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The genomic design of fruit metabolomes

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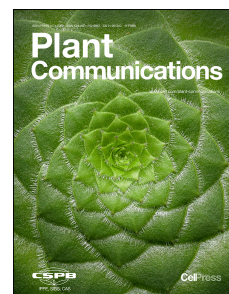
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1 **The genomic design of fruit metabolomes**

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19 **Short Summary**

20 A comprehensive understanding of the metabolic-genetic networks governing fruit
21 sensory traits (e.g., flavor and color) is essential for advancing genomic design breeding.
22 This review systematically elucidates these networks and recent advances in genomic
23 design breeding for targeted quality improvement, thereby providing a reference for
24 future fruit quality enhancement and intelligent breeding.

Abstract

As a major source of vitamins, minerals and dietary fibers, fruits are critical elements for ensuring global dietary sufficiency. Domestication and improvement boosted fruit yield and disease resistance but reduced flavor and aroma. With the rapid development of multiomics and gene editing, such as genomics, metabolomics and CRISPR-Cas9, improving fruit quality through genome design has become feasible. However, the sensory traits of fruits, including sugar, acid, aroma and color, are complex regulated by multiple genes, presenting a current challenge in the study of quantitative inheritance. Metabolomics, through reverse genetics, are more intuitively reflect gene expressions and protein-protein interactions than other omics in fruit. Establishing correlations between metabolites and phenotype changes, and integrate metabolomics and other omics data are crucial aspects of metabolomics research focused on fruit quality and genomic breeding. This paper provides a comprehensive review of research advancements in the metabolomics of fruit sensory traits, alongside the future prospects of integrating genomic design of metabolomics, aiming to deepen the understanding of multi-omics technologies, promoting the application and advancement of metabolomics in fruit, and establishing a robust theoretical foundation for improving fruit sensory quality.

Keywords: Metabolomics, Genomic breeding, Color, Flavor, Aroma, Horticulture

46 Introduction

47 Metabolomics, emerging in the late 1990s following genomics and proteomics, serves
48 as a critical bridge between genotype and phenotype (Fiehn 2002; Shen et al. 2023;
49 Nicholson and Lindon 2008). This technology has been widely applied in the medical
50 field, particularly in disease diagnosis, prediction of disease progression, and evaluation
51 of drug metabolism efficacy (DeBerardinis and Keshari 2022). Gradually, it also plays
52 a vital role in agricultural and forestry breeding, livestock diseases prevention, as well
53 as food chemistry processing technique. However, unlike the widely applied in
54 Arabidopsis (Wu, Tohge, et al. 2018; Huang, Jiang, et al. 2019), tobacco (Goetz et al.
55 2017), tomato (Gao et al. 2019; Klee and Tieman 2013; Zhu et al. 2018), etc. the
56 complexity and environmental sensitivity of metabolites in fruits development, along
57 with challenges in sample handling and high costs, have constrained the development
58 of metabolomics technologies in fruits research.

59 With natural selection and domestication over the past century, yield and disease
60 resistance have emerged as the primary objectives of fruit cultivation and breeding
61 (Zhou, Muyle, and Gaut 2019). However, the phenomena of ‘peach lacking peach
62 flavor’ (Cao et al. 2022) and ‘tomato lacking tomato flavor’ (Gao et al. 2019; Zhu et al.
63 2018), have become pressing issues that demand urgent solutions. Moreover, color
64 reflects flavor-related metabolism and also significantly influences consumers’ fruit
65 quality assessment. The complex interplay between fruit sensory traits-sugar, acid,
66 aroma, and color-requires comprehensive and in-depth research. Under the complex
67 interactions within metabolic networks, single-trait breeding approaches demonstrate
68 significant limitations. Therefore, systematically elucidating metabolic pathways and
69 their regulatory networks is essential. For instance, some intermediates or derivatives
70 from the carotenoid metabolic process also contribute to the composition of volatile
71 organic compounds (VOCs) (Nisar et al. 2015). High sugar content promotes the
72 synthesis and accumulation of anthocyanins, and variations in anthocyanin levels are

associated with flavor-related traits such as fruit astringency and antioxidant properties (Jaakola 2013). The intricate network interconnecting taste, color, and aroma demands extensive and in-depth investigation.

Breeding 4.0 (Wallace, Rodgers-Melnick, and Buckler 2018) refers to the intelligent, precision breeding phase supported by modern technologies such as genomics (Crossa et al. 2017), big data, and artificial intelligence (Huang et al. 2022) which will significantly accelerate the breeding process. Compared with traditional breeding methods, it places greater emphasis on in-depth mining and utilization of genetic information. Nevertheless, in light of the remarkably intricate genetic background and high level of heterozygosity characteristic of fruit trees, as well as the fact that agronomic traits are often influenced by both genes and cultivation environment, research on the sensory traits of fruits is relatively limited. This article primarily discussed the latest research progress in metabolomics related to fruit sensory traits, summarized the differences and connections in metabolomics of fruits among different species, the application of genomic design in fruit sensory traits, and the development trends and directions of fruit sensory traits genomic design in the future, which will provide theoretical support for targeted improvement of fruit quality and offer a roadmap for accelerating the breeding of high-quality fruit varieties.

The fruit sensory traits lost during fruit domestication

Fruits play a pivotal role in enhancing global food security through multiple dimensions. According to Food and Agriculture Organization (FAO), the global cultivated area and yield for fruits in 2021 was shown in Figure 1A (<https://www.fao.org/faostat/en/#data>). However, the domestication is achieved through long-term artificial selection and the refinement of genetic resources, yielding fruits that better suit the growers' preferences and requirements, accompanied by the reduction and loss of fruit flavor (Zhang and Hao 2020; Zhao et al. 2019).

With the historic breakthrough of the human genome “Telomere-to-Telomere” (T2T) (Miga et al. 2020), T2T-related research in fruits had been reported (Figure 1B). Grape stands as the pioneer among fruits to have its genome sequenced (Figure 1) (Jaillon et al. 2007), and concurrently, the genome information of diverse species is undergoing incessant updates (Velasco et al. 2007; Girollet et al. 2019; Shi et al. 2023). Subsequently, genome information of papaya (Ming et al. 2008), apple (Daccord et al. 2017; Zhang et al. 2019; Velasco et al. 2010), strawberry (Edger et al. 2019; Jin et al. 2023; Zhou et al. 2023; Shulaev et al. 2011), banana (D’hont et al. 2012; Huang et al. 2023), melon (Ruggieri et al. 2018; Garcia-Mas et al. 2012; Li et al. 2023), sweet orange (Xu et al. 2013; Wu, Terol, et al. 2018), peach (Initiative et al. 2013; Cao et al. 2021), etc. has been reported and continuously updated (Wu et al. 2013; Chagné et al. 2014; Sun et al. 2023; Deng et al. 2022; Guo et al. 2013; Han et al. 2023; Huang et al. 2013; Huang et al. 2016; Liu et al. 2014; Yang, Han, et al. 2023; Wu et al. 2014; Ming et al. 2015; Qin et al. 2017; Luo et al. 2020; Xiao et al. 2017; Teh et al. 2017; Lin et al. 2017; Wang, Li, et al. 2022; Rendón-Anaya et al. 2019; Zhu et al. 2019; Sahu et al. 2019; Wang, Luo, et al. 2020; Colle et al. 2019; Wang 2021; Jiang et al. 2020; Chen, Xie, et al. 2021; Bao et al. 2023). This genomic information will provide a solid theoretical foundation for precise breeding, including the precise mapping of genes related to fruit flavor, the uncovering its genetic mechanisms, and the exploration of high-quality wild germplasm resources for targeted flavor improvement.

Numerous differential metabolites have been discovered through metabolomic analyses of wild and cultivated fruits (Figure 1C) (Jing et al. 2023; Ren et al. 2021; Huang et al. 2022; Renner et al. 2021; Xiao et al. 2023). For instance, wild apples contain significantly larger amounts of substances associated with astringency, sourness, and bitterness-such as tannins and organic acids-than cultivated varieties, which indicates that the accumulation of such substances has decreased markedly during apple domestication (Liao et al. 2021). A decrease in acidity and an increase in sugar content were also observed during the domestication from sour jujube to cultivated jujube

(Huang et al. 2016). Notably, sugar content exhibits a negative correlation with fruit size in tomato. Interestingly, elevated levels of volatile organic compounds (VOCs) can enhance perceived sweetness, challenging the conventional view that fruit size correlates weakly or not at all with flavor-related traits (Tieman et al. 2017; Goulet et al. 2012; Klee and Tieman 2018). In summary, integrating multi-omics data to build a comprehensive regulatory network, precisely editing key genes via gene editing, and combining with machine learning can quickly, accurately, and directionally breed new fruit varieties, providing technical support for fruit domestication and quality improvement.

The genetic basis and anabolic pathway of fruit sensory traits

Currently, over 300,000 plant metabolites have been identified, which are classified into primary and secondary metabolites based on sources and functions. **fruit sensory** carbohydrates, lipids and nucleotides, are crucial for plant life and growth, while secondary metabolites including alkaloids, phenols and flavonoids, mainly function in stress responses and in aspects like protection and competition. The genetic basis and anabolic pathway of metabolites associated with fruit sensory traits-sugars, organic acids, pigments (for color), and VOCs (for aroma)-are illustrated and supported by Figure 2.

Fruit sugar, organic acids, VOCs, and pigment biosynthesis are interconnected metabolic processes that all rely on carbon sources derived from photosynthesis (Figure 2, Figure 3). These pathways diverge at a central metabolic junction-phosphoenolpyruvate (PEP). Sugar metabolism provides essential carbon skeletons not only for the tricarboxylic acid (TCA) cycle, which leads to organic acid accumulation, but also for the biosynthesis of VOCs through lipid, amino acid, and terpenoid pathways, and for pigment production, including carotenoids via the MEP pathway and anthocyanins via the phenylpropanoid pathway. Light signaling, particularly through

the transcription factor HY5, plays a crucial role in the coordinated regulation of these metabolic branches. Furthermore, organic acid levels can exert feedback inhibition on sugar metabolism, contributing to a complex and dynamic metabolic network that maintains the balance of carbon flux among fruit quality-related traits.

Sugar metabolism: dominant sucrose accumulation and regulation

The sweetness of fruits is mainly attributed to soluble sugars such as fructose, glucose, sucrose, as well as other compounds including starch, sorbitol, inositol, galactose, mannitol, pyruvate, and gluconic acid (Yamaki and Ishikawa 1986). The predominant sugar varies significantly among fruit species and varieties: hexose (fructose and glucose) is the major soluble sugar in grapes and apples (Zhu et al. 2023). However, based on the proportion of fruit sugar components and clustering analysis results, the types of fruit sugar accumulation in loquat (Sortino et al. 2022; Liu, Song, et al. 2024) and watermelon (Ren et al. 2021; Umer et al. 2020) germplasm resources can be classified into sucrose accumulation type and hexose accumulation type, respectively (Supplemental Table 1).

Among soluble sugars, sucrose accumulation holds dominance in evolution (Ren et al. 2021). This primacy stems from sucrose's role as the primary sugar for long-distance transport in plants, as well as its core functions in energy storage and signaling (Chen, Zhang, et al. 2021). Compared to other monosaccharides like fructose, sucrose offers significant evolutionary advantages due to its greater chemical stability and lower osmotic pressure, facilitating efficient transport and bulk storage, which is crucial for coping with environmental stress and energy allocation. Recent in-depth evolutionary analyses (e.g., comparative genomics, phylogenetic analysis) have successfully identified multiple key gene families and their members controlling sucrose content. These genes are critically involved in sucrose biosynthesis (e.g., Sucrose Phosphate Synthase genes, SPS) (Vimolmangkang et al. 2016), transport (e.g., Sucrose

Transporter genes, SUT/SUC, sugars will eventually be exported transporter, SWEETs) (Xue et al. 2022; Stein and Granot 2019), and catabolism (e.g., Sucrose Synthase genes, Susy, Invertase genes, INV) (Wei et al. 2021). Crucially, the functions of these key candidate genes, screened through evolutionary analysis, have been directly validated using stable genetic transformation techniques (e.g., transgenic overexpression, gene knockout/knockdown) in various model plants and crops (Ren et al. 2021; Deng, Mai, and Niu 2019). Experimental evidence confirms that modulating the expression of these genes significantly alters sucrose accumulation levels, thereby impacting plant growth, development, yield, and stress tolerance.

Sugar metabolism is orchestrated by transcription factors (bHLH /MYB/WRKY, etc.) (Zhang et al. 2023; Cao et al. 2016) that dynamically balance synthesis-transport-storage in response to energy/stress signals, while being reprogrammed by epigenetic marks (e.g., DNA methylation, histone modification) (Huang, Liu, et al. 2019; Ma et al. 2021; Li et al. 2020) and environmental cues (hormones/stress/microbes), collectively shaping carbon partitioning. Beyond sucrose, soluble sugars play multifaceted roles in fruit quality: Sorbitol serves as a Rosaceae-specific carbon transporter with low osmolarity and antioxidant capacity (Li et al. 2018); fructose delivers high sweetness and osmoregulation, glucose supplies energy substrates and pigment glycosylation precursors; trehalose and raffinose families enhance stress tolerance by stabilizing biomacromolecules. Through coordinated carbon partitioning (e.g., sorbitol-to-fructose conversion optimizing sugar/acid ratio), signaling (glucose-HXK pathway), and cellular homeostasis (trehalose-mediated membrane protection), these sugars collectively sculpt fruit flavor, color, and postharvest resilience.

Acid metabolism: dynamic balance of organic acids

The organic acids present in fruits encompass malic acid (MA), citric acid (CA), tartaric acid (TA), quinic acid, succinic acid, oxalic acid, acetic acid, and AsA (Vitamin C), etc.

(Guo et al. 2019). Fruits can be classified into MA-type (e.g. apples), CA-type (e.g. lemons), and TA-type (e.g. grapes) according to the dominant organic acid types. In addition, amino acids are constituents of fruit flavor (Kader 2008; Klee 2010), for example glutamic acid is responsible for “umami” or “savory”, while alanine or lysine is highly associated with sweetness, and phenylalanine or tyrosine contributes to bitterness (Song et al. 2019).

The accumulation of organic acids in fruit is primarily governed by the balance between their biosynthesis, interconversion, transport and degradation rates, which are regulated by a network of interconnected metabolic pathways (Etienne et al. 2013; Hu et al. 2016). Among these, the tricarboxylic acid (TCA) cycle serves as the central route for organic acid biosynthesis. Citric and malic acids are the predominant components, synthesized via key enzymes such as citrate synthase (CS), phosphoenolpyruvate carboxylase (PEPC) (Zhi et al. 2021), and malate dehydrogenase (MDH), and degraded via malic enzyme (ME), aconitase (ACO) (Liu, Zhao, et al. 2024), and isocitrate dehydrogenase (IDH) (Zhang et al. 2021). In addition, the γ -aminobutyric acid (GABA) shunt, acetyl-CoA-associated pathways, and glycolytic branches also contribute to the complexity of organic acid metabolism (Sheng et al. 2017). Organic acid transporters (Aluminum-activated malate transporters, ALMT) on the plasma membrane can also regulate the dynamic balance of organic acids in the cytoplasm, ensuring the continuity and stability of metabolism (Bai et al. 2012).

Additionally, organic acids accumulation is not the result of a single pathway, but rather the coordinated regulation of multiple metabolic pathways at different developmental stages and among various organelles. During the early developmental stage: Glycolysis, together with PEPC and MDH, synergistically promotes the synthesis of organic acids. In the middle stage of cell expansion: The vacuolar storage capacity increases, and organic acids are sequestered into the vacuoles. At the ripening stage: The expression of degrading enzymes such as ME and IDH rises, leading to a decrease in acidity. These

processes are finely regulated by transcription factor (bHLH /MYB/WRKY, etc.), enzymatic activity, and environmental cues, ultimately giving rise to the diverse organic acid profiles characteristic of different fruit species. Environmental impacts: Insufficient light, elevated temperature, calcium deficiency, and other factors can all inhibit the accumulation of organic acids. Notably, during fruit development, the dynamic changes in organic acids are more pronounced and sensitive than those of sugars-sugars often accumulate steadily from early development to maturity, while organic acids undergo drastic shifts (e.g., rapid synthesis in early stages, gradual degradation in ripening), making them the key variable in adjusting flavor balance.

Color metabolism: Pigment synthesis and coloration

Anthocyanins: Anthocyanins, widely distributed water-soluble pigments in plants, belong to flavonoid compounds with a basic C₆ (A ring)-C₃ (C ring)-C₆ (B ring) carbon skeleton structure (Winkel-Shirley 2001; Zhang et al. 2020; Liang et al. 2008). Due to methylation and hydroxylation substitution reactions at the R1 and R2 positions of the B ring, various anthocyanin types such as pelargonidin (Pg), cyanidin (Cy), peonidin (Pn), delphinidin (Del), malvidin (Mv) and petunidin (Pt) are formed (Figure 4). Anthocyanins types are varied in different fruits, for example, apple is dominated by cyanidin 3-galactoside, while grapes mainly contain cyanidin-3-O-glucoside and malvidin-3-O-glucoside (Supplemental Table 1).

The biosynthetic and metabolic pathway of anthocyanins is a complex and finely regulated process, which has been relatively well studied so far (Figure 2). The anthocyanin synthesis pathway can be divided into three stages: (1) Precursor synthesis stage (Phenylpropanoid pathway). This stage starts from the aromatic amino acid phenylalanine and produces flavanone-type precursor substances. (2) Flavonoid backbone biosynthesis stage. This is a core step in forming the flavonoid skeleton and also a branching point that distinguishes different classes of compounds such as

flavanones, flavanols, and anthocyanins. (3) Modification and sequestration stage. Anthocyanins are inherently unstable and are often transported to vacuoles for stable storage after undergoing glycosylation, acylation, and methylation modifications.

Anthocyanin metabolism is subject to complex multi-level regulation, encompassing multiple aspects such as transcriptional levels (Amato et al. 2019), post-transcriptional modifications, hormone signals, and environmental factors (LaFountain and Yuan 2021). Among them, the MYB-bHLH-WD40 (MBW) complex (Hu et al. 2016) serves as the most important core of transcriptional regulation. Meanwhile, plant hormones such as ethylene (Ni et al. 2023), abscisic acid (ABA) (Lama et al. 2020), auxins (Wang, Han, et al. 2020) and jasmonic acid (JA) (An et al. 2021), as well as environmental signals like temperature (Ryu et al. 2020) and light (Alabd et al. 2022), also play key roles in regulating anthocyanin synthesis.

Carotenoids: Composed of isoprene skeleton, carotenoids belonging to lipid-soluble pigments are most located in the plastids. Typically, over 1200 types of natural carotenoids establish them as the second most plentiful natural pigments on the earth (<http://carotenoiddb.jp/>) (Nisar et al. 2015; Sun et al. 2022). They can be grouped into two based on their chemical structure with or without oxygen: carotenes (e.g. α -carotene, β -carotene, lycopene) and xanthophylls (like lutein, zeaxanthin). Carotenoids' color and photoprotective ability depend on the number of conjugated double bonds. Carotenoids are abundantly accumulated in fruits such as citrus and mango. Among them, lycopene, possessing functions like antioxidation, cardiovascular protection and even cancer prevention, is ubiquitously existent in tomatoes, watermelon, guava, papaya, grapefruit (Story et al. 2010). They also act as precursors for plant hormones like ABA and strigolactone, participating in their synthesis and metabolism (Alder et al. 2012).

The metabolism of carotenoids is a dynamic balance process of “synthesis-

degradation”, which is precisely regulated by a series of enzymes and genes. The metabolic bias (synthetic accumulation or degradative transformation) of different fruits determines the final composition of carotenoids. Carotenoid synthesis initiates via either the mevalonic acid (MVA) pathway in the cytoplasm or the methylerythritol phosphate (MEP) pathway in plastids, with the core steps completed in plastids (Figure 3). It can be divided into three stages: (1) Precursor synthesis stage. Centered on the MEP pathway, including 1-deoxy-D-xylulose-5-phosphate synthase (DXPS), geranylgeranyl pyrophosphate synthase (GGPS); (2) Carotenoid backbone synthesis stage. phytoene synthase (PSY), phytoene desaturase (PDS), ζ -carotene desaturase (ZDS); (3) Cyclization and modification stage. β -cyclization branch (β -cyclase, LCYB, hydroxylase, HYDB) and α -cyclization branch (LCYB and α -cyclase, LCYE) (Figure 2). The degradation of carotenoids mainly occurs through oxidative cleavage and is divided into specific and non-specific degradation. Carotenoids could be catalyzed by carotenoid cleavage dioxygenases (CCDs) and 9-cis-epoxycarotenoid dioxygenases (NCEDs) to generate physiologically active products, such as aroma substances (such as β -ionone) and xanthoxin (a precursor for ABA synthesis), respectively (Figure 3). Carotenoids also be catalyzed by non-specific enzymes such as lipoxygenase (LOX) and occurs during fruit senescence or under stress conditions.

Carotenoid biosynthesis is regulated at multiple levels. Transcription factors such as MYB (Wu et al. 2020), bHLH, and AP2/ERF can modulate the expression of key biosynthetic genes by binding to their promoter regions. Plant hormones, particularly ethylene and abscisic acid (ABA), influence the expression of carotenoid-related genes during fruit ripening through signal transduction pathways. In addition, environmental factors such as light and temperature affect carotenoid accumulation by modulating regulatory signaling networks.

Betalains: Unlike carotenoids and anthocyanin, the biosynthesis of betalains has not

been fully elucidated (Polturak et al. 2018; Chen, Xie, et al. 2021; Gandía-Herrero and García-Carmona 2013). Betalains accumulate in vacuoles and are classified into two types: betacyanin (red-purple) and betaxanthins (yellow-orange), both of which are abundant in pitaya (Hatlestad et al., 2012; Hatlestad et al., 2015). Recent studies have identified transcription factors such as WRKY, MYB, and ERF as key regulators of betalains biosynthesis (Hatlestad et al., 2015; Cheng et al., 2017). Notably, betalains and anthocyanins exhibit mutual exclusivity across plant species, with no known example of their co-occurrence in the same organism (Figure 3) (Maeda and Dudareva, 2012). This exclusive distribution is hypothesized to arise from evolutionary divergence or potential metabolic redundancy, where the simultaneous presence of both pigment pathways may be unnecessary or even detrimental to the plant's physiological efficiency.

Aroma metabolism: Volatile compound synthesis and regulation

Currently, over 2000 aromatic compounds have been detected in fruits (Sánchez-Rodríguez et al. 2019; El Hadi et al. 2013; Hui et al. 2010; Liu, He, and Song 2018). Comprising esters, alcohols, aldehydes, ketones, terpenoids, etc., volatile organic compounds (VOCs) act as a self-protection mechanism of plants against diseases, pests and herbivores, also contribute to their unique aroma characteristics (Supplemental Table 1, Figure 1) (García-Gómez et al. 2020; Xia et al. 2020; Zhang, Wu, et al. 2024; Li et al. 2021; Mayuoni-Kirshinbaum and Porat 2014). Apples are dominated by esters and alcohols such as ethyl butyrate and hexanol, emitting a fresh, sweet fruity aroma (Yang et al. 2021; Espino-Díaz et al. 2016). Strawberries contain esters and aromatics like methyl acetate and phenylethanol, which produce a rich, sweet fragrance, while grapes feature terpenes and alcohols including geraniol and linalool, presenting floral and fruity notes (Schwab, Davidovich - Rikanati, and Lewinsohn 2008). Mangoes contain aldehydes and terpenes such as hexanal and myrcene, exhibiting a tropical

fruity scent (Li et al. 2017). Citrus fruits are characterized by monoterpenes like limonene and terpinene, releasing a typical citrus aroma (Zhang et al. 2017; Nguyen et al. 2009). These differences not only determine the unique flavor characteristics of fruits but also provide a basis for aroma fingerprint information in breeding (Xiao et al. 2021).

The synthesis of fruit VOCs involves multiple metabolic pathways and enzyme-catalyzed reactions. Straight-chain aldehydes, alcohols, and esters (especially in apples and bananas) are primarily synthesized via the lipoxygenase (LOX) pathway; branched-chain ones, via the amino acid and β -oxidation pathways, with key enzymes like alcohol acyltransferases and alcohol dehydrogenases (Zhang, Ma, et al. 2024; Abbas et al. 2023; Besada et al. 2017; Obando-Ulloa et al. 2008; Eduardo et al. 2010; Chen et al. 2018). Terpenoids are synthesized through the MEP and MVA pathways, while polyphenols and phenylpropanoids come from the shikimic acid/phenylpropanoid pathway (Lin, Massonnet, and Cantu 2019; Liu, Zhao, and Li 2022). TPS h/d/a/b/g enzyme families are primarily responsible for the biosynthesis of terpenoid compounds in plants (Jia et al. 2022). In addition, carotenoids can be converted into β -ionone, pseudoionone, and geranylacetone by carotenoid cleavage dioxygenases (CCDs) (Figure 3). Phenylethanol and benzaldehyde are derived from phenylalanine through the phenylpropanoid pathway, where phenylalanine ammonia-lyase (PAL) is a crucial enzyme. During early fruit development, LOX pathway-dominated C6 aldehydes/alcohols serve as defensive VOCs; at the expansion stage, enhanced MEP pathways drive light-protective monoterpene accumulation; while maturation triggers explosive synthesis of ester/lactone compounds via AAT gene activation to facilitate seed dispersal attraction (George et al. 2023; Liu et al. 2023).

The accumulation of volatile organic compounds (VOCs) in fruits is a highly spatiotemporally specific biological process. It is not only constrained by the availability of precursor substances and the expression of metabolic enzymes, but also

finely regulated by complex regulatory networks, including TFs regulate, hormone signaling (e.g. ethylene) (Tobaruela et al. 2021), and environmental (e.g. temperature and light) response mechanisms (Yan et al. 2018). Among these TFs, the AP2/ERF family is particularly important in the biosynthesis of fatty acid derivatives and terpenoids (Feng et al. 2020), while MYB family are broadly involved in the regulation of phenylpropanoids and aromatic compounds and the bHLH and WRKY families often act as co-regulators with MYB or ERF transcription factors (Lu et al. 2021).

Metabolic crosstalk and coordinated regulation of fruit sensory traits

The tetrad of fruit sensory traits-sugars, acids, aroma, and color-interact via a coordinated metabolic network (Zhang et al. 2023). This regulation is not only reflected in the resource allocation for substance synthesis but also achieves precise coordination through signal transduction, substrate competition, and transcriptional regulation, providing a systematically targeted breeding approach for fruit quality improvement.

Sugars act as the central hub directing carbon flux and signaling. As the end products of photosynthesis, sugars not only serve as the basis for energy and substance synthesis in fruits but also act as core signaling molecules that regulate other sensory traits. For example, the accumulation of sucrose in apple fruits inhibits the activity of phosphoenolpyruvate carboxylase (PEPC) (Wei et al. 2021). Sucrose and sorbitol function as molecular triggers that activate anthocyanin biosynthesis in peach flesh, whereas fructose appears to attenuate pigmentation intensity by inducing transcriptional repressors (Wang, Cao, et al. 2022).

Organic acids (e.g., citric acid, malic acid) bridge sugars, pigments and aroma by regulating intracellular microenvironments (e.g., vacuolar pH) and substrate availability. For example, anthocyanin stability depends highly on pH: they stay as stable red cyanidin under acidic conditions ($\text{pH} < 5$); but when pH rises (e.g., vacuolar

pH exceeds 6 due to malic acid degradation), they easily isomerize into colorless or brown forms. In citrus, citric acid maintains vacuolar acidity (pH 3.5 - 4.5) to stabilize carotenoids (e.g., β -cryptoxanthin) — reduced citric acid from metabolic imbalance causes carotenoid oxidation and faded color. Additionally, acidic conditions activate ester-synthesizing enzymes (e.g., AAT), promoting alcohol-to-ester conversion (e.g., hexanol to ethyl hexanoate); neutral/alkaline conditions inhibit this, shifting aroma from "fruity" to "grass-like".

The synthesis of VOCs and color (pigments) is often coordinated through shared transcriptional regulators and signaling pathways, with the MYB-bHLH-WD40 (MBW) complex and ethylene signaling as core regulatory nodes. Multi-target regulation by the MBW complex is key to this coordination. In strawberry fruits, the complex formed by *FaMYB10* and *FabHLH3* not only activates anthocyanin synthesis genes (e.g., *FaANS*) but also upregulates ester synthesis genes (e.g., *FaAAT1*), enabling the simultaneous accumulation of anthocyanins (red) and methyl acetate (sweet aroma) during ripening. As a ripening signal, ethylene coordinates aroma and color metabolism through the ROS (reactive oxygen species) signaling network. In apples, ethylene treatment upregulates the expression of LOX and DFR (anthocyanin synthase), enabling the fruit to accumulate ethyl hexanoate while synthesizing cyanidin (red). This ethylene-ROS mediated coordination explains why "fully ripe" fruits often have both rich aroma and vivid color.

The metabolic crosstalk network of fruit sensory traits provides a "multi-target synergy" improvement strategy for precision breeding, avoiding quality imbalance caused by single trait improvement. In the future, combining multi-omics data to construct a "sugar-acid-aroma-color" interaction network model, supplemented by machine learning or artificial intelligence (AI) to predict key regulatory nodes, will enable the "customized" design of fruit sensory traits. For example, apple varieties with "high sugar and low acid-strong fruity aroma-bright red color" or citrus varieties with "low

sugar and high acid-fresh floral aroma-orange color" can be directionally cultivated to meet diverse consumer demands.

The genomic design of fruit sensory traits

Plant precision breeding refers to a breeding strategy that utilizes modern biotechnological means to precisely identify, manipulate, and aggregate the genetic basis of target traits, thereby achieving directional improvement of crop traits (Figure 4) (Mascher et al. 2024). The rapid development of precision breeding stems from three major social needs: food security pressure, climate change challenges, and the demand for consumption upgrading. The progress in core technologies of precision breeding is reflected in gene editing technologies (including the optimization and innovation of the CRISPR-Cas system, epigenetic editing, and the optimization of delivery systems) (Mou et al. 2024), high-throughput genomics and molecular design (including pan-genome research and artificial intelligence-assisted design), and applications of synthetic biology (including artificial chromosomes and metabolic pathway reconstruction) (Li et al. 2024). However, these technologies have gradually been applied in crops such as rice (Wang et al. 2017) and wheat (Lin et al. 2020), while research in the field of fruit quality breeding remains relatively limited (Ma, Ma, and Zhou 2023).

uORFs fine regulation: As key regulatory sequences in the 5' untranslated region of mRNA, uORFs can precisely regulate the expression of downstream main genes by fine-tuning their translation efficiency through means such as base editing. For example, the conserved uORF of the strawberry *FvebZIPs1.1* gene was edited using the plant-efficient cytosine base editor (A3A-PBE), yielding 7 new uORF mutations in the T0 generation, with homozygous mutants significantly increasing fruit sugar content without affecting plant growth, which proves that precise editing of uORFs can finely regulate quantitative traits in fruit trees and that new genotypes and traits can be stably

transmitted through asexual reproduction (Xing et al. 2020). This technology has opened up a new path for quality improvement in strawberries and other asexually propagated fruit trees, and is expected to cultivate varieties with different sweetness levels to meet diverse market demands.

Research demonstrates that targeted knockout of the *SICDPK27* and *SICDPK26* genes in tomatoes enhances fruit sweetness while maintaining optimal weight and yield (Zhang, Lyu, et al. 2024). This breakthrough provides critical insights into the genetic regulation and molecular pathways governing sugar accumulation in tomato fruits. Using a red-fruited tomato as the material, a strategy employing multiplex gene editing technology has been developed to rapidly and precisely create seven distinct tomato varieties with different fruit colors (Yang, Ali, et al. 2023). This approach has been shown to have no significant impact on key agronomic traits, including single fruit weight, yield per plant, soluble solid content, and vitamin C concentration (Yang, Ali, et al. 2023). The research has successfully edited the *VvDXSI* gene in grapes through the CRISPR-Cas9 technology, significantly increasing the content of monoterpenoids and creating a muscat flavor in non-muscat grape varieties (Yang et al. 2024).

The regulatory strategy that precisely extends genetic modification to upstream elements has begun to take shape in fruit quality breeding. While relevant research cases remain relatively limited, it has already offered new insights and approaches for fruit quality improvement. Going forward, as research advances and technologies continue to innovate, more breakthroughs are anticipated in this field, which will inject new momentum into the development of the fruit industry.

Challenges and prospects

Although these precision breeding technologies are being increasingly applied in crop stress resistance and quality breeding, they still face numerous challenges. On one hand,

the fruit sensory traits are jointly regulated by multiple genes and environmental factors, making it highly challenging to decipher their complex genetic networks. It is necessary to further strengthen interdisciplinary research to deeply explore key genes and regulatory elements. On the other hand, despite continuous optimization of gene-editing technologies, off-target effects remain difficult to completely eliminate. Developing more precise and efficient gene-editing tools and off-target detection technologies is crucial to ensuring the safety of precision breeding.

With the continuous development of technologies such as metabolome detection and genome sequencing, the coverage and identification accuracy of metabolites will be further improved, providing data support for the joint analysis of traits and genes. In addition, the continuous development of new gene-editing technologies and tools, as well as the deepening integration of multi-omics, artificial intelligence and precision breeding, will also enable the precise design and regulation of fruit sensory traits or other complex plant traits.

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Author contributions

Y.F.Z. conceived and designed the manuscript. H.X wrote the manuscript. Z.J.L, W.W. L. and C.C.L. revised the manuscript with contributions from Y.L.P and X.W.Y. All of the authors read and approved the final manuscript.

502

503 Figure 1 Research on world fruit production, genome, and metabolome development.
 504 (A) The fruit production and harvest area in the world. (B) The genome and genome
 505 update of various fruit. (C) The metabolite evolution during domestication.

506 Figure 2 Major pathways of the primary and secondary metabolites in fruits. The
 507 pathways are constructed based on the KEGG pathways and literature references.

508 Abbreviations: 4CL, 4-coumarate-CoA ligase, 5GT, UDP-glucose flavonoid 5-O-
 509 glucosyltransferases, AACT, Acetoacetyl-CoA thiolase, AAT, alcohol acyltransferase,
 510 ADH, alcohol dehydrogenase, ANS, anthocyanidin synthase, C4H, cinnamate 4-
 511 hydroxylase, DODA, 4,5-levodopa-extradiol-dioxygenase, CHI, chalcone isomerase,
 512 CHS, chalcone synthase, CHYB2, β -carotene hydroxylase2, CMK, 4-(Cytidine 5'-
 513 diphospho)-2-C-methyl-D-erythritol kinase, CMS, 4-Diphosphocytidyl-2-C-methyl-
 514 D-erythritol synthase, CoA, coenzyme, ACS, citrate synthase, CRTISO, carotene cis-
 515 trans isomerase, CYP76AD, Cytochrome P450, CYP97, carotene epsilon-
 516 monooxygenase, DFR, dihydroflavonol-4-reductase, DXR, 1-deoxy-D-xylulose-5-
 517 phosphate reductoisomerase, DXS, 1-deoxy-D-xylulose-5-phosphate synthase, F3'5'H,
 518 flavanone 3',5'-hydroxylase, F3H, flavanone 3-hydroxylase, F3'H, flavanone-3'-
 519 hydroxylase, GA3P, glyceraldehyde 3-phosphate, GGPP, geranylgeranyl diphosphate,
 520 HMGR, 3-hydroxy-3-methylglutaryl-CoA reductase, HMGS, 3-hydroxy-3-
 521 methylglutaryl-CoA synthase, IV, invertase, LCYB, lycopene β -cyclase, LCYE,
 522 lycopene ϵ -cyclase, LDOX, leucoanthocyanidin dioxygenase, MDH, malate
 523 dehydrogenase, MEP, 2-methyl-D-erythritol-4-phosphate, MST, monosaccharide
 524 transporters, MVA, mevalonate pathway, NCED5, 9-cis-epoxycarotenoid
 525 dioxygenase5, OMT, O-methyl transferases, PAL, phenylalanine ammonia-lyase, PDS,
 526 phytoene desaturase, PEPC, phosphoenolpyruvate carboxylase, PSY, phytoene
 527 synthase, SPS, sucrose phosphate synthase, SS, sucrose synthase, SUT, sucrose
 528 transporter, SWEET, sugars will eventually be exported transporter, TPS, terpene

synthases, TST, tonoplast sugar transporters, UFGT, UDP-glucose flavonoid 3-O-glucosyltransferase, ZDS, ζ -carotene desaturase, ZEP, zeaxanthin epoxidase, Z-ISO, ζ -carotene isomerase.

Figure 3 The relationship between sugar, acid, pigments, and aroma components in fruits. CCD, carotenoid cleavage dioxygenase.

Figure 4 The genomic design of fruit sensory traits: from metabolites biosynthesis to precision breeding.

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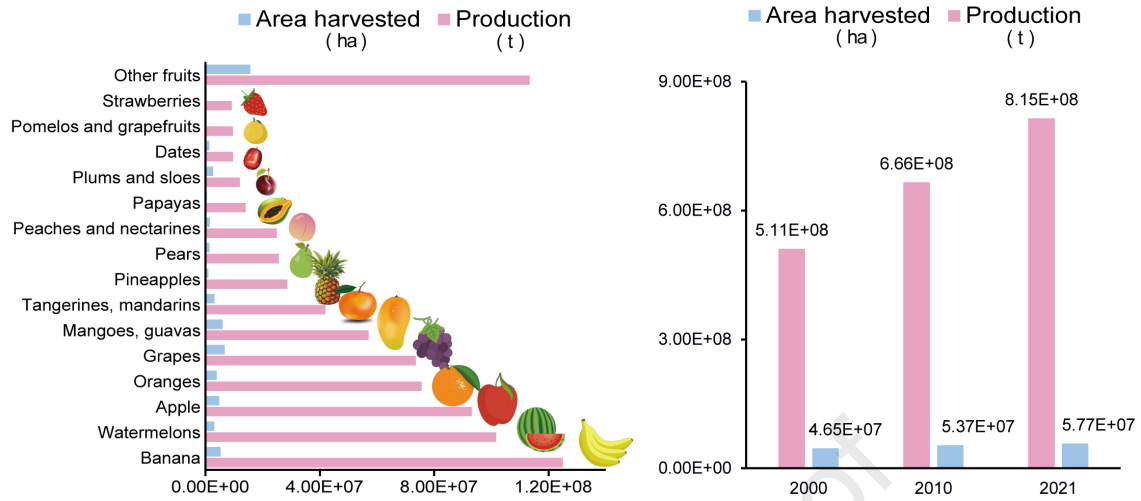
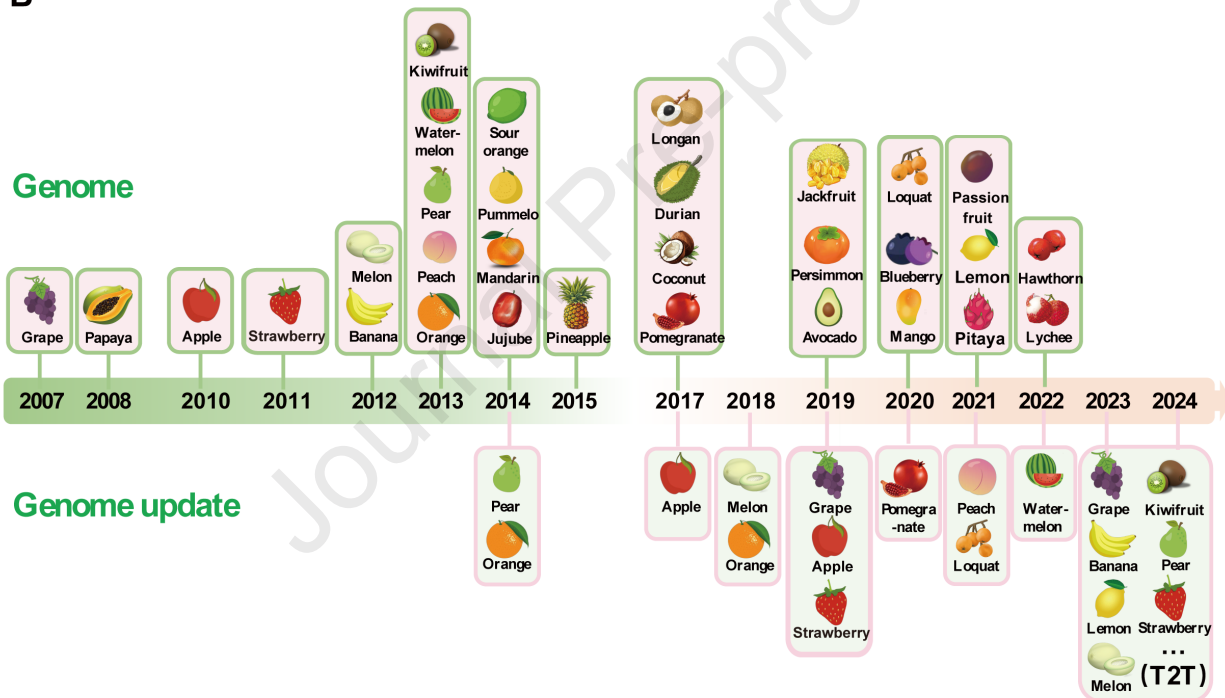
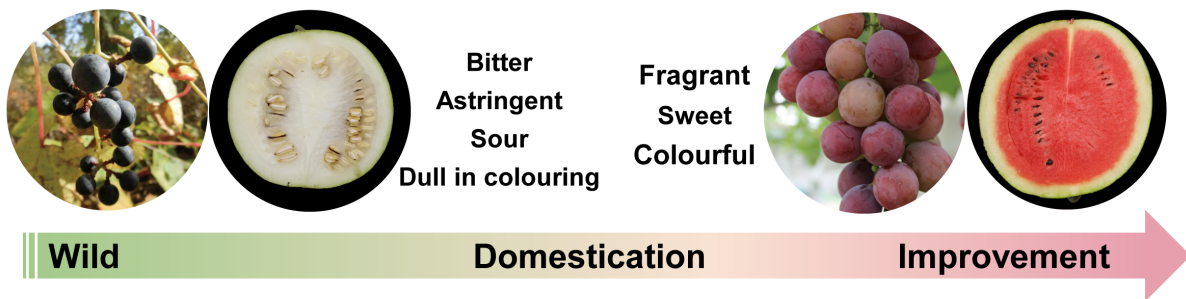
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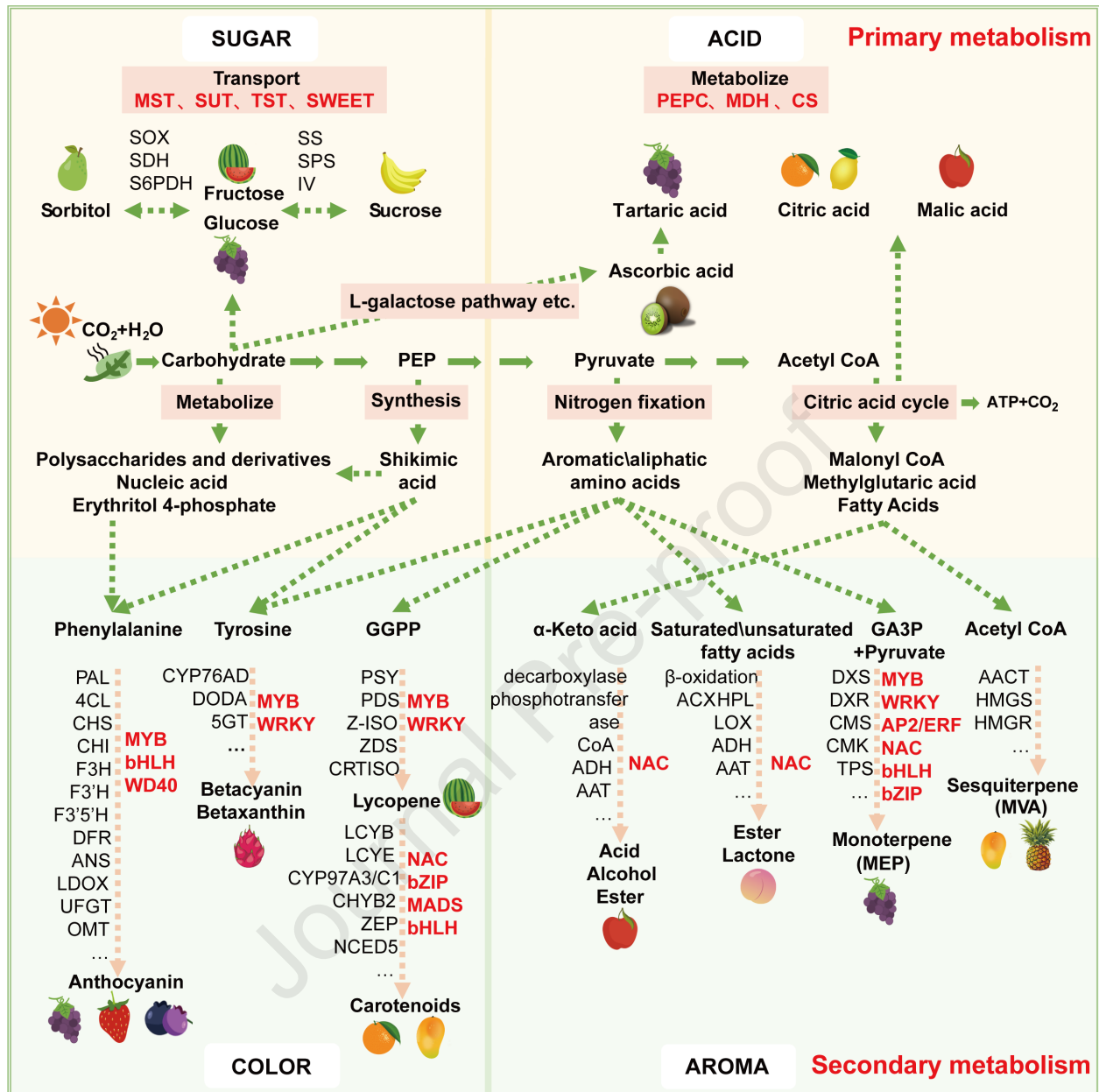
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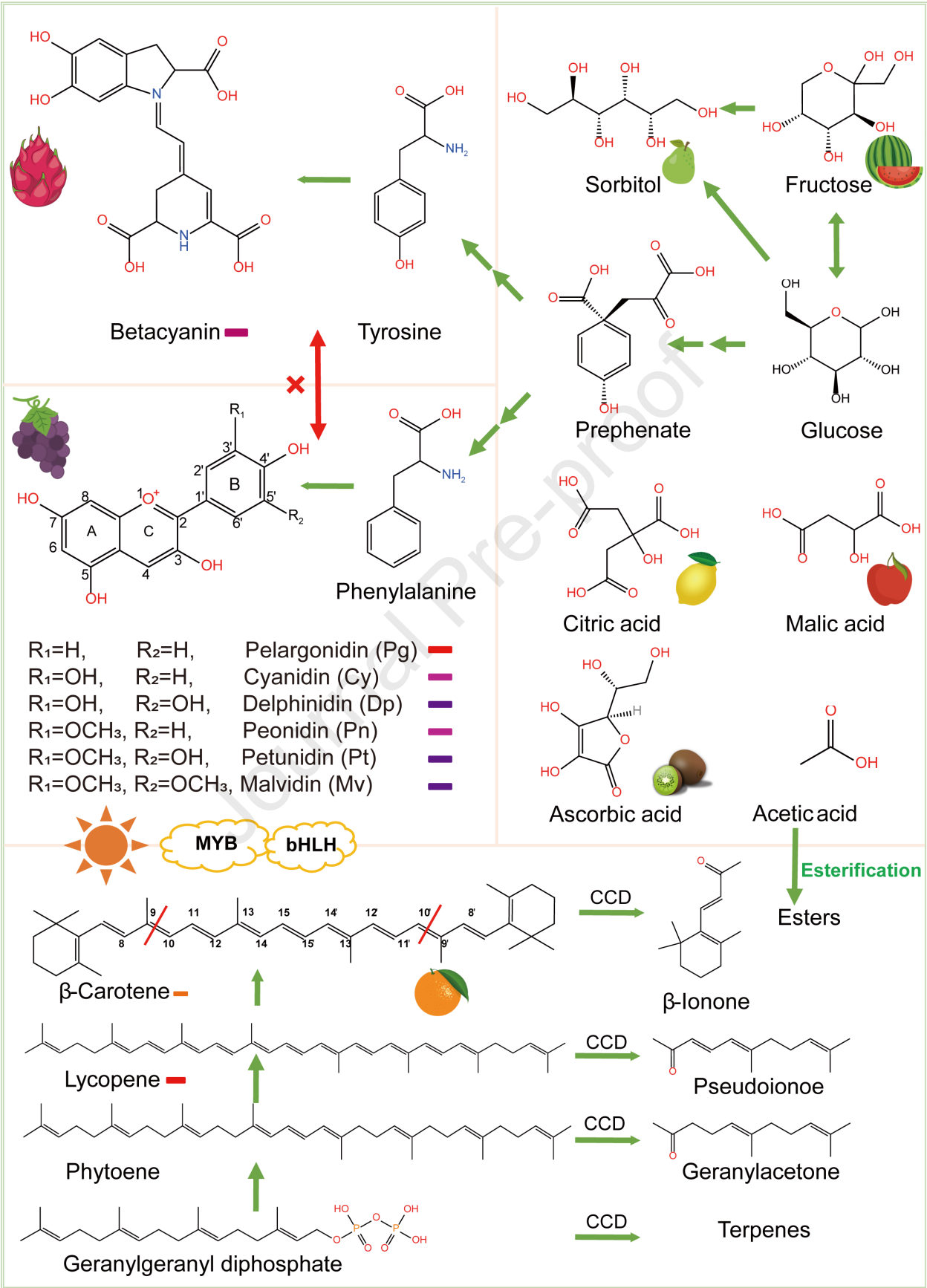
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