. Studies have shown that different red pigmentation patterns are regulated by distinct R2R3-MYB transcription factors: PeMYB2, PeMYB11, and PeMYB12 are associated with background coloration, spot formation, and venation patterns, respectively. In harlequin types, the random distribution of spots and blotches is associated with regulatory disruption involving PeMYB11, insertion of the retrotransposon HORT1, and interactions with miR858 and MYB repressors, leading to diverse pigmentation patterns (Lu et al., 2024a). Therefore, patterned coloration fundamentally arises from uneven pigment deposition under specific spatial and temporal gene expression, rather than simple color combination.

## 2.2 Flower form and structural variation

In addition to flower color, floral form and structural characteristics are critical criteria for evaluating ornamental value and cultivar classification in *Phalaenopsis*. The flowers exhibit a typical zygomorphic structure, consisting of three sepals, two lateral petals, and a highly specialized labellum, with a central column. This structure forms the basis of the characteristic “butterfly-like” appearance and defines the primary directions of floral variation. At the level of petals and sepals, significant variation exists among cultivars in terms of length, width, thickness, and curvature, resulting in diverse forms such as flat, cup-shaped, and elongated morphologies (Figure 2) (Indraloka and Rahayu, 2022; Hartati and Samanhudi, 2024). Standard cultivars typically exhibit well-spread petals and strong symmetry, whereas improved cultivars may incorporate wavy margins or increased curvature to enhance visual novelty. Quantitative analyses indicate that sepal and petal dimensions vary significantly among cultivars and serve as important indicators for classification and diversity evaluation.



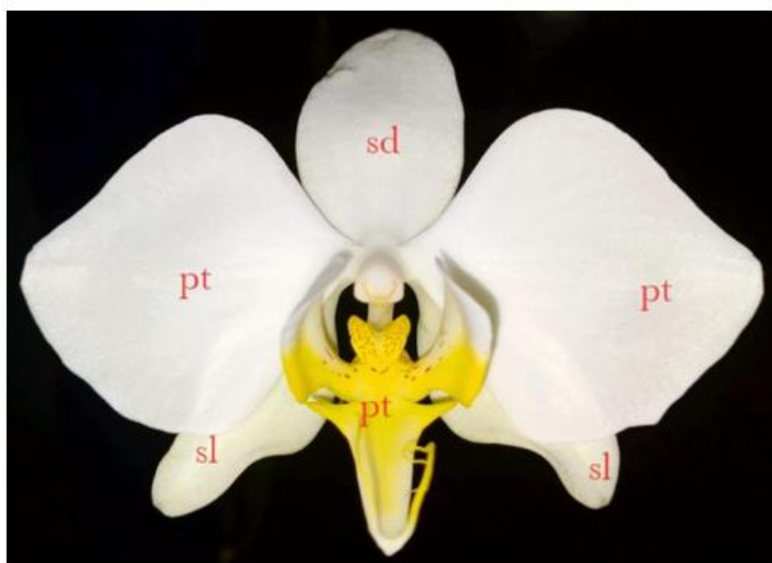


Figure 2 Floral morphology of *Phalaenopsis* sp (Adopted from Indraloka and Rahayu, 2022)

Image caption: sd=sepal dorsal, pt=petal, sl=sepal lateral (Adopted from Indraloka and Rahayu, 2022)

Petal texture represents an important microstructural feature influencing ornamental perception. *Phalaenopsis* petals can generally be categorized into waxy and velvety types: waxy petals have tightly arranged epidermal cells and a thicker cuticle, resulting in a glossy appearance, whereas velvety petals possess conical cells and a thinner cuticle, producing a softer visual effect. This indicates that floral aesthetics are not solely determined by macroscopic shape but are also influenced by microscopic structure, affecting both visual and tactile perception. The labellum is the most variable and diagnostic floral structure, exhibiting substantial variation in size, lobe differentiation, curvature, and color contrast. In some cultivars, a well-developed and vividly colored labellum forms a strong visual focal point, whereas in others, it contributes to overall harmony. Molecular studies have shown that *MADS-box* genes such as *SEPALLATA-like* and *AGL6-like* play key roles in labellum formation, and alterations in their expression can result in petal-to-labellum transformations, producing novel floral forms. Thus, the labellum serves not only as a descriptive trait but also as a key structure for understanding genetic regulation of floral morphology (Indraloka and Rahayu, 2022).

Flower size (flower diameter) is another critical factor influencing market positioning. Large-flowered cultivars are typically used for high-end displays, medium-sized cultivars offer balanced adaptability, and small-flowered types are more suitable for home gardening. Studies have shown that flower diameter is associated with coordinated variation in petal size and labellum proportion, resulting from both cell division and expansion processes, which are regulated by plant hormones such as auxins, cytokinins, and gibberellins (Guan et al., 2025). Therefore, variation in floral form reflects an integrated outcome of developmental regulation and market-oriented selection.

### 2.3 Inflorescence and whole-plant architecture

Inflorescence structure and overall plant architecture are key traits linking individual flower aesthetics to whole-plant commercial performance. *Phalaenopsis* typically produces racemose inflorescences, but significant variation exists among cultivars in peduncle length, inflorescence orientation, and flower arrangement (Pramanik et al., 2022). Inflorescences may be erect, arching, or pendulous, largely depending on the degree of lignification of the floral axis. Highly lignified inflorescences provide better mechanical support and are suitable for standardized potted plant production, whereas more flexible inflorescences create a dynamic and artistic visual effect, suitable for decorative applications.

Branching ability and spike number directly determine flower quantity and spatial complexity. Highly branched cultivars produce more flowers and achieve a fuller visual effect, while single-spike large-flowered types emphasize individual flower quality. These differences reflect distinct resource allocation strategies, often

described as “single-spike large-flower” versus “multi-spike multifloral” commercial types. Inflorescence length and flower number per spike show considerable variation and are key quantitative indicators for distinguishing market types. In addition, flower arrangement patterns, including density and curvature, significantly influence the overall visual presentation.

Whole-plant architecture results from the integration of inflorescence traits and vegetative growth, reflecting plant height, leaf number, and spike distribution. Compact plant types are well suited for home gardening, whereas taller or spreading forms are preferred for landscape and public space applications. Studies have shown that vegetative traits such as biomass and leaf number can predict subsequent flowering performance, indicating that plant architecture reflects cumulative growth status. Notably, structural and metabolic traits may be co-regulated; for example, genes involved in anthocyanin metabolism can also influence branching and floral organ development (Lou et al., 2023). Furthermore, cultivation practices such as paclobutrazol application can modify plant architecture by reducing spike length and improving compactness (Lu et al., 2024b). Therefore, inflorescence and plant architecture are not only outcomes of genetic selection but also important targets for cultivation management.

### 3 Mechanisms Underlying Trait Variation in *Phalaenopsis*

#### 3.1 Genetic factors

The variation in flower color and morphological traits in *Phalaenopsis* is fundamentally rooted in its genetic background. Significant genetic differentiation exists among species, wild germplasm, and hybrid cultivars in pigment metabolism, floral organ development, and inflorescence formation, collectively determining the diversity of flower color types, floral structures, and plant architecture. Studies based on hybrid populations derived from *Phalaenopsis aphrodite* and *P. equestris* have revealed extensive segregation in traits such as flower color and size. Genome-wide association analyses have identified multiple quantitative trait loci (QTLs) and 35 candidate genes associated with these traits, many of which are involved in anthocyanin biosynthesis (Hsu et al., 2022). These findings indicate that ornamental traits in *Phalaenopsis* are complex quantitative traits controlled by multiple genes and their interactions.

At the molecular level, pigment metabolic networks constitute the core genetic mechanism underlying flower color formation. The accumulation intensity and spatial distribution of anthocyanins, flavonoids, and carotenoids form the basis of monochromatic, bicolored, and patterned phenotypes. Comparative studies of purple and white *P. amabilis* have shown that purple petals accumulate high levels of anthocyanins (mainly cyanidin derivatives), accompanied by upregulation of key structural genes, whereas white petals exhibit restricted metabolic flux and altered flavonoid composition, resulting in pigment deficiency. In *P. pulcherrima*, the transcription factors PpMYB1 and PpbHLH1 form a regulatory complex that activates key genes such as F3H, DFR, and ANS, thereby significantly promoting anthocyanin accumulation (Wen et al., 2025). These results demonstrate that differences in expression intensity and spatial regulation within pigment biosynthesis pathways are the direct genetic basis of flower color diversity.

The formation of complex color patterns is also governed by specific regulatory networks. Members of the R2R3-MYB transcription factor family play differentiated roles in various pigmentation patterns, with distinct genes regulating background coloration, spot formation, and venation. Their differential expression ratios determine the regional distribution of pigments across floral organs. In addition, structural genes such as CHS and F3'5'H not only affect color intensity but also influence branching and floral organ number (Lou et al., 2023), suggesting coordinated regulation between metabolic pathways and morphological development. Therefore, flower color, floral form, and plant architecture are not independent traits but may be interconnected through shared regulatory networks. In breeding practice, hybridization remains the primary approach for expanding trait diversity; however, due to polygenic control and complex genetic backgrounds, progeny often exhibit significant phenotypic segregation and low stability of desirable trait combinations (Hsu et al., 2022). Furthermore, distant hybridization may produce triploid or aneuploid individuals, which can negatively affect fertility and subsequent utilization (Sevillano et al., 2023).

### 3.2 Environmental factors

Beyond genetic control, environmental factors significantly influence the expression of *Phalaenopsis* traits by regulating physiological metabolism and developmental processes, with light and temperature being the most critical variables. Light conditions directly affect vegetative growth, thereby influencing flowering potential. Higher light intensity promotes biomass accumulation and leaf development, which are positively correlated with subsequent spike number and flower production. Moreover, appropriate light conditions enhance anthocyanin synthesis and improve color saturation, whereas insufficient light leads to paler coloration, and excessive light may cause tissue damage. Therefore, shading systems are commonly used in greenhouse production to optimize light conditions.

Temperature plays a decisive role in flowering regulation. Moderate low-temperature treatment is typically required to break floral bud dormancy and induce inflorescence initiation, whereas higher temperatures tend to maintain vegetative growth and delay flowering. In addition, temperature affects cell division and expansion processes, thereby influencing flower size and the degree of floral opening, ultimately impacting commercial quality. Thus, temperature not only determines the timing of flowering but also shapes floral morphology and inflorescence characteristics.

Environmental regulation of flower color also involves changes in cellular microenvironment and physiological status. For example, in blue-purple *Phalaenopsis*, flower coloration is influenced not only by pigment composition but also by vacuolar pH and the relative proportions of metal ions. Elevated pH and specific ion combinations can shift flower color from purple toward blue-purple hues (Zhao et al., 2024; Narbona et al., 2025). Furthermore, regulatory genes associated with pigmentation, such as MYB and bHLH, respond to environmental signals including light, low temperature, and hormonal cues (Wang et al., 2025b), indicating that environmental factors can modulate pigment accumulation through transcriptional regulation. Overall, environmental factors interact with genetic regulatory networks to produce substantial phenotypic plasticity, offering opportunities for production control while posing challenges for quality consistency.

### 3.3 Cultivation management factors

Cultivation management serves as a critical link between genetic potential and environmental conditions, directly influencing trait expression in *Phalaenopsis*. Nutrient supply is one of the most fundamental factors, as macronutrients such as nitrogen, phosphorus, potassium, and calcium not only affect vegetative growth but also play key roles in floral induction and inflorescence development. Appropriate nitrogen levels support normal growth, whereas excessive nitrogen may delay flowering and insufficient nitrogen may reduce flower number. Calcium supplementation has been shown to significantly increase leaf area, flower number, and dry weight while improving overall plant nutritional status (Alves et al., 2024), highlighting its importance in structural stability and flowering quality.

In controlled production systems, CO<sub>2</sub> concentration and nutrient solution management also significantly influence commercial traits. Elevated CO<sub>2</sub> levels can promote spike elongation, increase branching, and accelerate flowering, although flower number does not respond linearly to nutrient solution electrical conductivity, indicating the need for precise fertilization management. Additionally, practices such as shading, foliar fertilization, and temperature regulation can improve plant vigor and synchronize flowering, thereby enhancing product quality (Mubarok et al., 2024). These findings reflect a transition from conventional management to precision cultivation systems.

Furthermore, cultivation practices can indirectly affect trait formation by modulating gene expression. Regulation of genes such as CHS and F3'5'H not only influences flower color but may also affect branching and floral organ development (Figure 3) (Lou et al., 2023), while transcription factors such as MYB and bHLH respond to environmental and hormonal signals (Wang et al., 2025b). This indicates that cultivation management operates by influencing physiological signaling and gene regulatory networks to optimize phenotypic outcomes. Overall, well-designed management strategies are essential for improving trait stability, ensuring product uniformity, and maximizing economic value, serving as a crucial bridge between genetic potential and commercial production.

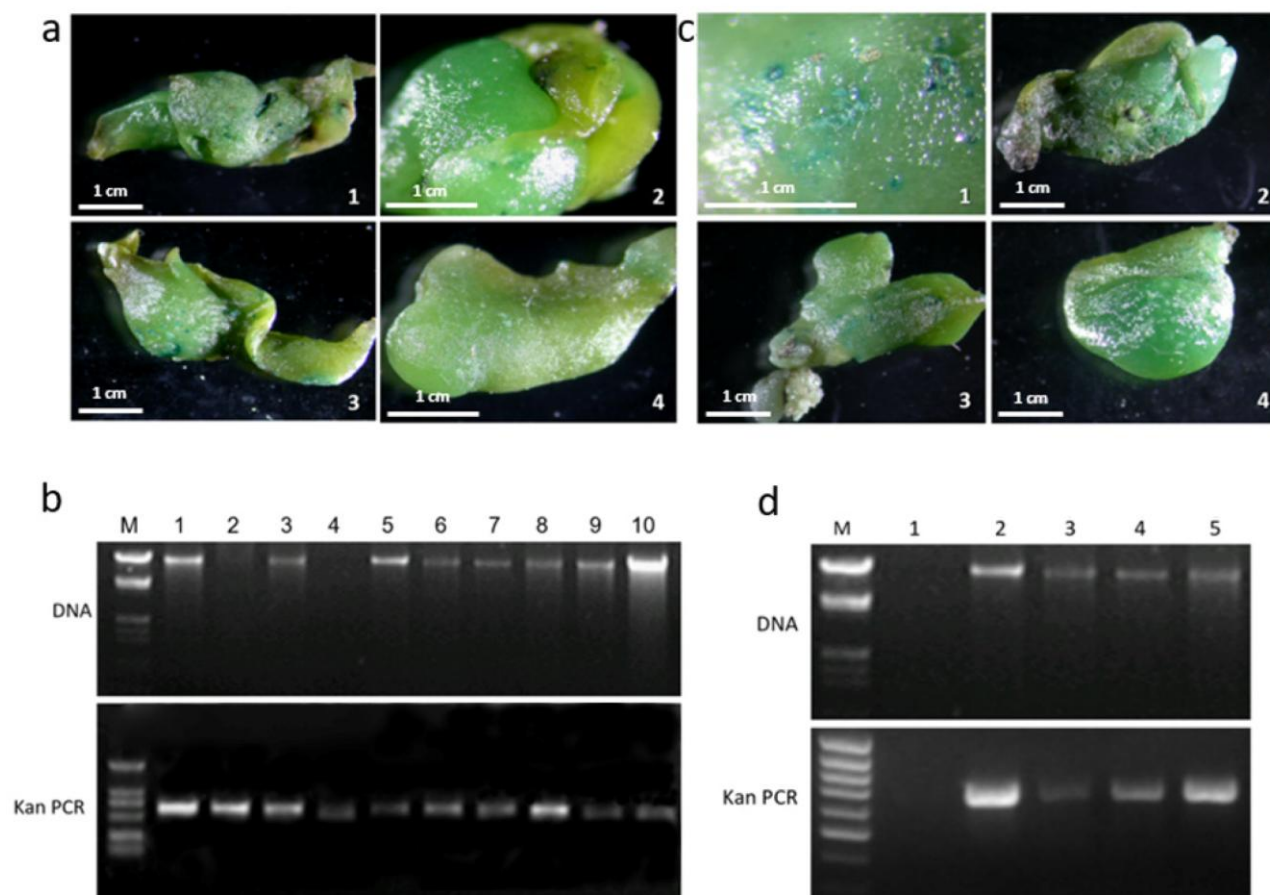


Figure 3 Screening of *Phalaenopsis* protocorms carrying PhCHS5 and PhF3'5'H after transformations (Adopted from Lou et al., 2023)

Image caption: (a) PhCHS5-transgenic *Phalaenopsis* protocorms; The image on the right is a close-focus image of the image on the left (b) Confirmation of the transformation of *Phalaenopsis* protocorms with PhCHS5 by PCR for Kan gene; M stands for marker, 1–10 stands for transformation seedlings; (c) PhF3'5'H-transgenic *Phalaenopsis* protocorms (Adopted from Lou et al., 2023)

## 4 Case Analysis of *Phalaenopsis*

### 4.1 Comparison of flower color and morphological traits among typical cultivars

In commercial *Phalaenopsis* production, significant variation exists among cultivars in flower color, pattern, floral morphology, and plant architecture. These differences collectively form the basis of varietal diversity and serve as key criteria for product grading and market segmentation (Hsu et al., 2022; Iiyama et al., 2024). Comparative analyses of representative commercial cultivars indicate that flower color and morphological traits are typically expressed as relatively stable trait combinations, which together define the ornamental style and commercial attributes of each cultivar. Standard large-flowered white cultivars are generally characterized by broad petals, symmetrical arrangement, and pure coloration, conveying a sense of elegance and formality suitable for high-end gift and wedding markets. *Phalaenopsis* Sogo Yukidian 'V3' is a representative example, featuring large flowers, a pure white perianth, strong structural integrity, and velvety petals, reflecting a classic and refined aesthetic.

In contrast, pink and purple-red cultivars often exhibit higher color saturation and stronger visual impact, making them more suitable for festive retail markets and prominent display settings. Bicolored and patterned cultivars further enhance individuality. For instance, 'Frigdaas Oxford' displays a yellow base color with red-purple patterns, and its thick, waxy petals not only enhance pattern visibility but also improve durability during transport and display (Han et al., 2025). In hybrid populations such as *P. intermedia* (*P. aphrodite* × *P. equestris*), offspring exhibit wide segregation in both flower size and color, ranging from small, vividly colored flowers to medium-sized pure white flowers (Hsu et al., 2022; Iiyama et al., 2024). This demonstrates that the diversity



observed in commercial cultivars fundamentally arises from recombination and directional selection of parental traits.

In terms of morphological traits, cultivars also differ significantly in flower diameter, peduncle length, inflorescence orientation, and flower number per spike. Analysis of 19 quantitative traits across 15 hybrid *Phalaenopsis* genotypes revealed distinct morphological groupings (Hartati and Samanhudi, 2024). Further studies on six species and 17 horticultural hybrids showed that inflorescence orientation varies from erect to semi-erect, arching, and pendant, and is closely associated with the degree of lignification in the inflorescence axis (Pramanik et al., 2022). The Indonesian cultivar Puspita Devi Agrihorti, for example, exhibits relatively large flowers (approximately 8.7-8.9×8.2-8.5 cm), long peduncles (50.6-88.2 cm), and 9-20 flowers per spike, showing clear differences from comparison cultivars such as Ayu Pujiastuty and Indu Pramesi (Figure 4) (Nurmalinda et al., 2023).



Figure 4 Candidate Varieties of *Phalaenopsis* 1 (Puspita Devi Agrihorti) (Adopted from Nurmalinda et al., 2023)

#### 4.2 Influence of trait differences on ornamental value

The ornamental value of *Phalaenopsis* arises from the integrated expression of flower color, morphology, and overall plant structure. Among these, flower color is the primary factor influencing first visual impression. Bright or highly contrasting colors tend to attract immediate attention, whereas soft and uniform color tones provide a more stable and enduring aesthetic appeal (Han et al., 2025). Consumer preference studies indicate that cultivars with harmonious combinations of color and pattern are more likely to be favored. For example, Puspita Devi Agrihorti achieved a first-choice preference rate of 35.9% in surveys, highlighting the importance of integrated color design in determining ornamental value (Nurmalinda et al., 2023).

Differences in floral morphology further enhance the viewing experience. Cultivars with large, symmetrical petals often present a fuller and higher-quality visual impression, while more elongated or loosely arranged floral forms convey a natural and dynamic aesthetic. The labellum (lip) plays a particularly important role in visual focus, with its structure and color contrast contributing to increased depth and complexity (Figure 5). Petal texture also influences perception; velvety petals enhance softness and elegance, whereas waxy petals increase glossiness and durability (Han et al., 2025).

In addition, the combination of flower size and flower number determines the mode of visual presentation. Cultivars with fewer but larger flowers emphasize individual floral refinement, whereas those with numerous smaller flowers create a fuller overall display. At the whole-plant level, the coordination between inflorescence structure and plant architecture is equally critical. Cultivars with erect, self-supporting inflorescences provide better display quality and a more orderly appearance (Pramanik et al., 2022). Therefore, ornamental value is not determined by a single trait, but by the synergistic interaction of color, floral form, and plant structure.



Figure 5 Different flower shapes of the *Phalaenopsis* orchid

#### 4.3 Impact of trait variation on market positioning

Variation in *Phalaenopsis* traits directly determines market positioning and product stratification. Different combinations of flower color, morphology, and plant architecture correspond to specific consumption scenarios and price segments, forming the basis for effective market segmentation (Gabellini and Scaramuzzi, 2022). In high-end gift markets, cultivars with large flowers, pure colors, and well-structured forms are preferred, particularly white or light-colored *Phalaenopsis*, which are widely used in weddings and formal occasions due to their strong cultural symbolism (Han et al., 2025).

In mass consumer and home gardening markets, trait preferences emphasize practicality and cost-effectiveness. Small-flowered, highly branched, and high-flower-number cultivars are more suitable for household display due to their compact form and abundant visual effect. At the same time, cultivars with self-supporting inflorescences and stable flowering performance are better suited for supermarkets and retail chains, where product uniformity and transport durability are critical (Pramanik et al., 2022).

Bicolored, patterned, and novelty cultivars are primarily targeted at differentiated and high-value markets. These products exhibit strong visual identity in both color and structural traits, catering to collectors and consumers seeking unique or personalized products (Badriah et al., 2024). For example, the strong consumer performance of Puspita Devi Agrihorti demonstrates that the combination of rich coloration and high flower number can establish

competitive advantages in regional markets (Nurmalinda et al., 2023). Under current consumption trends, *Phalaenopsis* product development is shifting from single-trait optimization to the integration of trait combinations with market positioning, which has become a key strategy for enhancing industry competitiveness.

## 5 Application in Commercial Horticulture

### 5.1 Cultivar selection and market matching

In commercial horticulture systems, the selection of *Phalaenopsis* cultivars must be precisely aligned with target consumer markets. Different consumer groups exhibit significant variation in aesthetic preferences, usage scenarios, and price sensitivity, thereby imposing distinct requirements on flower color, floral morphology, and plant architecture (Nurmalinda et al., 2023). Consequently, the commercial application of color and morphological traits is not merely an aesthetic decision, but a strategic configuration based on market segmentation and consumer behavior. With the development of data-driven marketing, cultivar selection is gradually shifting from experience-based approaches to more precise matching grounded in consumer preference data and channel-specific demand.

In high-end gift and interior decoration markets, consumers tend to prefer cultivars with pure colors, well-structured flower forms, and clear visual focal points. Such products emphasize ceremonial value and spatial aesthetics, making large-flowered white or light pink *Phalaenopsis* particularly advantageous (Nurmalinda et al., 2023). In contrast, mass-market consumers prioritize cost-effectiveness and spatial adaptability, favoring multifloral, highly branched, and compact cultivars that provide higher visual density within limited space (Gabellini and Scaramuzzi, 2022; Han et al., 2025). These differences highlight the distinct trait combinations required across market segments.

With increasing consumption upgrading and diversification of aesthetic preferences, demand for personalized products continues to grow. Younger consumers and horticultural enthusiasts are more inclined to select cultivars with complex color patterns, such as bicolored, spotted, or harlequin types, which enhance visual distinctiveness and command premium prices in niche markets (Badriah et al., 2024; Chen et al., 2024). As a result, modern cultivar selection has evolved from simple visual evaluation to a multidimensional decision-making process that integrates consumer demand, market positioning, and distribution channel characteristics (Gabellini and Scaramuzzi, 2022; Wei et al., 2022).

### 5.2 Production management and commercialization strategies

Production management is the key process through which the genetic potential of *Phalaenopsis* cultivars is translated into stable commercial value. The inherent advantages of a cultivar can only be fully realized under appropriate production systems that ensure uniformity and marketable quality (Han et al., 2025). Therefore, modern production management focuses on regulating plant development throughout the entire growth cycle—from vegetative growth to flowering—by controlling standards, uniformity, and floral quality.

Different cultivars require differentiated management strategies. Large-flowered cultivars typically demand enhanced nutrient supply and structural support to ensure flower size and integrity, whereas multifloral or highly branched cultivars require careful regulation of branching and flowering synchronization to maintain visual balance. Precise control of light, temperature, and nutrient conditions can significantly influence spike number, flower count, and plant uniformity. Additionally, leaf number and plant biomass can serve as reliable predictors of flowering performance, indicating that production management is not only a cultivation practice but also a tool for targeted optimization of trait expression.

At the commercialization level, efficient tissue culture systems ensure large-scale propagation and genetic uniformity of elite cultivars (Han et al., 2025), while flowering control technologies determine whether products can meet seasonal and festive market demands. Meanwhile, commercialization strategies increasingly depend on channel differentiation, with different distribution channels imposing varying requirements on plant uniformity, transport stability, and visual quality (Gabellini and Scaramuzzi, 2022; Wei et al., 2022). Therefore, production



systems must be closely aligned with marketing and distribution systems to enhance supply chain efficiency and market responsiveness.

### 5.3 Branding and product combination applications

In an increasingly competitive floriculture market, branding strategies and product combination approaches have become essential tools for enhancing the added value of *Phalaenopsis*. Flower color and morphological traits not only determine ornamental quality but also form the basis of brand identity and product differentiation (Gabellini and Scaramuzzi, 2022). As consumer demand shifts from functional to experiential consumption, *Phalaenopsis* products are transitioning from single potted plants to more design-oriented, scenario-based, and product-line-driven offerings.

Different combinations of traits support differentiated brand positioning. For example, white, round, and multifloral cultivars are well suited for “classic elegance” product lines targeting mainstream and premium decoration markets, whereas cultivars with rare colors or distinctive patterns can be positioned as premium or collector’s editions, emphasizing uniqueness and exclusivity (Badriah et al., 2024; Chen et al., 2024). In addition, the cultural symbolism associated with flower colors can be incorporated into brand narratives to enhance emotional value and consumer identification (Nurmalinda et al., 2023).

Product combination strategies further expand the application potential of *Phalaenopsis*. Miniature and multifloral cultivars can be integrated into mixed-planter designs to meet the demands of home decoration and lifestyle-oriented consumption (Gabellini and Scaramuzzi, 2022; Han et al., 2025). Moreover, *Phalaenopsis* can be combined with other ornamental plants or decorative materials to create ready-to-display products that require minimal consumer effort (Fauzia et al., 2023). By integrating trait advantages with branding strategies and product design, producers can significantly enhance product value and broaden application scenarios in the market.

## 6 Existing Problems and Development Trends

### 6.1 Current issues

Despite the rapid development of the *Phalaenopsis* industry, significant constraints remain in cultivar innovation and structural optimization, among which the homogenization of commercial cultivars is particularly prominent. Although the number of cultivars on the market continues to increase, most are derived from a limited set of core parental lines. Repeated complex hybridization within similar genetic backgrounds has led to convergence in flower color, flower form, and inflorescence types, resulting in a lack of truly novel trait combinations (Wang et al., 2025a). This phenomenon of “increased quantity but limited innovation” leads to visually similar products in the market, weak differentiation, and reduced attractiveness and competitiveness of new cultivars. In addition, the inefficient utilization of core germplasm resources, characterized by repeated use of favorable traits without systematic integration, further restricts the depth and breadth of cultivar innovation.

At the same time, insufficient trait stability has become a key factor limiting product quality improvement. Flower color and morphological traits in *Phalaenopsis* are highly sensitive to environmental variation, and fluctuations in light, temperature, and cultivation conditions can easily result in unstable coloration, morphological variation, and uneven flowering. In particular, high-value traits such as rare colors and complex patterns often exhibit unstable genetic expression, with segregation, degradation, or weakening occurring across different environments or propagation generations (Wu et al., 2022; Lou et al., 2023; Chen et al., 2024). Furthermore, genetic linkage effects hinder the independent selection of desirable traits, while ploidy abnormalities and cytogenetic instability arising from distant hybridization further complicate trait fixation and large-scale application (Sevilleno et al., 2023; Wang et al., 2025a).

At the production and industry chain levels, issues related to consistency control and supply-demand matching are also evident. Current cultivation practices largely rely on generalized management systems and lack precise, cultivar-specific optimization, resulting in considerable variation in plant growth and flowering performance. Meanwhile, the absence of unified grading standards across the industry leads to inconsistencies in quality evaluation among producers, thereby affecting market efficiency and brand recognition. In addition, while



production systems emphasize standardization and scale, consumer demand is increasingly oriented toward personalization and differentiation, creating a structural mismatch that constrains value chain coordination and value enhancement (Gabellini and Scaramuzzi, 2022).

## 6.2 Changes in market demand and consumer preferences

With consumption upgrading and accelerating urbanization, the *Phalaenopsis* market is shifting from traditional single potted plant consumption toward more diversified and scenario-based applications. Classic large-flowered white or pastel cultivars still dominate the mainstream market, but consumer interest in novel flower colors, compact combinations, and locally bred cultivars is steadily increasing (Nurmalinda et al., 2023). This trend indicates that the market is transitioning from a primarily standardized model to a dual structure combining standardization and differentiation, thereby placing higher demands on cultivar innovation.

Consumer behavior exhibits clear segmentation. Mass-market consumers tend to prioritize price, flower number, and ease of maintenance, with a strong emphasis on product stability and cost-effectiveness. In contrast, high-end consumers and hobbyists place greater value on rarity, uniqueness of flower color, and morphological novelty, and are willing to pay premium prices for distinctive traits. In gift-giving and emotional consumption contexts, *Phalaenopsis* has evolved from a purely ornamental plant into a product carrying cultural symbolism and emotional value, significantly enhancing its added value. This stratification of consumer demand is driving the market toward more refined and multi-tiered structures.

Meanwhile, application scenarios and sales channels continue to expand. *Phalaenopsis* has extended from traditional festive gifts to broader uses such as home decoration, commercial space design, and cultural-creative products. The rapid development of e-commerce and new retail models has increased the importance of visual presentation and packaging design, while also imposing higher requirements on product uniformity and logistics performance. In addition, green consumption concepts and cultural value recognition are gradually becoming important factors influencing consumer choices, promoting the industry toward sustainability and cultural integration (Gabellini and Scaramuzzi, 2022).

## 6.3 Future development directions

The future development of the *Phalaenopsis* industry will center on breeding innovation, with a focus on expanding the genetic base and alleviating cultivar homogenization. Interspecific and intergeneric hybridization to introduce rare flower colors, complex patterns, and desirable plant architectures represents an important pathway for achieving trait breakthroughs (Wu et al., 2022). Meanwhile, advances in genomics and molecular marker technologies, including QTL mapping and core germplasm resource development, are providing a solid foundation for marker-assisted breeding and precision selection (Hsu et al., 2022; Lai et al., 2024). Future breeding strategies are expected to shift from experience-based approaches toward data-driven and goal-oriented frameworks, thereby improving breeding efficiency and trait controllability.

At the technological level, the integration of conventional breeding with modern biotechnologies will become a major trend. Genome editing technologies such as CRISPR/Cas9 offer new opportunities for precise trait improvement, although they are still constrained by limitations in transformation efficiency and regeneration systems (Lou et al., 2023). At the same time, precision production systems based on environmental control and data analysis will contribute to improving flowering synchronization and quality stability (Cembrowska-Lech et al., 2023; Kaya, 2025). The application of high-throughput phenotyping and data modeling is also expected to provide more scientific decision support for production management.

From an industrial perspective, intelligent production and sustainable development will be key future directions. The application of the Internet of Things (IoT) and automated systems can enable precise environmental control, improve production efficiency, and reduce resource consumption. The integration of genomic, phenotypic, and environmental data will further promote the development of intelligent breeding and precision management systems (Xu et al., 2022; Farooq et al., 2024). In addition, optimizing resource use efficiency, developing circular agriculture models, and expanding cultural-creative and design-oriented horticultural products can enhance

industry value and facilitate the transition of the *Phalaenopsis* sector from traditional production toward a high-value, innovation-driven industry.

## 7 Conclusion

Flower color and morphological traits jointly determine the ornamental value, consumer preference, and market competitiveness of *Phalaenopsis*. On the one hand, the wide spectrum of flower colors—from pure white and soft pastel tones to highly saturated red, purple, and yellow, as well as complex bicolor or spotted patterns—provides diverse visual choices and emotional expressions for consumers, directly influencing first impressions and purchase intention. On the other hand, morphological traits—including flower size and fullness, petal and sepal morphology, labellum structure and pattern, inflorescence length and curvature, branching ability, flower number and arrangement, and overall plant architecture—not only affect aesthetic perception but also determine display performance, transportability, and application scenarios (e.g., potted plants, cut flowers, and long-term indoor decoration). In modern commercial horticulture, these traits are no longer merely static ornamental attributes; instead, they function as integrative indicators linking genetics, environment, and cultivation management, and serve as key tools for branding, product differentiation, and value enhancement. Overall, flower color and morphology constitute the core phenotypic basis for *Phalaenopsis* breeding, production planning, and marketing strategies, and are essential for sustaining industry vitality and innovation capacity.

Variation in flower color and morphological traits provides the foundation for market segmentation and diversified product development in *Phalaenopsis*. Differences in hue, brightness, and pattern enable breeders and enterprises to target specific consumer groups and cultural contexts—for example, white and light-colored cultivars are preferred in minimalist or Nordic-style settings, whereas bright red, purple, or golden cultivars are favored in festive and gift markets. Morphological variation further refines product positioning: large, round flowers with pendulous inflorescences are suitable for high-end display environments (e.g., hotel lobbies); compact plants with multiple spikes and medium-sized flowers are ideal for home and office decoration; while miniature and multifloral cultivars meet the preferences of younger consumers for small, refined, and easily arranged plants. At the production level, trait variation is also closely associated with cost control and supply chain efficiency. Cultivars with stable color expression, uniform morphology, and strong adaptability can reduce production risks and losses, whereas those with extended flowering duration and superior postharvest performance improve inventory turnover and facilitate long-distance distribution. Therefore, effective identification, utilization, and regulation of trait variation not only support the development of distinctive products and brands, but also promote deeper integration of the *Phalaenopsis* industry with diverse consumption scenarios such as home gardening, urban greening, and cultural-creative horticulture.

To fully exploit trait variation and promote the sustainable development of the *Phalaenopsis* industry, future efforts should focus on the coordinated advancement of breeding innovation, standardized production, and market-oriented strategies. In breeding, it is essential to integrate conventional hybridization with molecular-assisted selection and genomic technologies, systematically incorporating elite germplasm with novel colors, patterns, and morphologies while simultaneously improving stress tolerance, flowering stability, and postharvest longevity, thereby achieving the coordinated optimization of ornamental and production traits. In cultivation management, standardized and digitalized systems for regulating light, temperature, nutrition, and plant growth regulators should be established, alongside the adoption of intelligent production technologies (e.g., environmental control, phenotyping, and decision-support systems) to stabilize trait expression, reduce quality variation, and enhance production efficiency. From a market and industry perspective, stronger collaboration among breeders, propagators, producers, distributors, and retailers is required to design product portfolios based on seasons, holidays, and application scenarios, and to develop recognizable product lines and brands centered on clear trait profiles. Meanwhile, incorporating consumer preference research and aesthetic trends into breeding objectives, expanding applications in cultural, educational, and therapeutic contexts, and strengthening international cooperation and intellectual property protection for new cultivars will further enhance the global competitiveness, cultural influence, and long-term resilience of the *Phalaenopsis* industry.

## Conflict of Interest Disclosure

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

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## Review and Progress

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# Sweetness and Acidity Traits in Strawberry (*Fragaria* × *ananassa*): Research Progress and Perspectives

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**Abstract** Strawberry flavor quality is a pivotal factor determining its commercial value and consumer acceptance; among its attributes, sweetness and acidity serve as core sensory indicators that directly influence fruit palatability and market competitiveness. This paper systematically reviews the research progress regarding sweetness and acidity traits in strawberries. Drawing upon both sensory evaluation and physicochemical foundations, it analyzes the compositional characteristics of sugars and organic acids, as well as the dynamic patterns of their accumulation. Furthermore, the paper elucidates the metabolic pathways for carbohydrates and organic acids—including the regulatory mechanisms of key enzymes—and summarizes the genetic basis and molecular regulatory networks underlying these traits. Building upon this foundation, the study explores the impact of environmental factors and cultivation practices on sugar and acid accumulation, as well as the application of both traditional and molecular-assisted breeding techniques in quality improvement. Concurrently, through case studies of exemplary high-quality varieties, the paper reveals practical strategies and demonstrated outcomes for the improvement of sweetness and acidity traits. Finally, integrating the advancements in multi-omics technologies and precision breeding, the paper outlines future directions for research into strawberry flavor quality. This review aims to provide a theoretical basis and technical reference for the selection and breeding of high-quality, high-sweetness, and low-acidity strawberry varieties, as well as for the overall upgrading of the strawberry industry.

**Keywords** Strawberry; Sweetness; Acidity; Sugar-acid metabolism; Molecular breeding

## 1 Introduction

Strawberry (*Fragaria* × *ananassa*) is a globally important horticultural crop valued for its bright color, nutritional benefits, and distinctive flavor profile, making it a key component of fresh fruit markets and processed products worldwide (Barbey et al., 2021). However, decades of breeding focused on yield, firmness, appearance, and disease resistance have often led to a decline in perceived flavor quality, with many modern cultivars regarded as bland compared with wild relatives or older varieties (Porter et al., 2023). Recent sensory and multi-omics studies have highlighted flavor—particularly the balance of sweetness and acidity combined with characteristic aroma—as a central determinant of consumer satisfaction and a renewed priority for breeding programs. Within overall flavor, sweetness and acidity are core taste traits that directly influence both hedonic response and repeat purchase decisions.

Strawberry flavor perception arises from the integration of taste (sugars and organic acids), aroma (volatile organic compounds), and texture, with sweetness and acids providing the fundamental taste framework on which volatiles build complexity (Wang et al., 2025). Large sensory-chemical studies show that consumer liking is most strongly associated with sweetness intensity and strawberry flavor intensity, while sourness contributes less directly to overall preference yet still shapes the perceived balance of taste (Liu et al., 2023; Mezghina and Tikhonova, 2025). Biochemically, nonvolatile sugars such as glucose, fructose, and sucrose and organic acids such as citric and malic define the sweetness-acidity profile, and their ratio is often a better indicator of perceived flavor than absolute concentrations alone. In this context, dissecting the genetic, metabolic, and environmental determinants of sweetness and acidity has become essential for guiding both breeding and cultivation practices.

Consumer studies consistently indicate that strawberries are purchased and consumed primarily for their pleasant aroma and sweet taste, and that high sweetness and balanced acidity are key drivers of preference across diverse markets (Sturzeanu et al., 2025). Psychophysical and panel work has shown that overall liking is closely tied to

sweetness and strawberry flavor intensity and is undermined when sucrose and total volatile content are reduced by environmental or agronomic factors (Fan et al., 2021a). Quantitative analyses further demonstrate that relatively small increases in soluble solids content (SSC), strongly correlated with total sugars, can markedly increase the probability of a fruit being perceived as “sweet enough”, emphasizing the sensitivity of consumers to sugar levels within the commercial range. At the same time, excessive acidity or unbalanced sugar-acid ratios are associated with “not sweet enough” or overly sour perceptions even when sugar content is adequate, underscoring the importance of coordinated control of both traits.

Beyond sugars and acids, specific volatile compounds can enhance perceived sweetness independently of sugar concentration, effectively modulating the sensory impact of a given sweetness-acidity matrix (Liu et al., 2023). In large consumer panels and descriptive analyses, particular esters, terpenes, lactones, and other volatiles have been shown to correlate positively with sweetness intensity and liking, whereas green, astringent, or overripe notes detract from preference. These findings imply that breeding solely for higher SSC or lower titratable acidity is insufficient; instead, breeding and management must consider how sweetness and acidity interact with volatiles to shape overall flavor perception and market acceptance.

Internationally, research on strawberry flavor has progressed from simple physicochemical characterization toward integrated sensory, metabolomic, and genomic approaches aimed at resolving the complex basis of sweetness and acidity traits. Large-scale studies combining multi-season sensory data with profiles of sugars, acids, and up to more than 100 volatiles have identified chemical drivers of sweetness, sourness, and liking and provided predictive models that outperform those based on SSC and titratable acidity alone (Liu et al., 2023). Parallel advances in genomics, high-density SNP arrays, phased octoploid reference genomes, and transcriptomics have enabled the mapping of quantitative trait loci and identification of candidate genes for volatile synthesis, sugar accumulation, and organic acid metabolism, paving the way for marker-assisted and genomic selection targeting flavor components (Porter et al., 2023).

Recent reviews emphasize that cultivated strawberry, like tomato, is poised to benefit from genome-based breeding and even genome editing to restore and enhance key flavor attributes, including sweetness intensity and balanced acidity, while maintaining agronomic performance (Scott et al., 2021). Integrative metabolome-transcriptome analyses have begun to pinpoint nonvolatile compounds and biosynthetic pathways—such as citrate cycle and flavonoid metabolism—underlying sweetness, acidity, and related mouthfeel traits, providing new targets for manipulating taste quality. Looking forward, the convergence of consumer-driven sensory work, high-throughput chemistry, and multi-omics frameworks is expected to accelerate the development of cultivars with optimized sugar-acid profiles adapted to diverse environments, thereby aligning breeding outcomes more closely with evolving consumer expectations for flavor-rich strawberries (Lewers et al., 2020).

## **2 Material Basis and Metabolic Mechanisms of Strawberry Sweetness Formation**

### **2.1 Major sugar components and their dynamic changes (glucose, fructose, sucrose)**

Strawberry sweetness is mainly determined by three soluble sugars—glucose, fructose, and sucrose—which together account for about 99% of total fruit sugars and increase markedly during development from green to red stages (Xu et al., 2024). In many cultivated genotypes, glucose is often the most abundant carbohydrate and sucrose relatively low, although the exact proportions vary with cultivar and environment. Developmental profiling shows that total sugars and each of the three components are lowest in green fruit and highest in red fruit, paralleling the rise in total soluble solids and perceived sweetness (Topçu et al., 2022).

The dominant sugar can differ among genetic backgrounds. In some germplasm sets, sucrose is the main sugar in high-sugar cultivars, whereas fructose predominates in low-sugar types, indicating that sweetness depends not only on total sugar but also on sugar composition (Xu et al., 2024). In white-fleshed ‘Snow White’, fructose and glucose are at very low levels and often undetectable, while sucrose becomes the principal soluble sugar during ripening and is tightly associated with flavor formation. Similar patterns of strong sucrose accumulation during ripening, sometimes exceeding hexoses, have also been observed in wild species such as *F. nilgerrensis*, underscoring sucrose as a key driver of sweetness in some genetic backgrounds.

## 2.2 Carbohydrate metabolic pathways and regulation by key enzymes

Sucrose transported from leaves enters a metabolic network involving sucrose phosphate synthase (SPS), sucrose synthase (SS), and several forms of invertase (cell wall, vacuolar, and neutral), which together determine the balance between sucrose and hexoses in the receptacle (Wang et al., 2025). In Tochtotome fruit, sucrose rises rapidly in late development, while SPS and SS activities are relatively low, suggesting that sucrose accumulation is driven more by limited breakdown than by enhanced synthesis (Khammayom et al., 2022). Acid invertase activity declines early but increases again at ripening, leading to abundant hexoses and explaining why ripe red fruits frequently contain glucose as the major sugar despite strong late sucrose accumulation (Topçu et al., 2022).

Genome-wide analyses reveal a large invertase (INV) gene family in octoploid strawberry, with polyploidy-driven amplification and many members showing fruit-preferential expression. Among them, cell wall invertase FaCWINV1 is markedly upregulated during development, strongly expressed in ripe fruit, and significantly correlated with total sugar content, indicating a central role in sucrose unloading and sink strength establishment (Wang et al., 2025). Transcriptional studies also show that SPS transcripts increase sharply at late stages, while SS and acid invertase transcripts often decrease or fluctuate, supporting a model in which coordinated regulation of these enzymes and their genes channels carbon toward sugar accumulation as fruit ripen (Osatuke and Pritts, 2021).

## 2.3 The influence of developmental stages and environmental factors on sweetness

Strawberry fruit development from green through white/turning to red stages is accompanied by coordinated changes in sugars, hormones, and other metabolites that shape sweetness. Multi-stage analyses show that sucrose, glucose, and fructose all rise as fruit ripen, but sucrose is most tightly linked to ripening progression and activation of ripening-related genes (Osatuke and Pritts, 2021). In white-fleshed strawberries, total soluble solids, total sugar, and sucrose increase strongly while total acid and anthocyanins decrease, and transcriptomic data highlight enrichment of “starch and sucrose metabolism” and hormone signaling pathways, indicating that sucrose accumulation and plant hormones jointly regulate maturation and flavor development.

Environmental conditions, especially temperature, further modulate sweetness by altering sugar accumulation patterns. In greenhouse-grown strawberries, a larger day-night temperature differential during fruit development is associated with higher soluble sugar content and overall better fruit quality, whereas elevated temperatures late in the season reduce soluble sugars despite similar radiation and humidity, underscoring temperature’s dominant effect on sweetness (del Olmo et al., 2020). Comparative studies across farms likewise find soluble solids and titratable acidity to be positively associated with air temperature differential during ripening, while fertilization, pesticide intensity, and microbial inputs have little consistent influence on sugar levels. These findings emphasize that developmental programming of carbohydrate metabolism interacts strongly with thermal conditions to determine final sweetness.

## 3 Material Basis and Regulatory Mechanisms of Strawberry Acidity Formation

### 3.1 Major organic acid species (citric acid, malic acid, etc.)

Strawberry acidity is primarily determined by the composition and concentration of organic acids in the receptacle tissue. In cultivated *Fragaria × ananassa*, citric acid is generally recognized as the predominant organic acid, with malic acid as the second major component, and both together account for most of titratable acidity that shapes basic sourness perception. Studies on white-fleshed strawberry further confirm that citric and malic acids are much higher than other detected acids such as 2-oxobutyric, methylmalonic, suberic, and ascorbic acids, reinforcing their central role as the main acidity-forming components in different genetic backgrounds (Wang et al., 2025).

Comparative work in wild species highlights that the organic acid spectrum can diverge markedly from cultivated types. In *Fragaria nilgerrensis*, isocitric, succinic, and methylmalonic acids dominate the profile, while many other organic acids remain relatively stable across development, suggesting that different strawberry species rely on distinct TCA-cycle intermediates to support fruit metabolism and flavor formation (Ikegaya, 2023). Despite this diversity, across fleshy fruits more broadly, citrate and malate emerge as the two organic acids that most

consistently accumulate and contribute to respiratory supply, osmotic regulation, and taste quality during development and ripening (Wei et al., 2025).

### 3.2 Organic acid metabolism and regulation by related enzyme systems

Organic acid levels in strawberry fruit reflect a dynamic balance among synthesis, degradation, and compartmentation within the tricarboxylic acid (TCA) cycle and associated pathways. Metabolomic and transcriptomic analyses in cultivated strawberries with contrasting flavor show that structural genes encoding isocitrate dehydrogenase, 2-oxoglutarate dehydrogenase, succinate dehydrogenase, fumarate hydratase, and malate dehydrogenase are strongly associated with citric and malic acid content, and that numerous transcription factors (WRKY, MYB, NAC, bZIP, bHLH, AP2) are tightly co-expressed with these genes (Šimková et al., 2024). In kiwifruit, which shares similar acid profiles, high citric acid accumulation is driven by elevated citrate synthase (CS) activity combined with reduced aconitase and NAD-dependent isocitrate dehydrogenase, whereas malic acid accumulation mainly depends on NAD-malate dehydrogenase and phosphoenolpyruvate carboxylase, illustrating how synthesis and degradation fluxes jointly determine titratable acidity.

Recent functional work in strawberry has begun to resolve upstream regulatory nodes that connect primary carbon metabolism with citric acid pools. Overexpression of cytosolic glyceraldehyde-3-phosphate dehydrogenase (FaGAPC2) or pyruvate kinase (FaPKc2.2) reduces citric acid content and alters ripening progression by suppressing phosphoenolpyruvate carboxykinase (FaPEPCK) expression, decreasing PEPCK and glutamate decarboxylase activities, and promoting glutamine synthase-mediated diversion of carbon and nitrogen, thereby favoring citrate consumption through amino acid metabolism (Xu et al., 2024). In contrast, overexpression of FaPEPCK promotes ripening from full red to dark red while simultaneously decreasing citrate synthase activity and citric acid content, indicating that PEPCK-driven anaplerotic flux and CS-mediated synthesis constitute distinct control points for late-stage citrate decline (Xu et al., 2024). Exogenous modulation of enzyme activities, such as by selenomethionine treatment, also reduces total acids, citric acid, and malic acid by down-regulating CS, NAD-malate dehydrogenase, and NADP-malic enzyme, thereby increasing the sugar-acid ratio and improving perceived flavor (Jia et al., 2023).

### 3.3 Patterns of acidity change during fruit ripening

Strawberry fruit acidity is highly stage-dependent, reflecting reconfiguration of central metabolism as the fruit transitions from growth to ripening and eventual over-ripeness. Metabolic profiling across seven developmental stages in cultivated *F. × ananassa* shows that organic acids are among the major polar metabolites, with TCA-cycle activity shifting markedly during the transition to the red and over-ripe stages, when respiration and carbon partitioning are strongly remodeled (Wei et al., 2024). In the cultivar ‘Albion’, titratable acidity decreases by nearly 15% during ripening, with citric acid showing an overall descending pattern and malic acid fluctuating irregularly, while ascorbic acid increases, indicating that total acidity decline is largely driven by reduced citrate content and partial remodeling of the acid spectrum (Wang et al., 2025).

More detailed time-course studies reveal that citric acid content does not necessarily decrease monotonically but can show a rise-fall pattern in late development. In ‘Benihoppe’, citric acid concentration increases from initial red to full red and then declines toward dark red, suggesting that different regulatory modules dominate at successive ripening stages (Xu et al., 2024). Consistently, non-destructive assessments across multiple cultivars show that as strawberries ripen from green to over-ripe, total organic acid content generally decreases while sugars and the sugar-acid ratio increase, although the magnitude and exact timing of changes vary among genotypes (Yang et al., 2023). In white-fleshed ‘Snow White’, total acid and titratable acidity decline as soluble solids and total sugars rise, with citric and malic acids remaining the predominant acids throughout, illustrating how coordinated reductions in major organic acids underpin the shift from sour to sweeter, milder flavor during maturation.

## 4 Genetic Basis and Molecular Regulation of Sweetness and Acidity Traits

### 4.1 Inheritance patterns and QTL mapping of related traits

Sweetness and acidity in cultivated strawberry are complex quantitative traits controlled by multiple loci with relatively small individual effects, strongly influenced by environment. Early linkage maps based on ‘Redgauntlet’



× ‘Hapil’ established collinearity with the diploid *Fragaria* reference genome and enabled dissection of fruit quality QTL, providing a structural framework for mapping sugar and acid-related traits in the octoploid background (Porter et al., 2023). Subsequent metabolite-focused QTL work detected 133 mQTL for 44 primary metabolites, soluble solids content (SSC), titratable acidity (TA), and pH, with only 12.9% stable across years, underlining strong genotype × environment interactions for sugar-acid balance (Alarfaj et al., 2021).

Specific genomic regions contributing to sweetness and acidity have now been repeatedly identified. Pedigree-based analysis in U.S. breeding populations mapped a moderate-effect SSC QTL on linkage group (LG) 6A and TA QTL on LGs 2A and 5B, together explaining up to 22% of phenotypic variance for acidity-related traits. Independent F<sub>1</sub> and F<sub>2</sub> populations and GWAS have revealed additional SSC QTL on chromosomes 3B and 6A, often with antagonistic effects on yield, and co-localized QTL blocks in homoeology group V controlling sucrose, raffinose, and organic acids, suggesting hotspots for coordinated regulation of sweetness and acidity (Liu et al., 2020).

#### 4.2 Key functional genes and transcriptional regulatory networks

High-resolution QTL and multi-omics analyses are beginning to pinpoint functional genes underlying sugar and acid variation. Genome-wide association combined with eQTL mapping has implicated a starch synthase 4 gene and a sugar transporter 2-like gene within major SSC QTL on chromosomes 3B and 6A, linking allelic variation in carbohydrate metabolism and transport to differences in soluble sugar accumulation and SSC-yield trade-offs (Liu et al., 2020). Similarly, mQTL in homoeology group V co-controlling sucrose, raffinose, and succinic acid co-localize with genes involved in sugar interconversion and transport, such as UDP-glucose 4-epimerase and SWEET-type sugar transporters, indicating pleiotropic regulators of both sweetness and acidity (Alarfaj et al., 2021).

At the transcriptional level, integrated metabolome-transcriptome studies identify broad networks connecting sweetness, acidity, and other non-volatile flavor components. Comparative analyses of three *F. × ananassa* cultivars with contrasting flavor profiles showed that differences in fructose and citric acid contents were associated with differential expression of structural genes in the citrate cycle, phenylpropanoid, and flavonoid pathways, highlighting central metabolic nodes that affect both acid accumulation and downstream flavor traits (Natarajan et al., 2020). In parallel, genome-wide surveys of the MYB transcription factor family identified 407 FaMYB genes, with specific loci predicted to regulate sugars and organic acids; several MYBs showed cultivar- and ripening-dependent expression linked to fruit quality, nominating them as key regulators of sugar-acid metabolism and transport (Figure 1).

#### 4.3 Progress in the application of molecular markers and gene editing technologies

Rapid advances in strawberry genomics are transforming sweetness and acidity improvement from purely phenotypic selection to genomics-assisted strategies. High-density SNP arrays (IStraw90, IStraw35) and ddRAD-based maps have enabled finer QTL resolution for SSC, TA, and SSC/TA, and marker haplotypes in validated regions such as LG 6A for SSC and LG 2A/5B for TA are now available to support marker-assisted selection for improved sugar-acid balance. In some cases, functional markers linked to sugar metabolism genes (e.g., UDP-glucose 4-epimerase) differentiate high- and low-sugar genotypes with >80% accuracy, illustrating the potential of trait-specific markers for routine screening in breeding programs (Wang et al., 2022).

Beyond markers, genome-scale resources and CRISPR technologies are opening prospects for direct manipulation of sweetness and acidity pathways. Phased octoploid reference genomes, dense SNP arrays, and extensive fruit transcriptomes now allow precise localization of genes controlling sweetness intensity and acid metabolism, while early CRISPR applications in *Fragaria* demonstrate the feasibility of targeted editing of fruit quality genes, including those for volatile synthesis and sugar perception. Recent reviews emphasize that integrating marker-assisted and genomic selection for SSC with editing of key metabolic and regulatory genes (e.g., sugar transporters, MYBs) will accelerate the development of cultivars combining high sweetness, balanced acidity, and strong agronomic performance (Liu et al., 2020).

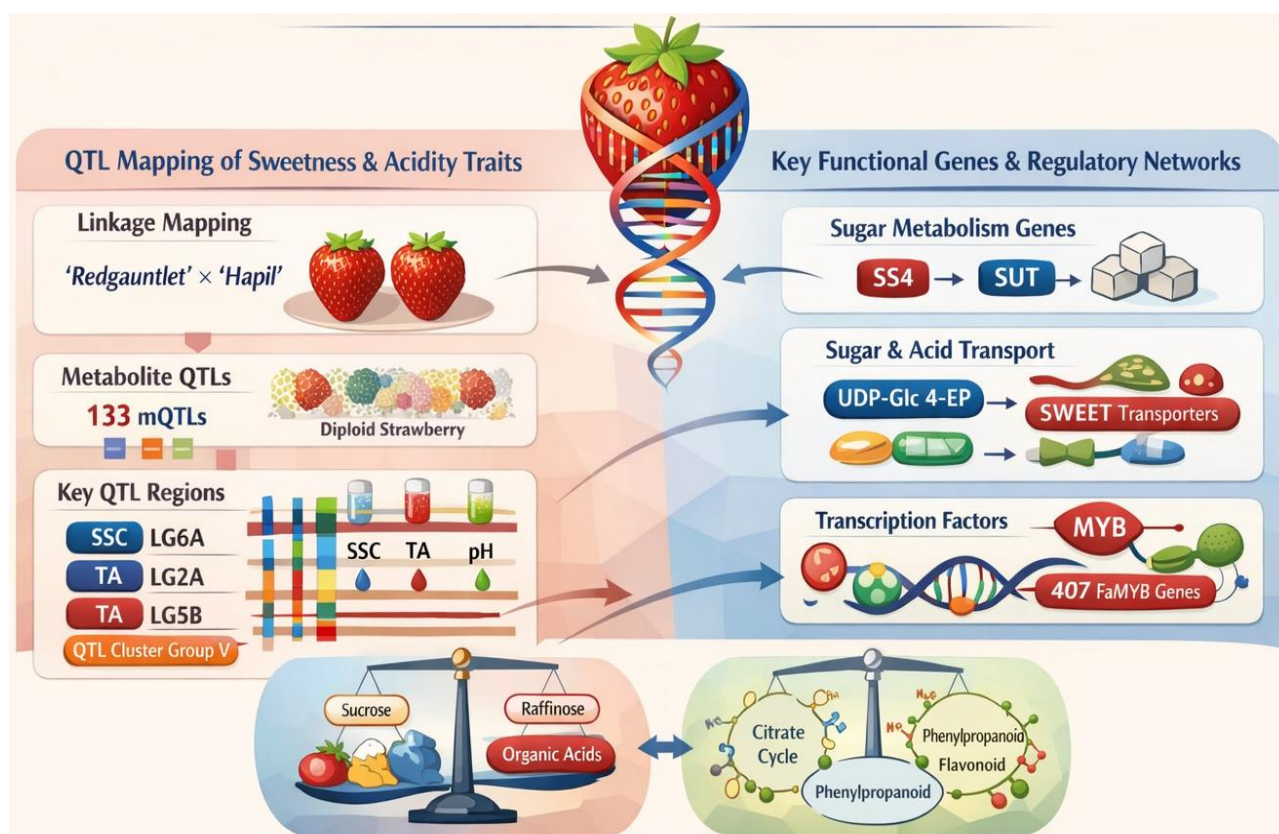


Figure 1 The genetic basis and molecular regulation of sweetness and acidity traits in cultivated strawberry (*Fragaria × ananassa*)

## 5 The Impact of Environmental and Cultivation Measures on Sweetness and Acidity Traits

### 5.1 The regulatory roles of light, temperature, and water conditions

Light quantity and quality strongly influence strawberry sugar and acid accumulation, especially in protected cultivation where natural light is limiting. In autumn-spring greenhouses, combining elevated CO<sub>2</sub> with LED supplemental light increased yield by over 50% compared with ambient conditions, while significantly increasing soluble sugar content and decreasing titratable acidity, thereby enhancing perceived sweetness (Tang et al., 2023). More precise chromatic control of LED spectra showed that supplemental light generally raised soluble solids by about 7% and titratable acidity by 27%, with color temperature and illuminance determining the exact balance between sugars and acids and thus flavor intensity (Patel et al., 2023).

Light treatments can also modulate sweetness-acidity traits after harvest. Continuous red LED exposure during cold storage improved total soluble solids and maintained firmness, while reducing weight loss relative to dark storage, indicating better retention of sweetness and texture (Kilic et al., 2021). By contrast, blue light combined with salicylic acid during refrigerated storage stabilized total soluble solids and titratable acidity at relatively low but constant levels, while markedly improving antioxidant capacity and delaying decay, thus conserving an acceptable sugar-acid balance over an extended storage period (Xu et al., 2023).

Temperature and water status interact to shape field sweetness-acidity profiles. Across multiple farms, soluble solids and titratable acidity were both positively associated with the air temperature differential (day-night difference) during ripening, whereas contrasting fertilization and input regimes showed no consistent effect on SSC or TA, suggesting that mesoclimate is a primary driver of basic taste attributes (Li et al., 2024). In greenhouse experiments manipulating irrigation levels, moderate deficit irrigation reduced yield and titratable acidity but increased soluble sugars, the sugar-acid ratio, and water-use efficiency, indicating that carefully controlled water stress can enhance sweetness perception without severely compromising quality (Jiang et al., 2023).

## 5.2 The impact of cultivation modes (protected vs. open-field) on quality

Comparisons of strawberries grown in high tunnels versus open-field systems indicate that protection modifies microclimate and can alter acidity and phytochemical profiles. In coastal Virginia, ten cultivars grown simultaneously in high tunnels and open field showed no significant environmental effect on total soluble solids, but titratable acidity and anthocyanin content were higher under high tunnels, implying a slightly tarter flavor with more intense color in protected systems (Osatuke and Pritts, 2021). A separate metabolite-focused study likewise found that titratable acidity was highest in high-tunnel ‘Albion’, while soluble solids and pH did not differ significantly between cultivation modes, suggesting that tunnels mainly enhance organic acid and phenolic accumulation rather than basic sweetness (Šimková et al., 2024).

Light-filtering structures such as colored shade nets provide a more targeted approach to modifying flavor-related traits under protection. Under beige and blue photosensitive nets, total soluble sugars increased by about 42% compared with unshaded controls, and beige nets also raised titratable acidity by 24%, resulting in fruit with both higher sweetness and more pronounced sourness (Devi et al., 2024). In contrast, greenhouse LED supplemental lighting with controlled color temperature increased soluble solids and titratable acidity concurrently but reduced fruit firmness and single-fruit weight, highlighting trade-offs between sweetness-acidity enhancement and certain physical quality attributes in protected cultivation (Patel et al., 2023).

## 5.3 The impact of fertilization and post-harvest treatments on sugar and acid accumulation

Nutrient management significantly affects basic taste components, although effects can differ among fertilizer types and rates. Under protected fertigation, supplying 100% of the recommended NPK dose produced the highest total soluble solids, total sugars, and TSS:acidity ratio, while simultaneously minimizing titratable acidity, thus clearly shifting flavor toward greater sweetness and milder sourness (Aragón-Ramírez et al., 2025). In contrast, a comparison of organic, chemical, and combined fertilization showed that organic fertilizer generated fruit with higher soluble solids and glucose but lower firmness and vitamin C, and did not significantly alter citric acid content, suggesting that organic inputs may enhance sweetness primarily via increased sugars without strongly changing major organic acids (Cvelbar Weber et al., 2021).

More detailed work on nitrogen, calcium, and nano-fertilizers indicates that conventional N and Ca fertilization can markedly modify sugars, organic acids, and volatiles, often with negative consequences for overall flavor. Higher N and Ca doses increased certain aldehydes associated with grassy notes, while nano-fertilizer treatment improved phenolic content and fruity esters, illustrating that some innovative inputs can improve flavor-related metabolite profiles even when basic sugars and acids are only moderately affected (Ikegaya, 2023). Postharvest light and signaling treatments further modulate sugar-acid traits: red LED storage increased total soluble solids, whereas combined blue light and salicylic acid maintained low but stable TSS and titratable acidity, helping preserve an acceptable sugar-acid ratio while extending shelf life (Kilic et al., 2021; Xu et al., 2023).

# 6 Breeding Strategies for Improving Strawberry Sweetness and Acidity Quality

## 6.1 Traditional breeding methods and the selection of superior varieties

Conventional strawberry breeding has historically relied on controlled hybridization among elite cultivars followed by multi-year field selection for yield, disease resistance, appearance, and organoleptic quality, including sweetness and acidity balance. Long-term evaluations show that recurrent selection can generate cumulative genetic gain for soluble solids content (SSC) and titratable acidity (TA), confirming that both traits possess exploitable heritable variation and can be shifted upward or downward according to breeding goals (Pedrozo et al., 2023).

Selection of superior varieties increasingly integrates sensory panels and detailed physicochemical measurements. Studies comparing cultivars under commercial-like conditions demonstrate wide variability in SSC, TA, SSC/TA ratio, and volatile composition, with certain cultivars such as ‘Flavorfest’, ‘Albion’, and FL 00-51 consistently achieving higher sweetness, better flavor ratings, and more favorable SSC-TA combinations across harvests and environments (Liu et al., 2023). Multivariate approaches combining yield, SSC, TA, color, and bioactive compounds further support simultaneous selection for production and taste traits, enabling identification of hybrids suited to both fresh consumption and processing markets.

## 6.2 Molecular-assisted breeding and genomic selection

Molecular tools now complement traditional selection by enabling more precise manipulation of sweetness and acidity traits. High-density SNP arrays and pedigree-based QTL analyses have identified loci for SSC on linkage groups/chromosomes 3B and 6A and for TA and pH on 2A, 5B, and 4C, providing markers that can be implemented in marker-assisted selection to shift sugar-acid balance (Porter et al., 2023). Genome-wide association and expression-QTL integration have further pinpointed candidate genes such as starch synthase 4 and sugar transporter 2-like underlying major SSC QTL, facilitating haplotype-based selection for enhanced sugar accumulation (Fan et al., 2021b).

Genomic selection (GS) is emerging as a powerful strategy where sweetness, acidity, and yield are controlled by many loci of small effect. Large multi-parental populations genotyped with SNP arrays and phenotyped for fruit quality and yield show that genomic prediction is effective for complex traits, although a negative correlation between total soluble sugars and marketable yield highlights a key trade-off that GS must manage. Recent reviews emphasize that declining genotyping costs and availability of phased octoploid genomes will make GS for SSC/yield balance feasible in seedling populations, allowing breeders to enrich for sweeter, well-balanced genotypes early in the breeding pipeline.

## 6.3 Synergistic improvement of multiple traits and comprehensive evaluation of flavor quality

Improving sweetness and acidity cannot be separated from broader flavor and agronomic performance. Large sensory-chemical studies reveal that overall liking is driven primarily by sweetness intensity and strawberry flavor, with sourness playing a lesser direct role, and that specific volatiles can enhance perceived sweetness independently of sugar content (Barth et al., 2020). Descriptive analysis and consumer work consistently show that cultivars combining adequate SSC, moderate TA, and rich ester- and terpene-dominated volatile profiles achieve superior flavor ratings, whereas imbalanced acids or atypical volatile patterns can undermine acceptability even in high-sugar fruit (Liu et al., 2023).

Modern flavor-oriented breeding strategies advocate a multi-trait, consumer-driven framework in which sensory data guide the prioritization of chemical targets—sugars, organic acids, and key volatiles—and these, in turn, drive genetic target discovery and marker development (Jouquand et al., 2008). Multi-year, multi-environment evaluations using integrated sensory, metabolite, and genomic data allow breeders to select genotypes with stable sweetness, balanced acidity, desirable aroma, and acceptable yield across harvest dates and production systems (Patel et al., 2023). Such comprehensive evaluation supports the release of cultivars that deliver consistently high flavor quality while meeting grower requirements for productivity and shelf life.

## 7 Case Study: Selection and Evaluation of High-Quality, High-Sweetness, Low-Acidity Strawberry Varieties

### 7.1 Analysis of quality characteristics in typical varieties

High-sweetness, low-acidity cultivars are favored where consumers prefer mild, dessert-type strawberries with intense sweetness and relatively soft sourness. Comparative work across 25 cultivars shows wide inter-cultivar variation in soluble sugars and organic acids, with some genotypes achieving both high sugar content and favorable sugar/acid ratios, reflected in superior total quality index (TQI) scores (Milosavljević et al., 2023). Such cultivars are prime candidates as “high-sweetness” types, because they combine elevated sugars with moderate acidity and beneficial bioactive compounds, aligning with increasing demand for fruits that are both palatable and nutritionally valuable (Ikegaya et al., 2021).

Cultivar-specific evaluations under greenhouse or soilless systems further highlight materials with desirable sensory profiles. In a soilless comparison of four Japanese cultivars, ‘Guimeiren’ exhibited the highest sweetness index, while ‘Tochiotome’ combined relatively high soluble solids and sugar/acid ratios with comparatively low organic acid levels, producing a sweet yet not overly tart taste. Similarly, studies in Greece reported that ‘Sabrina’ had the highest pH and SSC/TA index and was perceived as the sweetest among three commercial cultivars, illustrating how individual varieties can naturally express a high-sweetness, lower-acidity profile under suitable conditions (Ikegaya et al., 2021).



## 7.2 Measurement and comparison of indicators related to sweetness and acidity traits

Quantitative evaluation of high-sweetness, low-acidity types relies on integrated measurement of sugars, acids, and derived indices. Across numerous cultivars, soluble solids (SSC), titratable acidity (TA), and the SSC/TA ratio have been established as core indicators of eating quality, with high SSC and moderate TA yielding balanced “sweet-tart” profiles. In multi-cultivar surveys, SSC and TA ranges are often broad, allowing selection of genotypes that exceed breeding targets (e.g.,  $\geq 8\%$  SSC and  $\approx 0.8\%$  TA) or express higher SSC/TA ratios indicating greater perceived sweetness and milder acidity (Klakotskaya et al., 2023).

Beyond bulk metrics, detailed profiling of individual sugars and acids improves discrimination among candidate cultivars. HPLC-based analysis of 25 cultivars showed that variation in glucose, fructose, sucrose, citric acid, and malic acid strongly differentiates genotypes and underpins differences in TQI, with some cultivars like ‘Sandra’ excelling in both primary metabolites and overall quality score (Milosavljević et al., 2023). Soilless-culture work in Japanese varieties found fructose and glucose as major sugars and citric acid as the dominant organic acid, but identified ‘Tochiotome’ as having higher TSS/TA and total sugars/total organic acids ratios than other cultivars, clearly linking compositional profiles to sweetness-acidity traits.

## 7.3 Evaluation of breeding strategies and practical application outcomes

Recent breeding and selection efforts emphasize integrating multi-trait quality data to identify high-performing, sweet, low-acid materials suitable for diverse environments. Large multi-location trials demonstrate that germplasm (genotype) explains more variation in SSC and TA than location, and that a subset of genotypes concurrently meets modern breeding goals of  $\geq 8\%$  SSC and  $\sim 0.8\%$  TA, making them attractive parents for combining sweetness and acceptable acidity in new cultivars (Klakotskaya et al., 2023) (Figure 2). Cluster analyses of dozens of cultivars using yield, SSC, TA, and SSC/TA effectively group genotypes with similar target traits, helping breeders prioritize those with naturally high sugar/acid balance and good agronomic potential (Xu et al., 2025).

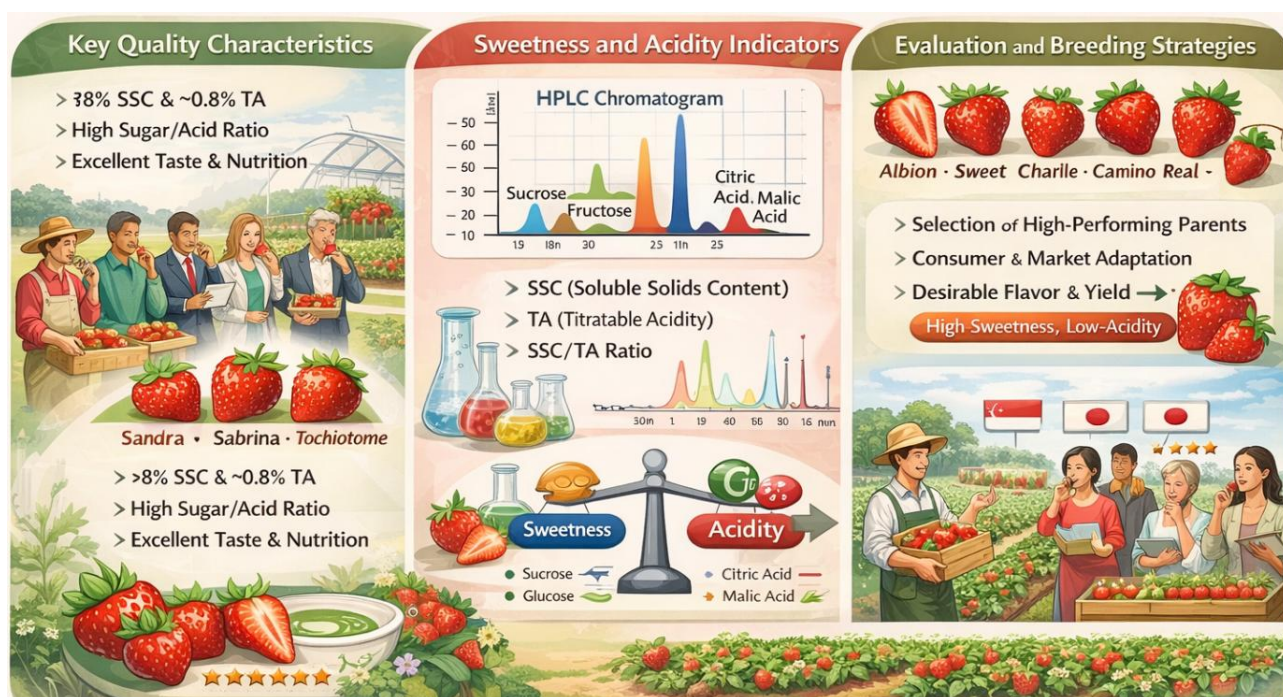


Figure 2 The selection and evaluation of high-quality, high-sweetness, low-acidity strawberry cultivars

On-farm and market-oriented evaluations confirm that such selection strategies translate into tangible improvements in consumer satisfaction and market fit. In a cross-regional quality assessment, strawberries with higher SSC and lower TA were preferred by both Singaporean and Japanese consumers, although Singaporean assessors favored especially low acidity, indicating that high-sweetness, low-acidity cultivars are particularly suitable for certain export markets (Radović et al., 2025). Sensory and chemical studies in Texas similarly

identified cultivars like ‘Albion’, ‘Sweet Charlie’, ‘Camarosa’, ‘Camino Real’, and ‘Chandler’ as ideal for local conditions because they combined high °Brix and favorable TSS/TA ratios with desirable flavor volatiles, underscoring the success of breeding programs that explicitly target balanced sweetness and acidity alongside regional adaptation (Scott et al., 2021).

## 8 Future Directions for Strawberry Sweet-Sour Quality

Multi-omics approaches in cultivated strawberry now combine phased genomes, transcriptomes, metabolomes, and volatile GWAS to dissect flavor genes and regulatory elements. An integrated framework in octoploid strawberry exploited genomic heterozygosity and metabolomic diversity to link allele-specific expression and structural variants with key flavor volatiles, demonstrating how such datasets can systematically uncover flavor genes. Conjoint metabolome-transcriptome analyses across cultivars with contrasting flavor have further highlighted fructose and citric acid as central non-volatile drivers of sweetness and acidity, and revealed that citrate cycle, phenylpropanoid, and flavonoid pathways are major regulatory hubs.

Future research will likely deepen integration of sugar-acid metabolism with broader flavor networks using expanded omics resources. Integrative analyses in contrasting cultivars already identify candidate structural genes and transcription factors associated with soluble sugars, organic acids, and vitamin C, indicating that coordinated regulation of multiple quality components can be mapped at pathway level. At the same time, comparative metabolomics across diverse wild *Fragaria* accessions shows that amino acids, sugars, and anthocyanins co-vary with flavor, suggesting that extending multi-omics to wild relatives will enrich sweet-sour regulatory models and provide novel alleles for breeding.

Precision flavor breeding is moving toward genomics-informed strategies that explicitly target sweetness, acidity, and key volatiles. Large-scale sensory-chemical studies have identified sugars, two main acids, and sets of volatiles that enhance sweetness and liking, while genetic association analyses mapped loci for ester production that can be targeted by marker-assisted selection. A broader review of strawberry flavor breeding emphasizes that phased haplotype genomes, SNP arrays, and extensive fruit transcriptomes now allow localization of genes for volatile synthesis, anthocyanins, and sweetness perception, paving the way for more precise manipulation of flavor traits.

Genomic selection and marker-assisted breeding for quality traits are expected to expand as genotyping costs fall and prediction models mature. Genomic-informed studies in multi-parental populations reveal a negative correlation between total soluble sugars and yield, and identify QTNs for perceived acidity and other traits, supporting combined use. Updates from breeding programs adopting DNA testing show that high-throughput markers for disease resistance and fruit quality are already being used to cull seedlings efficiently, illustrating how precision breeding pipelines can be scaled in practice.

Future progress in sweet-sour improvement will depend on aligning biochemical targets with consumer sensory preferences. Large multi-year consumer and descriptive-panel studies demonstrate that overall liking is driven mainly by sweetness and strawberry flavor intensity, not sourness, and reveal volatile compounds that enhance perceived sweetness independently of sugars, providing concrete chemical targets for breeding and quality control. Bayesian modeling of soluble solids-sweetness relationships further refines selection criteria by quantifying how small SSC changes shift the probability of achieving above-average sweetness in sensory panels.

Industrial application will likely leverage these insights across fresh and processed product chains. Studies relating cultivar traits to consumer preference show that higher sweetness and strawberry flavor predict better acceptance in fresh fruit, while work on strawberry-flavored dairy products indicates that consumers prefer high sweet taste, relatively low acid taste, and strong strawberry aroma, even when delivered by added flavorings.

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

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## Feature Review

## Open Access

**Variation in Secondary Metabolite Traits of *Leonurus japonicus* and Their Functional Implications in Gynecological Applications**

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**Abstract** *Leonurus japonicus*, a widely used medicinal herb in traditional Chinese medicine, plays an important role in the treatment of gynecological disorders. This study systematically reviews the variation in secondary metabolic traits of *L. japonicus* and explores their functional associations with gynecological efficacy. The major classes of secondary metabolites, including alkaloids, flavonoids, and phenolic acids, exhibit significant variability across different germplasms, environments, and developmental stages. These variations are closely regulated by complex biosynthetic pathways and gene expression networks. Pharmacological evidence indicates that these metabolites contribute to key therapeutic effects such as promoting blood circulation, regulating menstruation, and exerting anti-inflammatory and antioxidant activities. Furthermore, metabolomic analyses reveal strong correlations between specific compounds and clinical efficacy, highlighting the importance of metabolic profiling in quality evaluation. A case study comparing samples from different geographical origins further demonstrates that metabolic differences significantly influence therapeutic outcomes. Overall, this work provides a comprehensive framework for understanding the biochemical basis of *L. japonicus* efficacy and supports future applications in precision breeding and standardized utilization.

**Keywords** *Leonurus japonicus*; Secondary metabolites; Metabolic variation; Gynecological efficacy; Metabolomics

**1 Introduction**

*Leonurus japonicus* Houtt., commonly known as Chinese motherwort, has been esteemed for centuries in East Asian traditional medicine, particularly for its pivotal role in gynecological health. Its earliest documentation appears in the ancient Chinese pharmacopeia, Shennong Bencao Jing, where it was described as the “sacred medicine of gynecology” due to its efficacy in treating menstrual irregularities, postpartum hemorrhage, and other reproductive disorders (Shang et al., 2014; Wang et al., 2025). Over the past decades, *L. japonicus* has remained widely used in both traditional and modern clinical practice for conditions such as dysmenorrhea, amenorrhea, and blood stasis. This enduring popularity has driven extensive phytochemical and pharmacological research into its therapeutic mechanisms.

Central to the medicinal efficacy of *L. japonicus* is its rich repertoire of secondary metabolites-organic compounds essential for plant defense and ecological adaptation (Yeshe et al., 2022; Elshafie et al., 2023). These include alkaloids, flavonoids, phenolic acids, terpenoids, and other bioactive compounds, which exhibit diverse biological activities. Studies have shown that these metabolites regulate uterine contraction, exert anti-inflammatory effects, and protect against oxidative stress, thereby supporting their gynecological applications. In addition, environmental factors such as light, temperature, and soil conditions can influence the composition and accumulation of these compounds.

Despite significant progress in identifying over 280 compounds from *L. japonicus*, the biosynthetic pathways underlying their production remain incompletely understood. Recent genomic studies have revealed gene clusters associated with specialized metabolism and highlighted evolutionary mechanisms contributing to metabolite diversity (Li et al., 2023; Wang et al., 2024). Moreover, both genetic variation and environmental conditions can lead to substantial differences in metabolite content, which has important implications for medicinal quality and standardization. Multi-omics approaches are increasingly being used to elucidate the regulatory networks governing metabolite biosynthesis and accumulation.

Given this context, the present review aims to synthesize current knowledge on the variation in secondary metabolite traits of *L. japonicus* and explore their functional implications in gynecological applications. It focuses on the relationship between metabolic diversity and pharmacological efficacy, as well as the underlying genetic and environmental determinants. By integrating ethnobotanical knowledge with modern molecular research, this study seeks to provide a comprehensive framework for the standardized utilization and future development of *L. japonicus*.

## 2 Botanical Characteristics and Resource Distribution of *Leonurus japonicus*

### 2.1 Taxonomic status and morphological characteristics

*Leonurus japonicus* Houtt. is an herbaceous species in the family Lamiaceae, subfamily Lamioideae, and belongs to the small genus *Leonurus*, which comprises roughly 25 species distributed mainly across temperate to tropical Eurasia (Oak et al., 2021). Within the genus, *L. japonicus* is closely related to other medicinal taxa such as *L. cardiaca* and *L. sibiricus*, but differs in both chromosome number ( $2n = 20$ ) and characteristic accumulation of leonurine, features that support its taxonomic separation and pharmacological distinctiveness (Yang et al., 2022). Floral and pollen micromorphology studies show that *L. japonicus* shares the typical Lamiaceae traits of zygomorphic, bilabiate corollas and bi-reticulate pollen exine, reinforcing its placement in Leonureae while also providing diagnostic features to distinguish it from congeners.

Morphologically, *L. japonicus* is an annual or biennial herb reaching up to 1-1.5 m, with square stems, opposite leaves, and verticillaster inflorescences typical of Lamiaceae (Rojas-Sandoval and Acevedo-Rodríguez, 2022). Leaves are palmately lobed and serrate, while the purple to pink bilabiate flowers bear abundant glandular and non-glandular trichomes that contribute to both defense and secretion of aromatic and medicinal compounds. In China, the plant flowers mainly from June to September and fruits from September to October, though in tropical regions it can flower throughout the year, reflecting notable phenological plasticity (Figure 1) (Huang et al., 2020).

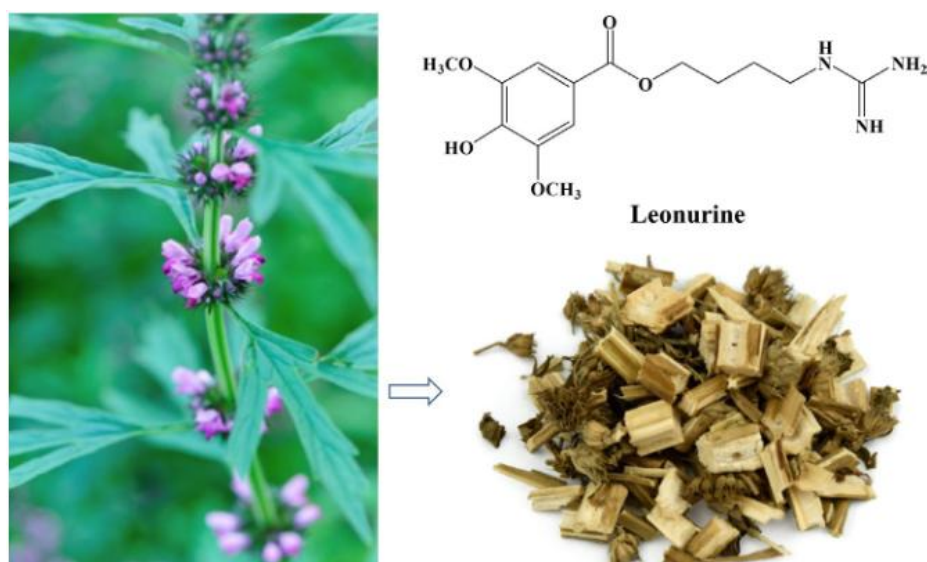


Figure 1 The photograph of *Leonurus japonicus* Houtt. and the structure of leonurine (Adopted from Huang et al., 2020)

### 2.2 Geographic distribution and ecological adaptability

*Leonurus japonicus* is native to East Asia but now shows a nearly cosmopolitan distribution, occurring in temperate and tropical regions of Asia, parts of Europe, and the Americas as an introduced or naturalized species (Hu et al., 2025). Within China, it is widely distributed from lowlands to montane areas, supporting its long history of use and large domestic demand as a medicinal resource. Habitat-suitability modeling indicates that its global and national centers of occurrence are concentrated in Southeast Asia, southern and eastern China, and extended regions such as South America and the Gulf of Mexico, underscoring its strong capacity for range expansion (Chen et al., 2024a).

Ecologically, *L. japonicus* prefers moist environments and is commonly found along field margins, riverbanks, disturbed ground, and grasslands from sea level up to about 3400 m (Rojas-Sandoval and Acevedo-Rodríguez, 2022). The species tolerates semi-shade but grows best in full sun and on a wide range of soils with pH 4-8, highlighting broad edaphic adaptability. Niche-modeling studies further reveal that precipitation in the warmest quarter and temperature in the coldest quarter are key climatic factors shaping its distribution, and future climate scenarios predict a northward and upward shift in suitable ranges, with expansion at higher latitudes (Wang et al., 2023a).

### 2.3 Genetic diversity and germplasm resources

Genetic studies based on complete chloroplast genomes and plastome hotspot regions have shown that *L. japonicus* in China possesses relatively low average nucleotide diversity ( $\pi \approx 0.00029$ ) but is structured into four well-supported clades, reflecting historical divergence influenced by geological events such as the uplift of the Hengduan Mountains and Quaternary climate oscillations. Sliding-window analyses identified variable intergenic spacers (petN-psbM and rpl32-trnL) that serve as cost-effective markers for genotype discrimination and provide useful tools for monitoring population structure in germplasm collections (Wang et al., 2023b). AFLP and ISSR marker analyses across multiple accessions and provenances have also revealed rich polymorphism and clear clustering, confirming that substantial genetic variation persists despite localized bottlenecks (Chen et al., 2009; Wang, 2009).

At a broader phylogenetic scale, ITS-based analyses within *Leonurus* and comparative genomic work with *L. sibiricus* indicate that *L. japonicus* forms distinct genetic lineages, with chromosome-level genome assemblies now available to support fine-scale exploration of biosynthetic and adaptive traits (Yang et al., 2022; Arabova et al., 2025). Recent work combining DNA barcoding (ITS + plastid loci) with HPLC profiling has further shown that genetic groupings among different geographic origins correlate with variation in active ingredient content, although environmental factors also contribute significantly to metabolite differences (Figure 2) (Han et al., 2023; Hu et al., 2025). These findings highlight the importance of conserving diverse wild populations and developing genotype-informed germplasm banks to secure both genetic diversity and the spectrum of secondary metabolite phenotypes relevant to gynecological applications.

## 3 Types and Composition of Secondary Metabolites in *Leonurus japonicus*

*Leonurus japonicus* exhibits a chemically diverse profile with over one hundred secondary metabolites, including alkaloids, flavonoids, phenolic acids, and terpenoids, which collectively contribute to its gynecological effects such as uterotonic, anti-inflammatory, and antioxidant activities. Although pharmacopoeial standards often rely on single markers like leonurine, modern analyses reveal complex multi-component interactions influenced by plant origin and processing (Zhao et al., 2022; Han et al., 2023). Advanced chromatographic and metabolomic studies have further identified over 130 compounds, highlighting key groups such as alkaloids, flavonoids, and terpenoids as central to its therapeutic functions.

### 3.1 Alkaloids

Alkaloids are widely regarded as the primary signature metabolites of *Leonurus*, distinguishing *L. japonicus* from many other Lamiaceae that are dominated by terpenoids alone (Zhang et al., 2018; Li et al., 2023). Leonurine, a guanidine-type pseudoalkaloid, together with betaine-type alkaloids such as stachydrine and trigonelline, represents the major nitrogen-containing constituents quantified in pharmacopoeial materials and in pharmacokinetic studies. Targeted LC-MS/MS analysis across different plant parts has confirmed these three molecules as the principal activity-related substances, with measurable stability and reproducible content suitable for use as quality markers (Zhao et al., 2022). Multi-omics comparison between *L. japonicus* (high-leonurine) and *L. sibiricus* (trace-leonurine) further shows that leonurine accumulation is species-specific and controlled by a specialized biosynthetic pathway, explaining why Chinese motherwort is particularly rich in this gynecological alkaloid.

Functionally, leonurine and stachydrine are strongly implicated in the uterine and cardiovascular actions that justify traditional indications such as regulation of menstruation, treatment of dysmenorrhea, and promotion of



postpartum lochia discharge (Zhang et al., 2018). Ethnopharmacological and pharmacological syntheses emphasize that these alkaloids exert uterotonic effects, improve uterine blood flow, and modulate platelet aggregation and vascular tone, linking them directly to relief of blood-stasis-type gynecological syndromes and prevention of thrombotic complications in the puerperium (Shang et al., 2014; Zhang et al., 2023). Leonurine additionally exhibits cardioprotective, neuroprotective, and anti-oxidative activities, which may benefit women with comorbid cardiovascular risk or stress-related menstrual irregularities. The recent elucidation of leonurine biosynthesis-highlighting arginine decarboxylase, UDP-glucosyltransferase, and serine-carboxypeptidase-like acyltransferase as key enzymes-creates opportunities to breed or engineer high-leonurine lines, thereby optimizing uterotonic and cardioprotective potential in gynecological formulations.

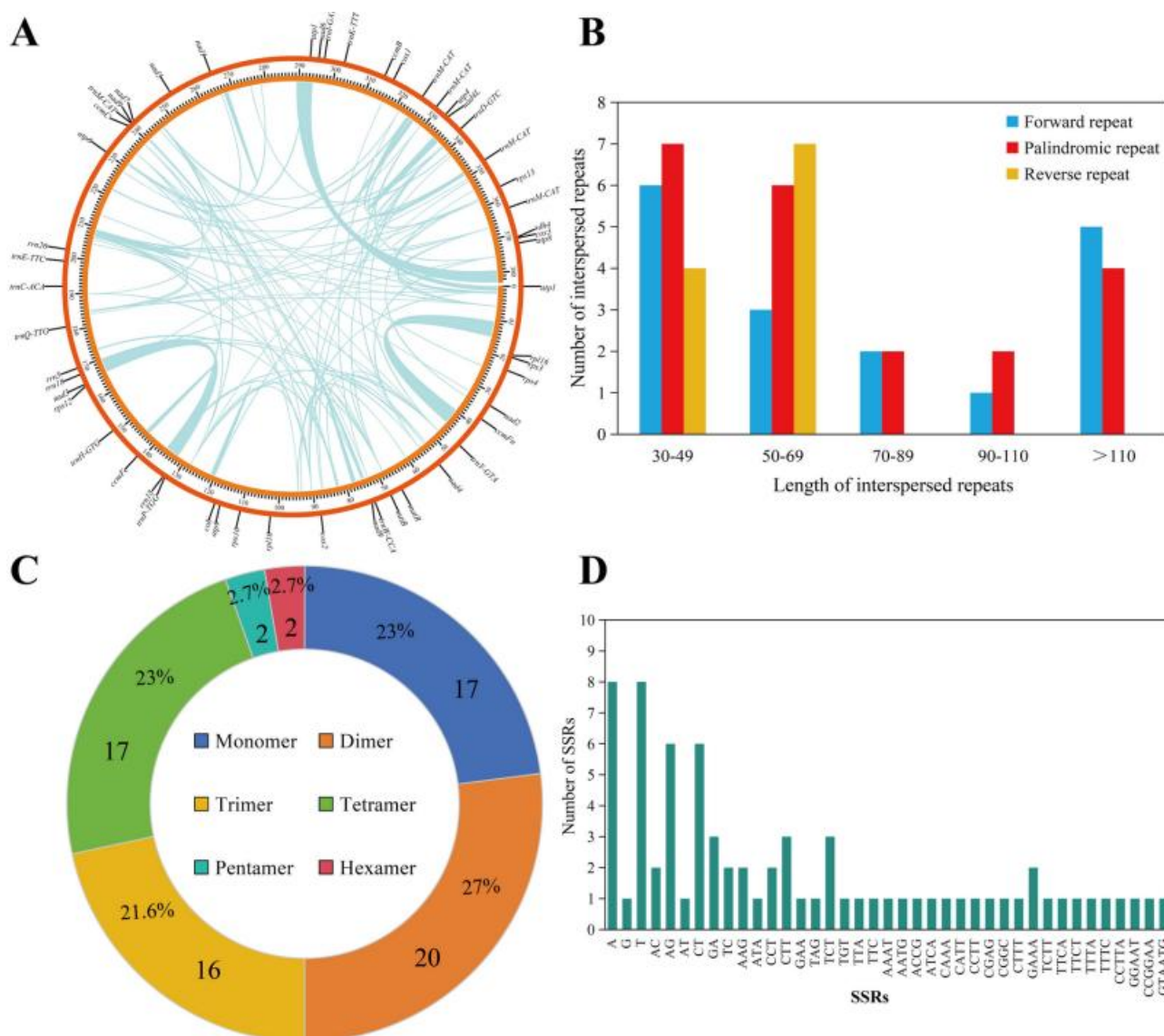


Figure 2 Repeat sequence analysis of the *L. japonicus* mt genome (Adopted from Hu et al., 2025)

Image caption: (A) The distribution of repeat sequences. The outer circle displays different genes. The blue inner arc indicates repeat sequences that are greater than or equal to 30 bp in length. (B) Histograms of lengths and classes of different DSRs. Different colors represent different types of DSRs. The x-axis and y-axis indicate the length and quantity of DSRs, respectively. (C) Proportion of different types of SSRs. Different colors represent different types of SSRs. (D) Statistical histograms of various SSRs. The x-axis displays different SSRs, while the y-axis shows the length of each SSR (Adopted from Hu et al., 2025)

### 3.2 Flavonoids and phenolic acids

Flavonoids and phenolic acids constitute a second dominant class of secondary metabolites in *L. japonicus*, widely distributed in aerial parts and readily enriched by polar extraction (Malave et al., 2020; Morais et al., 2023).

Quantitative assays show that ethanolic and hydroalcoholic extracts contain substantial amounts of total phenolics and flavonoids, with compounds such as chlorogenic, caffeic, caffeoylmalic, and ferulic acids, as well as rutin and quercetin, consistently identified in LC-MS analyses. Earlier isolation work from aerial parts yielded a panel of flavonoids including apigenin, luteolin, kaempferol, quercetin, and myricetin, alongside simple phenolic acids such as gallic and syringic acids, many of which display strong free-radical-scavenging activity in DPPH assays (Qu et al., 2006). More recent metabolomic studies on *Leonurus* spp. confirm that phenylpropanoids-including rare caffeoylglucaric acids-and classical flavonoids are quantitatively dominant in the phenolic fraction, emphasizing their central contribution to the plant's antioxidant capacity (Olennikov and Chirikova, 2016).

These phenolic constituents are closely linked to activities relevant for gynecological health, especially anti-oxidative, anti-inflammatory, vascular-protective, and tissue-repair effects that accompany uterine and pelvic pathologies. Antioxidant testing consistently demonstrates that phenolic-rich partitions (e.g., ethyl acetate fractions) and individual flavonoids such as luteolin, kaempferol, and quercetin exhibit higher radical-scavenging power than reference antioxidants, supporting their role in limiting oxidative damage during menstrual pain or postpartum recovery (Qu et al., 2006). In a wound-healing model, hydroalcoholic extracts with higher flavonoid content accelerated inflammatory resolution, wound contraction, and collagen synthesis, suggesting that polyphenols from *L. japonicus* can facilitate repair of reproductive-tract and perineal injuries associated with childbirth or gynecological surgery. Phenolic acids such as chlorogenic and caffeic acid, together with rutin and related flavonoid glycosides, also correlate with anti-inflammatory, vasodilatory, and enzyme-inhibitory activities in *Leonurus* species, providing mechanistic support for their use in relieving pelvic congestion, dysmenorrhea, and microvascular complications associated with gynecological disorders (Angeloni et al., 2021).

### 3.3 Volatile oils and other bioactive compounds

Beyond alkaloids and phenolics, *L. japonicus* produces essential oils and a suite of terpenoid and minor constituents that add further pharmacological dimensions, particularly antimicrobial and anti-inflammatory effects relevant to gynecological infections and postpartum care. Hydrodistillation of the herb (Yimucao) and fruits (Chongweizi) reveals marked variation in essential-oil profiles between parts: herb oil is dominated by sesquiterpenes and diterpenes, with phytone, phytol, caryophyllene oxide, and  $\beta$ -caryophyllene as major components, whereas fruit oil is richer in aliphatic hydrocarbons and bornyl acetate. These compositional differences translate into distinct bioactivities; Yimucao oil shows broad-spectrum activity against Gram-positive bacteria, while Chongweizi oil is largely inactive, underscoring the herb's particular value for managing genital and puerperal infections in traditional practice (Xiong et al., 2013). The predominance of  $\beta$ -caryophyllene, a sesquiterpene with known anti-inflammatory and analgesic potential, further suggests synergism with uterotonic alkaloids and phenolics in alleviating pelvic pain and inflammatory gynecological conditions.

In addition to essential oils, numerous labdane-type diterpenoids, ionone derivatives, terpenoid acids, and triterpenes have been isolated from the aerial parts of *L. japonicus*, many of them newly characterized in the last decade (Zhong et al., 2015; Wei et al., 2023). Several labdane diterpenes, including novel epimeric pairs, significantly inhibit nitric oxide production and pro-inflammatory cytokine release in LPS-stimulated macrophages, partly by blocking NF- $\kappa$ B signaling, thereby providing a non-alkaloid anti-inflammatory axis that may contribute to relief of uterine inflammation, endometritis, or pelvic inflammatory disease. Other terpenoids such as leojaponic acids A and B and triterpenes like ursolic acid exhibit enzyme-inhibitory and cytoprotective activities, which, together with minor phenylethanoid glycosides and iridoids documented in the genus, broaden the spectrum of biological actions relevant to women's health (Wu et al., 2016; Angeloni et al., 2021). Collectively, the volatile and terpenoid fractions complement the hormone-modulating and hemodynamic actions of alkaloids with antimicrobial, anti-inflammatory, and tissue-protective effects, forming a multi-target phytochemical ensemble well-suited to complex gynecological syndromes that involve infection, inflammation, pain, and impaired uterine involution.

## 4 Variation in Secondary Metabolic Traits and Influencing Factors

### 4.1 Metabolic differences among germplasms and varieties

*Leonurus japonicus* exhibits substantial intraspecific variation in secondary-metabolite traits that is closely tied to its genetic diversity across populations. Phylogenetic work based on concatenated plastid and nuclear markers has divided Chinese germplasm into four deeply divergent clades, with divergence events linked to geological uplift and Quaternary climate shifts (Wang et al., 2023a). This population structure provides a genomic framework for chemotype formation, because nucleotide diversity “hotspots” and clade differentiation are expected to underlie differences in biosynthetic capacity and regulatory networks influencing alkaloids, flavonoids, and terpenoids. At the same time, comparative genomics within the genus shows that leonurine accumulation is species-specific, driven by duplication and neofunctionalization of a UGT-SCPL gene cluster in *L. japonicus* but not in the low-leonurine species *L. sibiricus*, emphasizing how relatively recent gene-level changes can create marked metabolic contrasts between otherwise related lineages (Li et al., 2023).

Chemotaxonomic analysis of accessions from multiple provenances confirms that germplasms differ not only in overall metabolite content but also in the relative proportions of leonurine and other active markers important for gynecological efficacy (Han et al., 2023). High-performance liquid chromatography combined with multivariate statistics has resolved origin-specific clusters, in which some populations consistently show higher levels of key uterotonic and cardioprotective constituents than others, even under similar analytical conditions. These chemotype differences likely translate into variable clinical potency for indications such as regulating menstruation or promoting postpartum uterine involution, and they underscore the need to match germplasm to pharmacopoeial standards when developing standardized modern preparations. Integrating genome information with metabolite profiling-linking specific clades or alleles to leonurine and phenolic contents-offers a path toward breeding elite lines with optimized secondary-metabolite profiles for gynecological applications.

### 4.2 Regulation of metabolism by environmental factors

Environmental conditions strongly modulate secondary-metabolite accumulation in medicinal plants, and *L. japonicus* is no exception. A multi-origin study combining phylogenetics and chemical analysis showed that differences in active-ingredient profiles among regions could not be explained by genetics alone, implying a major contribution of local climate and edaphic conditions to observed metabolic variation (Han et al., 2023). In parallel, ecological modeling at the species level has identified precipitation patterns and temperature regimes-especially precipitation of the warmest quarter and minimum temperature of the coldest month-as key determinants of ecological suitability, with highly suitable habitats tending to support plants with higher expression of medicinal markers (Chen et al., 2024a). These findings suggest that water availability and thermal stress shape secondary metabolism in the field, for example by influencing pathways for alkaloids and phenylpropanoids that underpin gynecological indications such as hemostasis and uterine activation.

More broadly, reviews on plant secondary metabolism under abiotic stress demonstrate that light intensity and spectrum, temperature, soil moisture, nutrient status, and salinity can all shift both the quantity and profile of secondary metabolites, often through transcriptional regulation of biosynthetic genes (Jan et al., 2021). Even modest variation in a single factor-such as soil water or fertility-can significantly alter the levels of phenolics, terpenes, or alkaloids while other factors remain constant, indicating that cultivation practices for *L. japonicus* must carefully manage irrigation, fertilization, and shading to maintain consistent chemical quality (Yang et al., 2018). Climate-change-oriented syntheses further highlight that elevated temperature, drought, and changing CO<sub>2</sub> can either enhance or suppress specific metabolite classes, implying that future field production of motherwort may drift in chemotype unless adaptive agronomic strategies are implemented to stabilize uterotonic and anti-inflammatory components critical for gynecological efficacy (Qaderi et al., 2023).

### 4.3 Effects of developmental stages and harvesting time

Ontogeny exerts a powerful influence on secondary metabolism, and developmental regulation needs to be considered when defining optimal harvest windows for gynecological use of *L. japonicus*. General analyses of medicinal plants show that biosynthesis and storage of key secondary metabolites are tightly linked to organ

differentiation, flowering, and reproductive investment, resulting in stage-specific peaks of alkaloids, flavonoids, and volatile terpenoids (Li et al., 2020a). During early vegetative and pre-flowering phases, carbon allocation often favors phenylpropanoids and simple flavonoids that provide oxidative and UV protection, whereas later reproductive stages can shift metabolism toward terpenoid volatiles and lignified phenolics, altering the balance of compounds relevant to uterine and hemostatic actions. For *L. japonicus*, such ontogenic patterns imply that aerial parts harvested at different phenological stages (pre-flowering herb versus fruiting tops) may differ markedly in leonurine, flavonoid, and essential-oil content, potentially leading to variable gynecological outcomes if not standardized.

Evidence from related medicinal species illustrates how tightly secondary-metabolite dynamics can track developmental transitions and supports extrapolation to motherwort. In *Sophora japonica*, UHPLC-based metabolomics across five flower-maturity stages revealed pronounced shifts in 331 metabolites, with flavonoids and phenolic acids showing the strongest variation and early buds being richest in pharmacologically valued flavonoids suited for medicinal extraction (Wang et al., 2022a). Similarly, integrative omics of *Lonicera japonica* flowers demonstrated that simple phenylpropanoids and flavonoids accumulate predominantly at early stages, while terpenoid-backbone metabolites increase later, indicating a developmental switch in pathway dominance (Yang et al., 2019). Together with broader reviews on developmental control of medicinal plant metabolites, these results suggest that to maximize uterotonic alkaloid and antioxidant polyphenol content for gynecological formulations, *L. japonicus* should be harvested at carefully defined stages-likely around full flowering of the herb and specific maturity of the fruits-supported by stage-resolved metabolomic profiling and linked to traditional experiential criteria (Li et al., 2020b).

## 5 Biosynthetic Pathways and Molecular Regulation of Secondary Metabolites

*Leonurus japonicus* accumulates structurally diverse secondary metabolites-including leonurine, labdane-type diterpenoids and flavonoids-whose biosynthesis relies on conserved primary pathways such as shikimate, phenylpropanoid and terpenoid backbones that are broadly shared across angiosperms (Jan et al., 2021; Zhan et al., 2022). In many medicinal plants, the shikimate pathway supplies aromatic amino acids, which in turn feed into phenylpropanoid and flavonoid biosynthesis, creating the scaffold for tissue-specific and stress-responsive metabolite profiles relevant to pharmacological activity. Terpenoid and diterpenoid scaffolds in *L. japonicus* derive from plastidial and cytosolic isoprenoid pathways, with subsequent tailoring by cytochrome P450s, glycosyltransferases and acyltransferases producing lineage-specific compounds such as spiro-labdane diterpenoids and leonurine that underlie its distinctive gynecological uses. Integration of genomics and metabolomics in *Leonurus* indicates that diversification of specialized enzymes and gene clusters not only shapes total metabolite output but also species-specific differences between *L. japonicus* and low-leonurine relatives, highlighting an evolutionary tuning of biosynthetic capacity (Li et al., 2023).

### 5.1 Key metabolic pathways and enzymatic reactions

Multi-omics reconstruction of leonurine biosynthesis shows that this key guanidine-containing alkaloid arises from arginine via arginine decarboxylase (ADC), followed by uridine diphosphate glucosyltransferase (UGT)-mediated glycosylation and serine carboxypeptidase-like (SCPL) acyltransferase-catalyzed acylation, defining a concise route from primary nitrogen metabolism to a pharmacologically active secondary metabolite (Li et al., 2023). Comparative genomics between *L. japonicus* and *L. sibiricus* reveals that expansion and neofunctionalization of UGT-SCPL gene clusters in *L. japonicus* are central to its high leonurine content, illustrating how small changes in enzyme complement can dramatically shift the quantitative profile of medicinally important metabolites.

Labdane-related diterpenoids, including spiro-9,13-epoxy-labdane structures abundant in *L. japonicus*, are formed by a pairwise action of class II and class I diterpene synthases acting on geranylgeranyl diphosphate to generate peregrinol diphosphate and then epoxy-bridged labdane skeletons (Wang et al., 2022b). Functional characterization of six *L. japonicus* diTPSs indicates that LjTPS3 supplies the C-9-hydroxylated intermediate,



whereas LjTPS6 produces a mixture of labdane products; mutational analysis of a single active-site residue in LjTPS6 can shift product specificity toward a single 9,13-epoxy-labdane epimer, underscoring how subtle protein changes reprogram diterpenoid profiles.

## 5.2 Regulatory networks of related genes and transcription factors

Genome-level analyses of *L. japonicus* identify expanded gene families in specialized metabolism, particularly diterpenoid biosynthesis, suggesting that duplication and diversification of pathway genes provides a genomic substrate for regulatory rewiring of secondary metabolite output (Wang et al., 2024). In *Leonurus* WRKY transcription factor (TF) families, drought-responsive members (e.g., LjWRKY1, 4, 23, 44) show strong induction or repression under stress, and differentially expressed genes under drought are enriched in plant hormone signaling, MAPK cascades and secondary metabolite biosynthesis, implying a coordinated TF-centered network that links environmental cues to metabolite pathways (Guo et al., 2025).

Across plant species, transcription factors from WRKY, MYB, AP2/ERF, bHLH, bZIP and NAC families act as master regulators of secondary metabolism by binding cis-elements in promoters of biosynthetic genes and modulating their transcription in response to biotic and abiotic stimuli (Jan et al., 2021; Rabeh et al., 2025). Stress-inducible TFs often converge on precursor-producing steps such as the shikimate and phenylpropanoid pathways, creating regulatory nodes where environmental signals can adjust flux toward flavonoids, alkaloids or terpenoids; these principles are likely conserved in *L. japonicus* and underpin stress- and tissue-dependent variability in leonurine and labdane diterpenoids (Zhan et al., 2022).

## 5.3 Advances in molecular markers and metabolic regulation

The chromosome-level genome of *L. japonicus*, with over 22,000 annotated genes and clear expansion of specialized-metabolism families, provides a foundational resource for designing molecular markers targeting loci involved in diterpenoid and alkaloid biosynthesis and for associating allelic variation with chemotype differences among germplasm (Wang et al., 2024). Population-level work correlating ITS and plastid markers with inter-origin variation in active components already shows that genetic divergence only partially explains metabolite differences, emphasizing the need for pathway-anchored markers that can directly track biosynthetic capacity in breeding for stable gynecological quality traits (Han et al., 2023).

Multi-omics approaches in related medicinal species illustrate how integrating transcriptomics, metabolomics and co-expression network analysis can reveal key control points and candidate regulators for flavonoid and other secondary-metabolite pathways, offering a template for similar systems-level dissection in *L. japonicus* (Yang et al., 2019; Chen et al., 2024b). In such frameworks, hub TFs (including WRKYs) and tailoring enzymes like UGTs emerge as central levers of metabolic regulation; manipulating these nodes by marker-assisted selection, transgenic or genome-editing strategies could rationally enhance leonurine and labdane-diterpenoid profiles that contribute to uterotonic, hemostatic and anti-inflammatory effects in gynecological applications (Li et al., 2023; Guo et al., 2025).

# 6 Pharmacological Effects of *Leonurus japonicus* in Gynecological Disorders

*Leonurus japonicus*, known as a “sacred medicine of gynecology,” has long been used to treat menstrual disorders and postpartum conditions. Its major secondary metabolites, including alkaloids, flavonoids, and terpenoids, exert multi-target effects on circulation, inflammation, and endocrine regulation, supporting its therapeutic role (Shang et al., 2014; Li et al., 2019). Modern studies indicate that these compounds act synergistically through multiple pathways, providing a mechanistic basis for its traditional functions such as promoting blood circulation and alleviating gynecological disorders.

## 6.1 Mechanisms of promoting blood circulation and regulating menstruation

Animal models of trauma-induced blood stasis demonstrate that *L. japonicus* extracts significantly reduce plasma viscosity, platelet aggregation, fibrinogen, thromboxane B<sub>2</sub>, and plasminogen activator inhibitor-1, while increasing antithrombin III and tissue-type plasminogen activator, indicating coordinated antithrombotic and profibrinolytic effects that improve microcirculation (Zhang et al., 2023). In the same model, extract treatment

ameliorates local tissue injury and normalizes hemodynamic indices, supporting its use for pelvic “blood stasis” conditions that underlie dysmenorrhea and amenorrhea in traditional gynecology (Miao et al., 2019).

Leonurine and stachydrine also display vasodilatory, anti-platelet, and angiogenic activities, providing compound-level mechanisms for improved uterine blood supply and endometrial repair (Liao et al., 2023; Shi et al., 2022). Total alkaloid fractions from *L. japonicus* promote endothelial cell proliferation, migration, and tube formation via SRC/MEK/ERK signaling and accelerate wound healing *in vivo*, suggesting that enhanced neovascularization may contribute to the resolution of ischemic or stagnant uterine states associated with irregular menstruation and postpartum recovery (Li et al., 2019).

## 6.2 Anti-inflammatory and antioxidant activities

Motherwort total alkaloids attenuate bacteria-induced endometritis in rats, where treatment reduces inflammatory mediator overproduction and promotes endometrial repair through suppression of the PI3K/AKT/NF- $\kappa$ B axis and downstream cytokines (Ou et al., 2025). *in vitro*, these alkaloids inhibit lipopolysaccharide-triggered inflammatory responses in macrophages and human endometrial epithelial cells, highlighting a direct action on uterine immune-inflammatory microenvironments that are central to chronic endometrial pathology and infertility.

Broader pharmacological profiling shows that leonurine and stachydrine possess prominent anti-inflammatory and antioxidant properties, including inhibition of oxidative stress, modulation of NF- $\kappa$ B signaling, and reduction of tissue injury in cardiovascular and neuronal models (Liao et al., 2023; Wang et al., 2025). Crude *L. japonicus* extracts similarly downregulate TNF- $\alpha$ , IL-6, and IL-8 while enhancing anti-inflammatory IL-10 and antioxidant systems in trauma blood-stasis rats, indicating that both purified metabolites and complex mixtures can temper systemic and local inflammation relevant to pelvic pain, dysmenorrhea, and inflammatory gynecological disorders (Miao et al., 2019; Zhang et al., 2023).

## 6.3 Effects on uterine contraction and endocrine regulation

Classical and modern data converge to show that *L. japonicus* has marked effects on the uterus, including the ability to stimulate uterine smooth muscle and thereby assist in treating postpartum hemorrhage caused by uterine inertia (Shang et al., 2014). Bioassay-guided isolation has revealed that specific cyclopeptides and alkaloids, including leonurine, enhance contraction of rat uterine strips, while flavonoid glycosides exert the opposite, relaxing effect, explaining the herb’s clinically observed bidirectional regulation of uterine activity in dysmenorrhea versus postpartum bleeding. More recently, coumarins isolated from *L. japonicus* were found to have similarly opposite effects on uterine smooth muscle: bergapten promotes contraction by increasing intracellular Ca<sup>2+</sup> via L-type Ca<sup>2+</sup> channels and  $\alpha$ -adrenergic receptors, whereas osthole, an  $\alpha$ -receptor antagonist, reduces Ca<sup>2+</sup> influx and relaxes oxytocin-induced contractions (Fan et al., 2024). Beyond direct myometrial actions, network pharmacology analyses indicate that multiple motherwort components target endocrine-related molecules such as ESR1, AR, AKT1, and PPARG, suggesting integrated regulation of steroid hormone signaling in menstrual disorders (Wang et al., 2020).

Endocrine modulation by *L. japonicus* extends to ovarian steroidogenesis, where luteolin and luteolin-7-methylether suppress aromatase-mediated estrogen biosynthesis in human granulosa cells by inhibiting TPL2-MKK3/6-p38-CREB signaling (Shi et al., 2024). Luteolin-7-methylether (XLY29) decreases estradiol production in granulosa-like cells and downregulates aromatase promoter I.3/II without directly inhibiting catalytic activity, and *in vivo* lowers serum estradiol and alters estrous cycling in mice, suggesting potential applications in estrogen-excess conditions such as polycystic ovary syndrome (Du et al., 2020). A network pharmacology study focused on menstrual disorders further shows that 29 bioactive compounds from motherwort share core targets in endocrine, vascular, and inflammatory pathways, with hub genes including AKT1, PTGS2, ESR1, AR, and PPARG. Molecular docking indicates that many of these metabolites bind strongly to estrogen receptor and androgen receptor, providing a mechanistic bridge between traditional indications of “regulating menstruation” and modern concepts of hypothalamic-pituitary-ovarian axis and peripheral receptor modulation in gynecological endocrine disorders.

## 7 Functional Associations Between Secondary Metabolic Traits and Gynecological Effects

### 7.1 Correlation between key active components and pharmacological efficacy

Chemical-pharmacological correlation studies consistently identify leonurine, stachydrine and trigonelline as core active alkaloids whose plasma exposure and tissue distribution parallel the traditional gynecological indications of *Leonurus japonicus* (Zhao et al., 2022). Network pharmacology and pharmacokinetic analyses show that these alkaloids act on targets involved in vascular regulation, inflammation and endocrine pathways, linking their presence in different plant parts to effects on menstrual disorders, postpartum recovery and blood-stasis syndromes (Wang et al., 2020).

At the single-compound level, leonurine displays pleiotropic cardiovascular, anti-oxidant and anti-inflammatory actions, furnishing mechanistic support for motherwort's use in conditions characterized by pelvic ischemia, pain and microvascular dysfunction (Li et al., 2019). Other secondary metabolites, including labdane diterpenoids and flavonoids, contribute anti-platelet, anti-inflammatory and hormone-modulating activities, suggesting that distinct metabolite classes collectively underpin the multi-target efficacy observed in obstetrical and gynecological practice (Xiao et al., 2017; Zhang et al., 2018).

### 7.2 Impact of metabolic variation on therapeutic stability

Comparative analyses of *L. japonicus* from different geographic origins reveal significant intergroup differences in active-ingredient profiles, despite relatively modest genetic divergence, indicating that environmental factors and cultivation conditions strongly influence secondary metabolite composition (Han et al., 2023). Such chemotypic variation implies that the content of key alkaloids or diterpenoids may fluctuate among accessions, potentially leading to inconsistent clinical responses when crude drugs are sourced without standardized quality control (Wang et al., 2023b).

A systematic Q-marker study further demonstrates that leonurine, stachydrine and trigonelline differ in stability during storage, with time-dependent declines that are substantial enough to affect pharmacologically effective doses if not controlled (Zhao et al., 2022). By establishing content limits and stability windows for these markers, the work directly links metabolic degradation dynamics to therapeutic reliability, providing a quantitative framework for ensuring consistent gynecological efficacy in commercial preparations (Wang et al., 2024).

### 7.3 Functional association studies based on metabolomics

Integrated metabolomics and network pharmacology applied to leonurine show that changes in circulating metabolites map to pathways in glycerophospholipid, linoleic acid, tryptophan and glutamate metabolism, which are central to oxidative stress, inflammation and energy homeostasis (Rong et al., 2022). Regulation of these metabolic networks aligns with leonurine's protective effects in cardiovascular and metabolic models, reinforcing the idea that modulation of systemic metabolism is a key route through which *L. japonicus* components support uterine and pelvic vascular health in gynecological disorders (Li et al., 2019).

In parallel, metabolomic and multivariate analyses of whole-plant extracts identify dozens of absorbed prototypes and biotransformation products whose patterns differ across plant parts, yet cluster with gynecologically relevant targets in network models (Zhao et al., 2022). These association studies suggest that specific metabolite signatures-rather than single compounds alone-correlate with anti-inflammatory, endocrine-modulating and pro-circulatory effects, pointing toward metabolomics-driven definition of chemotypes optimized for menstrual regulation, endometrial repair or estrogen-related conditions (Shi et al., 2024).

## 8 Case Study: Comparative Analysis of Metabolic Variation and Gynecological Efficacy of *Leonurus japonicus* from Different Origins

### 8.1 Comparative analysis of chemical composition among different geographical origins

*Leonurus japonicus* exhibits pronounced intraspecific chemical variation, reflecting both genetic divergence and environmental heterogeneity across its distribution range. Multi-locus barcoding combined with HPLC profiling has shown that accessions from different origins cluster into distinct genetic lineages, and these clades partially parallel differences in contents of key alkaloids such as leonurine and stachydrine (Figure 3) (Han et al., 2023).

The integrated analysis indicates that metabolite divergence cannot be explained by genetics alone, and that ecological variables-particularly climate and edaphic conditions-shape local chemotypes, likely through modulation of stress-responsive and specialized-metabolism gene networks. Broad-scale ecological modeling further supports this view: areas with higher climatic suitability for *L. japonicus* tend to harbor plants with more favorable profiles of medicinal marker compounds, linking habitat quality to metabolite accumulation (Chen et al., 2024a).

High-resolution metabolomics has revealed that beyond a few alkaloid markers, the *L. japonicus* metabolome encompasses extensive diversity in flavonoids, phenylethanoid glycosides, terpenoids, and fatty-acid esters, with many of these constituents varying quantitatively among origins (Garrañ et al., 2019). Comparative surveys suggest that some regions produce material enriched in alkaloids and flavonoids, whereas others are relatively richer in terpenoid scaffolds, implying origin-specific pharmacological tendencies within the same species. Large-scale distribution modeling predicts a future poleward expansion and reshaping of suitable areas under climate change, raising the prospect that both the geographic supply and typical metabolite profiles of medicinal *L. japonicus* will shift over time (Chen et al., 2024b). Together, these data underscore that “origin” encodes a complex combination of genetic background, local environment, and resulting metabolite pattern, with direct relevance to quality evaluation.

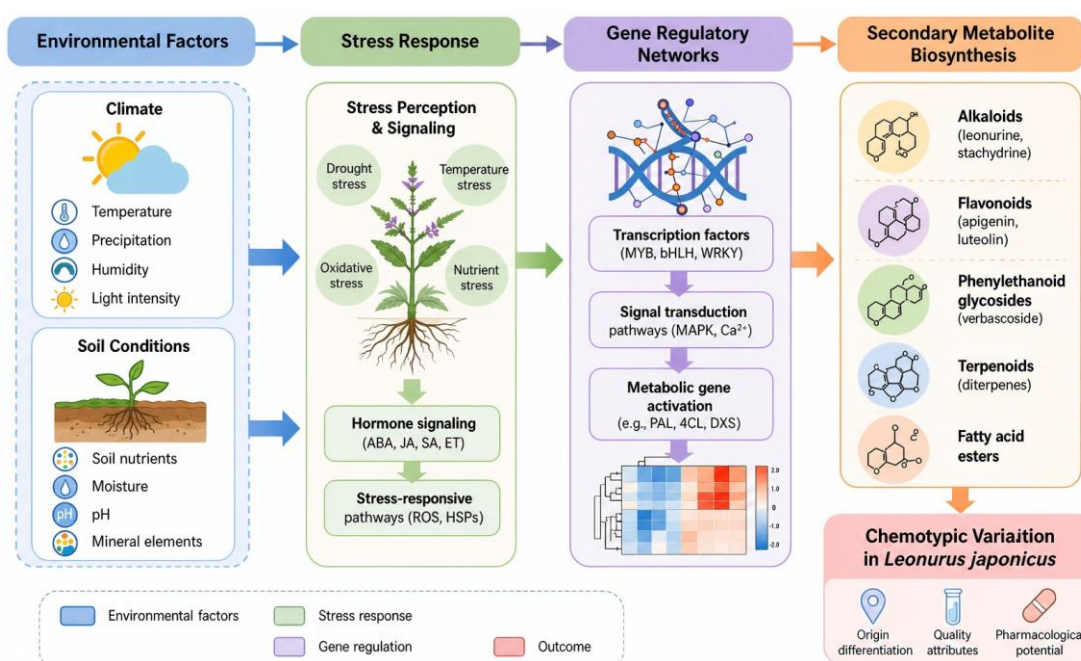


Figure 3 Conceptual model illustrating how environmental factors (climate and soil conditions) influence stress-responsive pathways and specialized metabolism gene networks, ultimately shaping chemotypic variation in *Leonurus japonicus* (Adopted from Han et al., 2023)

## 8.2 Pharmacodynamic evaluation (*in vitro* and *in vivo* models)

Pharmacodynamic studies integrating chemical profiling with bioassays have begun to clarify how origin-linked metabolite differences translate into gynecologically relevant activities. Total alkaloid fractions, dominated by leonurine-type and related bases, promote angiogenesis, endothelial migration, and collagen deposition via SRC-MEK-ERK signaling, supporting tissue repair after uterine or perineal injury (Shi et al., 2022). Parallel work in trauma-induced blood-stasis models demonstrates that whole-plant extracts rich in alkaloids and flavonoids improve hemodynamics, decrease platelet aggregation, and modulate vasoactive mediators, providing mechanistic support for traditional indications of “activating blood circulation” in dysmenorrhea and postpartum conditions (Zhang et al., 2023). Because the abundance of these bioactive constituents is origin-dependent, extracts from alkaloid-rich regions are expected to exert stronger pro-angiogenic and hemorheologic effects at equivalent doses (Han et al., 2023).



Gynecological inflammation models offer additional insight into how metabolite patterns shape efficacy. Motherwort total alkaloids significantly ameliorate bacteria-induced endometritis in rats, reducing inflammatory mediator overproduction and promoting endometrial repair through regulation of PI3K-AKT-NF- $\kappa$ B signaling (Ou et al., 2025). In parallel, combination formulas containing *L. japonicus* with other herbs show robust efficacy against bovine and rodent endometritis, lowering uterine bacterial load and inflammatory scores while improving oxidative status, consistent with a multi-component, multi-target anti-inflammatory mode of action (Tan et al., 2025). In endocrine-related disorders, *L. japonicus*-derived flavonoids such as luteolin and luteolin-7-methylether inhibit aromatase-mediated estrogen biosynthesis in granulosa cells and alleviate polycystic ovary syndrome (PCOS) phenotypes in mice, implicating origin-dependent flavonoid content in modulation of ovarian steroidogenesis (Du et al., 2020; Shi et al., 2024). Collectively, these *in vitro* and *in vivo* data indicate that variation in alkaloid and flavonoid levels across origins is likely to produce distinct profiles of uterotonic, anti-inflammatory, vascular, and endocrine activities.

### 8.3 Validation of correlations between metabolic profiles and clinical efficacy

Establishing robust links between origin-specific metabolite signatures and clinical gynecological outcomes requires coordinated chemical, pharmacokinetic, and clinical data. Multi-marker quality control work has identified leonurine, stachydrine, and trigonelline as quantitative “Q-markers” that are both pharmacodynamically relevant and sufficiently stable for routine measurement, enabling standardized comparison of materials from different regions and plant parts (Zhao et al., 2022). Broad metabolomic and genomic analyses demonstrate that *L. japonicus* accessions with higher expression of leonurine-biosynthesis genes accumulate more leonurine in aerial tissues, whereas closely related *Leonurus* species lacking these pathway innovations are essentially leonurine-free, highlighting a genetic basis for inter- and intra-specific differences in clinically important alkaloids. Integrating such markers with origin information allows retrospective correlation of clinical preparations-long valued for treating menoxenia, dysmenorrhea, amenorrhea, postpartum hemorrhage, and lochial disorders-with defined ranges of bioactive constituents (Shang et al., 2014; Miao et al., 2019).

Translational studies in gynecologically relevant models provide a bridge between chemistry and real-world therapeutic outcomes. Leonurine isolated from *L. japonicus* exhibits potent antimycobacterial activity against *Mycobacterium tuberculosis* and reduces mycobacterial load in a rat model of genital tuberculosis, directly linking an origin- and pathway-dependent alkaloid to improved uterine infection control (Gan et al., 2019). Similarly, motherwort-based formulations and extracts rich in leonurine and related secondary metabolites alleviate obstetric and gynecologic conditions such as postpartum hemorrhage, irregular menstruation, and dysmenorrhea in clinical and preclinical settings, in line with their vascular, uterotonic, anti-inflammatory, and endocrine-modulating activities (Wen et al., 2019). As ecological modeling now connects climatic suitability and gene expression with medicinal compound accumulation, origin-informed cultivation strategies can be used prospectively to produce chemotypes optimized for specific gynecologic indications, creating a feedback loop in which metabolic profiling, pharmacodynamics, and clinical efficacy mutually refine quality standards for *L. japonicus*-based therapies.

## 9 Conclusion and Future Perspectives

Research on *Leonurus japonicus* has firmly established it as a key medicinal plant in gynecology, with its therapeutic efficacy closely linked to a chemically diverse and dynamic secondary metabolite system. The plant contains abundant alkaloids, diterpenoids, and flavonoids, among which leonurine, stachydrine, and trigonelline are considered core bioactive compounds. These metabolites not only contribute to traditional indications such as regulating menstruation and promoting blood circulation but also serve as important quality markers connecting phytochemical variation with clinical consistency. Advances in chromatographic and metabolomic analyses have revealed substantial intra- and interspecific variation in these compounds, highlighting leonurine as a species-specific chemical signature distinguishing *L. japonicus* from related taxa such as *L. sibiricus*. More importantly, the integration of genomics, transcriptomics, metabolomics, and enzymology has enabled reconstruction of the leonurine biosynthetic pathway, identifying key enzymes such as arginine decarboxylase (ADC), UDP-glycosyltransferases (UGTs), and serine carboxypeptidase-like proteins (SCPLs). Gene duplication

and functional divergence within these pathways provide a mechanistic explanation for the high accumulation of leonurine in *L. japonicus*, thereby directly linking genetic architecture with pharmacologically relevant alkaloid traits.

At the functional level, the diverse metabolite profile of *L. japonicus* underpins its multi-target pharmacological activities, particularly in gynecological contexts. Total alkaloid fractions and enriched extracts have been shown to promote angiogenesis, accelerate tissue repair, and facilitate endometrial recovery through signaling pathways such as SRC/MEK/ERK and PI3K/AKT/NF- $\kappa$ B, supporting its traditional application in postpartum rehabilitation and inflammatory uterine conditions. Systems pharmacology approaches further demonstrate that multiple metabolite classes collectively modulate endocrine, vascular, and inflammatory networks, with hub targets including AKT1, ESR1, and PTGS2 serving as key regulatory nodes. Flavonoids such as luteolin and luteolin-7-methylether provide an additional layer of endocrine regulation by suppressing aromatase-mediated estrogen biosynthesis via pathways such as p38 MAPK/AKT and TPL2-p38-CREB, suggesting therapeutic potential in estrogen-related disorders including polycystic ovary syndrome. Meanwhile, labdane diterpenoids, particularly those localized in glandular trichomes, exhibit anti-inflammatory, antithrombotic, and anti-proliferative activities, expanding the spectrum of bioactive constituents involved in regulating uterine blood flow, thrombosis, and pelvic inflammation. Together, these findings support a multi-component, multi-target mode of action that bridges traditional concepts with modern molecular pharmacology.

Despite significant progress, important challenges remain in fully elucidating the relationship between metabolite diversity and gynecological efficacy. Existing studies are often fragmented across different extract types, plant tissues, developmental stages, and geographical origins, with relatively few investigations systematically linking natural variation in metabolite profiles to standardized clinical outcomes. Although genetic and environmental factors have been shown to influence metabolite composition, the specific ecological drivers and agronomic strategies for optimizing key bioactive compounds remain insufficiently defined. Furthermore, while network pharmacology and *in vitro* or animal studies provide valuable mechanistic insights, rigorously designed clinical trials that incorporate chemical quality and genetic background are still lacking. The expansion of genomic resources, including chromosome-level assemblies and organelle genomes, offers new opportunities for integrative research; however, comprehensive genotype-metabolite-phenotype association studies remain in their early stages. Future research should prioritize multi-omics integration across diverse germplasm to develop predictive models linking genome, environment, and metabolite traits to gynecological functions. Such efforts, combined with precision breeding strategies and improved quality control frameworks that incorporate multi-component fingerprints and pharmacokinetic data, will be essential for advancing the standardized, safe, and evidence-based application of *L. japonicus* in modern obstetrics and gynecology.

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### Conflict of Interest Disclosure

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

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