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Review

An Update on the Function, Biosynthesis and Regulation of Floral Volatile Terpenoids

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Abstract: Floral volatile terpenoids (FVTs) belong to a group of volatile organic compounds (VOC) that play important roles in attracting pollinators, defending against pathogens and parasites and serving as signals associated with biotic and abiotic stress responses. Although research on FVTs has been increasing, a systematic generalization is lacking. Among flowering plants used mainly for ornamental purposes, a systematic study on the production of FVTs in flowers with characteristic aromas is still limited. This paper reviews the biological functions and biosynthesis of FVTs, which may contribute a foundational aspect for future research. We highlight regulatory mechanisms that control the production of FVTs in ornamental flowers and the intersection of biosynthetic pathways that produce flower fragrance and color. Additionally, we summarize the opportunities and challenges facing FVT research in the whole genome and -omics eras and the possible research directions that will provide a foundation for further innovation and utilization of flowering ornamental plants and their germplasm resources.

Keywords: floral volatile terpenoids; function; biosynthesis; regulation

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1. Introduction

Plant volatile compounds (VOCs) biosynthesis occurs in almost all plant organs, including the roots, stems, leaves, flowers, fruits and seeds. They are widely used in perfumes, cosmetics and medicines, and seem promising for use in therapeutic gardens because some possess anxiolytic properties [1,2]. VOCs are lipophilic liquids with low molecular weights and high vapor pressures at ambient temperatures. They include terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives and amino acid derivatives, in addition to a few species- and genus-specific compounds not represented in these major classes. Floral volatile terpenoids (FVTs) are the most dominant VOCs, followed by particular phenylpropanoids/benzenoids [3,4].

The main FVTs—released into the air because of their high vapor pressures—are the hemiterpenes (C5), monoterpenes (C10), sesquiterpenes (C15) and a few diterpenes (C20) [5–7]. In addition, irregular volatile terpenoids with carbon skeletons ranging from C8 to C18 are derived from carotenoids. The homoterpenes that are often emitted from night-scented flowers and aerial tissues upon herbivore attack form a small part of the FVTs [3]. Among these FVTs, monoterpenes, such as limonene, ocimene, myrcene and linalool, and sesquiterpenes, such as farnesene, nerolidol and caryophyllene, are the most ubiquitous volatiles (Table 1) [4,8]. The FVTs identified so far in flowering plants are detailed in Table 1.

The mechanism of FVT production is complex, influenced by many environmental factors and associated with vital biological functions. Here, we focus on the biological functions of FVTs and the environmental factors, biosynthesis, transcriptional regulation

and modification of terpene skeletons that affects FVTs. We also discuss some possible applications of FVT research.

2. Biological Functions of FVTs

An important property of flowering plants is their scent, which plays a vital role in ecology, the economy and aesthetics. To date, numerous FVTs have been studied in flowering woody plants and herbs (Table 1). Most of these are ornamental plants that are very close to people's lives. Biologically, FVTs are involved in the attraction of pollinators [9], defense against herbivores [10], protection against pathogens and response to abiotic stress [11]. When it comes to human products, FVTs influence the taste and quality of foods and beverages [12,13]. They also contribute to the aromas of flowers and, consequently, to their ornamental value [14]. FVTs serve as major components of essential oils and are, therefore, key to the development of industries that utilize these natural products [15].

Table 1. Major FVTs and genes associated with their biosynthesis in flowering plants.

Latin Name	Family	Main FVT Compounds	Genes	Ref.
Actinidia deliciosa 'Hayward'	Actinidiaceae	(*E*,*E*)-α-farnesene, (*E*)-β-ocimene, (+)-germacrene D		[16]
Albizia julibrissin	Leguminosae	α-farnesene, (*Z*, *E*)-β-farnesene	*AjTPS2*, *AjTPS5*, *AjTPS7*, *AjTPS9*, *AjTPS10*	[17]
Camellia spp.	Theaceae	linalool and its oxides, geraniol, α-farnesene, hedycaryol	*CbTPS1*, *ChTPS1*, *CbTPS18*, *CbTPS25*, *CbTPS28*, *CbTPS33*, *CbTPS35 CsTPS29*, *CbTPS47*, *CbTPS48*, *CbTPS51*, *CbTPS52*	[18–20]
Cananga odorata var. fruticosa	Annonaceae	linalool	*CoTPS1*, *CoTPS2*, *CoTPS3*, *CoTPS4*	[21]
Chimonanthus praecox L.	Calycanthaceae	linalool, trans-β-ocimene, β-caryophyllene	*CpTPS1*, *CpTPS9*, *CpTPS10*, *CpTPS14*, *CpTPS16*, *CpTPS4*, *CpTPS9*, *CpTPS42*	[22–25]
Datura wrightii	Solanaceae	linalool and its enantiomers		[26]
Eurya japonica Thunb	Theaceae	α-pinene, linalool		[27]
Gardenia jasminoides	Rubiaceae	farnesene, *Z*-3-hexenyl tiglate, indole		[28]
Gelsemium sempervirens (L.) J. St.-Hil.	Gelsemiaceae	(*Z*)-α-ocimene, α-farnesene		[29]
Gossypium hirsutum	Malvaceae	(*3S*)-linalool	*GhTPS12*	[30,31]
Jasminum spp.	Oleaceae	α-farnesene, linalool, β-ocimene, germacrene-D		[32–36]
Laurus nobilis	Lauraceae	sesquiterpenes, γ-cadinene, δ-cadinene		[37]
Lonicera japonica	Caprifoliaceae	linalool		[38]
Magnolia champaca	Magnoliaceae	(*R*)-linalool, linalool and its oxides		[39]
Malus domestica	Rosaceae	(*E*)-linalool oxide		[40]
Murraya paniculata	Rutaceae	*E*-β-ocimene, linalool, α-cubebene		[41,42]
Myrtus communis L.	Myrtaceae	α-pinene, linalool, 1,8-cineole		[43]
Osmanthus fragrans	Oleaceae	linalool and its derivatives, α-ionone, β-ionone	*OfTPS1*, *OfTPS2*, *OfTPS3*	[44–47]
Paeonia spp.	Paeoniaceae	β-caryophyllene, linalool		[48,49]
Psidium guajava	Myrtaceae	α-cadinol, β-caryophyllene, nerolidol		[50]
Rosa spp.	Rosaceae	geraniol, linalool, nerolidol, myrcene, ocimene, citronellol	*NEROLIDOL SYNTHASE (NES)*, *RcLIN-NERS1*, *RcLIN-NERS2*	[51–56]

Table 1. *Cont.*

Latin Name	Family	Main FVT Compounds	Genes	Ref.
Styrax japonicas spp.	Styracaceae	linalool, α-pincnc, gcrmacrcnc D		[57]
Syringa oblata Lindl.	Oleaceae	*D*-limonene		[58,59]
Penstemon digitalis	Plantaginaceae	linalool and its enantiomers, *cis*-and *trans*-β-ocimene		[60–62]
Alstroemeria spp.	Alstroemeriaceae	(*E*)-caryophyllene, α-caryophyllene		[63]
Anthurium 'Mystral'	Araceae	eucalyptol, β/α-pinene, β-phellandrene, β-Myrcene		[64]
Antirhinum majus	Plantaginaceae	nerolidol, linalool, (*E*)-β-ocimene, myrcene		[65,66]
Arabidopsis thaliana	Brassicaceae	α-copaene, α-caryophyllene, β-elemene	*AtTPS21*, *AtTPS11*, and other 40 terpenoid synthase genes	[11,67–70]
Aristolochia gigantea	Aristolochiaceae	linalool, (*Z*,*E*)-α-farnesene, geraniol		[71]
Caladenia plicata	Orchidaceae	β-citronellol		[72]
Cannabis sativa	Cannabaceae	(+)-α-pinene, (−)-limonene, β-caryophyllene		[73]
Chrysanthemum indicum	Asteraceae	1,8-cineole, germacrene D, camphor		[74,75]
Citrus L.	Rutaceae	linalool, β-myrcene, α-myrcene, limonene		[76]
Clarkia breweri	Onagraceae	*S*-linalool, Linalool, linalool oxide	*linalool synthase (LIS)* gene	[77,78]
Clematis florida cv. 'Kaiser'	Ranunculaceae	linalool, linalool oxide, nerolidol	*CfTPS1*, *CfTPS2*, *CfTPS3*	[79]
Cymbidium spp.	Orchidaceae	(*E*)-β-farrnesene, nerolidol, linalool	*CgTPS7*	[80,81]
Dendrobium officinale	Orchidaceae	α-thujene, linalool, α-terpineol	*DoTPS10*	[82–84]
Dianthus caryophyllus L.	Caryophyllaceae	caryophyllene, caryophyllene oxide, linalool		[85–87]
Freesia hybrida. "Shiny Gold"	Iridaceae	linalool, β-ocimene, D-limonene	*FhTPS1*, *FhTPS2*, *FhTPS3*, *FhTPS4*, *FhTPS5*, *FhTPS6*, *FhTPS7*, *FhTPS8*	[88–90]
Gymnadenia conopsea (L.) R. Br.	Orchidaceae	β-myrcene, α-terpineol, (+)-cyclosativene, α-santalene, trans-α-bergamotene, (*Z*,*E*)-α-farnesene, (*E*,*E*)-α-farnesene		[91]
Hedychium coronarium	Zingiberaceae	β-ocimene, 1,8-cineole, linalool	*HcTPS1*, *HcTPS3*, *HcTPS5*, *HcTPS6*, *HcTPS7*, *HcTPS8*, *HcTPS10*, *HcTPS11*, *HcTPS21*	[92–96]
Hippeastrum spp.	Amaryllidaceae	eucalyptol, (*Z*)-β-ocimene		[97]
Lathyrus odoratus	Leguminosae	α-bergamotene, linalool, (−)-α-cubebene		[98]
Lavandula spp.	Lamiaceae	linalool acetate, linalool, lavandulyl acetate, α/β-Pinene	*LaLIMS*, *LaLINS*	[98–102]
Lilium spp.	Liliaceae	linalool, myrcene, (*E*)-β-ocimene, α-pinene, limonene	*LoTPS1*, *LoTPS2*, *LoTPS3*, *LoTPS4*	[103–105]
Maxillaria tenuifolia	Orchidaceae	β-caryophyllene, α-copaene, delta-decalacton		[106]
Mentha citrata	Lamiaceae	linalool and its enantiomers		[107]
Mimulus spp.	Phrymaceae	(*E*)-β-ocimene, d-limonene, β-myrcene	*OCIMENE SYNTHASE (OS)* gene	[108–110]
Narcissus spp.	Amaryllidaceae	myrcene, eucalyptol, linalool		[111,112]
Nicotiana spp.	Solanaceae	(*E*)-α-bergamotene, (*E*)-β-ocimene, 1,8-cineole	*NaTPS25*, *NaTPS38*	[113–117]

Table 1. *Cont.*

Latin Name	Family	Main FVT Compounds	Genes	Ref.
Nymphaea subg. Hydrocallis	Nymphaeaceae	linalool, farnesene, nerolidol		[118]
Ocimum basilicum L.	Lamiaceae	linalool		[119]
Petunia hybrida	Solanaceae	germacrene D, β-cadinene	*PhTPS1, PhTPS2, PhTPS3, PhTPS4*	[120]
Passiflora edulis Sims	Passifloraceae	linalool	*PeTPS2, PeTPS3, PeTPS4, PeTPS24*	[14]
Phalaenopsis spp.	Orchidaceae	α-pinene, trans-β-ocimene, linalool, geraniol and their derivatives	*PbTPS5, PbTPS7, PbTPS9, PbTPS10, PbTPS3, PbTPS4*	[121–123]
Plectranthus amboinicus (Lour.) Spreng	Lamiaceae	linalool, nerolidol		[124]
Polianthes tuberosa L.	Amaryllidaceae	germacrene D, 1, 8- cineole, α-terpineol		[125–128]
Rheum nobile	Polygonaceae	α-pinene		[129]
Salvia officinalis	Labiatae	myrcene, (+)-neomenthol, 1,8-cineole		[130]
Tanacetum vulgare	Asteraceae	α-pinene, 3-hexen-1-ol-acetate		[131]

2.1. Attraction of Pollinators

The most important biological function for FVTs is the attraction of pollinators to enhance propagation. Flower morphology, including flower structure, color, size and the arrangement of floral organs, is important for attracting pollinators. Flowers that produce FVTs are commonly pollinated by bees and moths [4]. Linalool and its enantiomers are reported as being attractive to pollinators including the *Megalopta* bee [132], bumblebees [60], honeybees [39] and hawkmoths, as well as moths and/or hornworms [25] such as the *C. praecox* L., *D. wrightii*, *M. champaca*, *P. digitalis* and *M. citrata* flowers (Table 1). Flowers that produce *E*-β-ocimene have been reported to be especially attractive to honeybees and bumblebees [107,133].

On the other hand, many flowers produce FVTs that repel herbivores or attract the enemies of herbivores [4], because plants will expose their most vulnerable tissues to insects and pathogens during pollination. Indeed, pollinators often become florivores during particular stages of their life cycles [134]. For example, (*E*)-β-caryophyllene was reported to increase floral resistance [11]; meanwhile, linalool, (*E*)-β-farnesene, (*E*)-α-bergamotene and particular homoterpenes or terpene derivatives help to protect plants from microbial pathogens by recruiting the enemies of pollinators and pests [6,61,112,135–137].

2.2. Enhancement of Plant Resistance

Scientists infer that plants would not need to produce terpenes to protect their tissues if fungi and pathogens did not exist. Indeed, FVT emission dramatically decreased after flowers were fumigated with a combination of antibiotics. One week after the fumigation, some flowers still did not emit particular FVTs [138]. The amount of the FVT emission reduction depended on the concentration of antibiotics [139]. Meanwhile, microflora affects FVTs [140]. VOCs (including FVTs) can be used as carbon sources by bacteria in some plants and thus, bacteria can reduce the emission rate of FVTs, which may lead to differences in floral aroma [141].

In addition, particular FVTs play key roles in the synergistic and antagonistic interactions among organisms and the environment [142]. For example, (*E*, *E*)-α-farnesene, enantiomers of β-ocimene and linalool are reported to influence multiple interactions between plants and other organisms during biological and abiotic trauma [103,104,133,143]. Germacrene D, bicyclogermacrene and germacrene D-4-ol have been reported to possibly mediate communications between floral organs [137].

3. Complexity of FVT Biosynthesis and Emission

The biosynthesis and emission of FVTs in flowering plants and cut flowers is complex and is not only regulated by the spatio–temporal expression of particular genes but is also affected by various environmental factors, such as light intensity, radiation, the composition of the atmosphere, ambient temperature and relative humidity [85,110]. The mechanisms that influence the biosynthesis and emission of FVTs in response to specific environmental factors are still to be studied [86].

3.1. Spatio–Temporal Regulation

The release of FVTs follows a spatio–temporal pattern. Generally, each flowering plant has a unique composition of FVTs and coordinates the rhythm of FVT emission with the activity of its pollinators [70,90,144,145]. When flowers are ready to be pollinated, they emit elevated levels of volatile compounds. Successful pollination leads to fertilization and decreases in the emission of floral scents, resulting in decreases in unproductive visits from pollinators [145,146]. For example, the emission of linalool from *P. lemonei* 'High noon' flowers appears highest—accounting for 40% of total volatiles—at the fully opened stage and decreases as the flower wilts [47]. The diel emission of FVTs and the composition of FVTs produced by fragrant orchid *G. conopsea* is consistent with the spatial variation of nocturnal and diurnal pollinators in southern Sweden [90]. Meanwhile, the emission of particular FVTs varies during the different stages of flower development. The monoterpenes and relatively few sesquiterpenes mainly form in buds. The proportion of terpenes is greatly reduced in open flowers. This phenomenon occurs in the flowers of most fragrant plants, including *Plumeria rubra* flowers [147], lemon basil (*O. citriodorum* Vis) [148], roses [55], *J. auriculatum* [32], *J. grandiflorum* flowers [34], styrax flowers [56], *M. tenuifolia* [105], *C. sativa* [72] and *C. goeringii* [79]. Moreover, the circadian rhythm strongly influences the release of FVTs including (*Z*)-β-ocimene and (+/−)-linalool from *lilium* 'Siberia' [104], myrcene and (*E*)-β-ocimene from snapdragon flowers, 1,8-cineole from *N. suaveolens* [116] and linalool and its enantiomers from *Jasminum* spp. (*J. auriculatum, J. grandiflorum, J. multiflorum* and *J. malabaricum*) [149]. The molecular mechanism linking the emission of particular FVTs to the circadian rhythm remains unknown.

Different plants release FVTs from various tissues and organs to serve specific biological functions. The maximum amounts of FVTs are synthesized at the top of the petunia flower tube directly below the unexpanded corolla, close to the developing stigma. This arrangement allows the stigma to absorb the most FVTs for resistance [119]. In *Lilium* 'Siberia' flowers, the expression of the *TPS* genes was prominent in flowering parts, especially in sepals and petals [104]. Specifically, *LoTPS1* and *LoTPS3* were localized to plastids and mitochondria, respectively [104]. The bisexual dimorphism of floral aromas reflects the evolution of flowering plants from hermaphroditic to dioecious plants. Researchers have found that the constituents and release of FVTs differ in pistils and stamens. In *E. japonica* flowers, α-pinene and linalool were identified as the major components of floral scents in females, hermaphrodites and males. The males emit particularly high levels of α-pinene relative to females and hermaphrodites. The emissions from males generally decrease as flowers senescence. In contrast, the emissions from females and hermaphrodites do not change significantly during senescence [26].

3.2. Luminous Intensity

Light directly affects floral scent emission, changing the qualities and quantities of light-induced fluctuations in the FVTs emitted from *Lilium* 'siberia' flowers [150], *P. bellina*, *P. violacea* and *Phalaenopsis* hybrid flowers [123], *Narcissus* sp. cut flowers [110] and *C. sinensis* leaves [151]. One study indicated that light intensity and the circadian clock influenced a Ca^{2+} signal that contributed to the biosynthesis and emission of monoterpenes in *Lilium* 'siberia' tepals [152].

3.3. Radiation

γ radiation greatly influences the biosynthesis and emission of FVTs. The concentration of linalool in the floral scent bouquet from *J. auriculatum* was increased twofold in 10 Gy gamma-irradiated variants relative to the control [31]. In addition, the researchers observed a significant increase in the expression of FVT biosynthetic pathway genes and enzymes in particular plants that were irradiated with ultraviolet (UV) light [153]. These data provide evidence that UV-B light affects FVT biosynthesis.

3.4. Composition of the Atmosphere

VOCs form the floral scent trails that are essential for plant–insect interactions. Tropospheric ozone (O_3) chemically degrades the floral scent trails, thus reducing the distance, specificity and efficiency of the VOC signal [154,155]. Moreover, elevated levels of O_3, carbon dioxide (CO_2), diesel exhaust and nitrogen inputs (e.g., atmospheric NOx, N deposition and soil N enrichment) contribute to the production of O_3—and have recently been reported to rapidly degrade floral volatiles [155–157]. Thus, these environmental factors decrease the distance of scent trails and negatively affect the orientation of pollinators toward floral sources [155].

3.5. Ambient Temperature and Relative Humidity

With global climate change, temperature and humidity are increasingly threatening floral maturation and the size, nectar volume, floral scent and pollinator visitation rates associated with it, and thus, the composition of the pollinator community for some flowering plants [32,157–160]. The enhancement of temperature and humidity have a significant effect on the amounts of floral scent components, especially FVTs from the *O. fragrans* cultivars [44], *P. axillaris* [161], *J. auriculatum* [32], *Lilium* 'Siberia' [162] and seven common Mediterranean species [163]. As a result, the attractive characteristics of the floral fragrances are diminished due to the changed compositions of FVTs and the release rates of particular FVTs, such as (*E*)-β-ocimene, (*E*,*E*)-α-farnesene and α- and β-pinene [160,164–166].

4. Biosynthesis of FVTs

FVTs are the dominant and most diverse group of floral VOCs and include 556 scent compounds [167]. They are produced from the C5 carbon precursors isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP) through two alternative pathways, the cytosol-localized mevalonic-acid (MVA) and the plastid-localized 2-c-methylerythritol 4-phosphate (MEP) pathway in flowers and other plant organs [3,113,168]. Generally, the MEP pathway requires seven enzymatic steps to produce IPP and DMAPP. It is mainly used for the biosynthesis of hemiterpenes (C5), monoterpenes (C10) and diterpenes (C20) [3]. The MVA pathway uses six enzymatic reactions to produce IPP and is mainly responsible for the biosynthesis of sesquiterpenes (C15) (Figure 1). One exception is that sesquiterpenes are produced from the IPP and DMAP synthesized by the MEP pathway only in snapdragon flowers [169]. Although the MVA pathway produces only IPP, the MEP pathway produces both IPP and DMAPP at a 6: 1 ratio. Isopentenyl diphosphate isomerase (IDI) plays a key role in reversibly converting IPP to its allylic isomer DMAPP and controlling the equilibrium between these two isomers [3]. FPP is the prenyl diphosphate precursor of the sesquiterpenes that are produced in the cytoplasm. FPPS catalyzes a condensation reaction that utilizes IPP and DMAPP as substrates in a 2:1 ratio. GPP is the prenyl diphosphate precursor of monoterpenes and is produced in the plastid by GPPS, which utilizes IPP and DMAPP as substrates in a 1:1 ratio [3]. Notably, IPP synthesized by the MVA pathway can be imported into mitochondria for the production of FPP, GGPP and GFPP, which serve as precursors for the biosynthesis of other terpenoids [170].

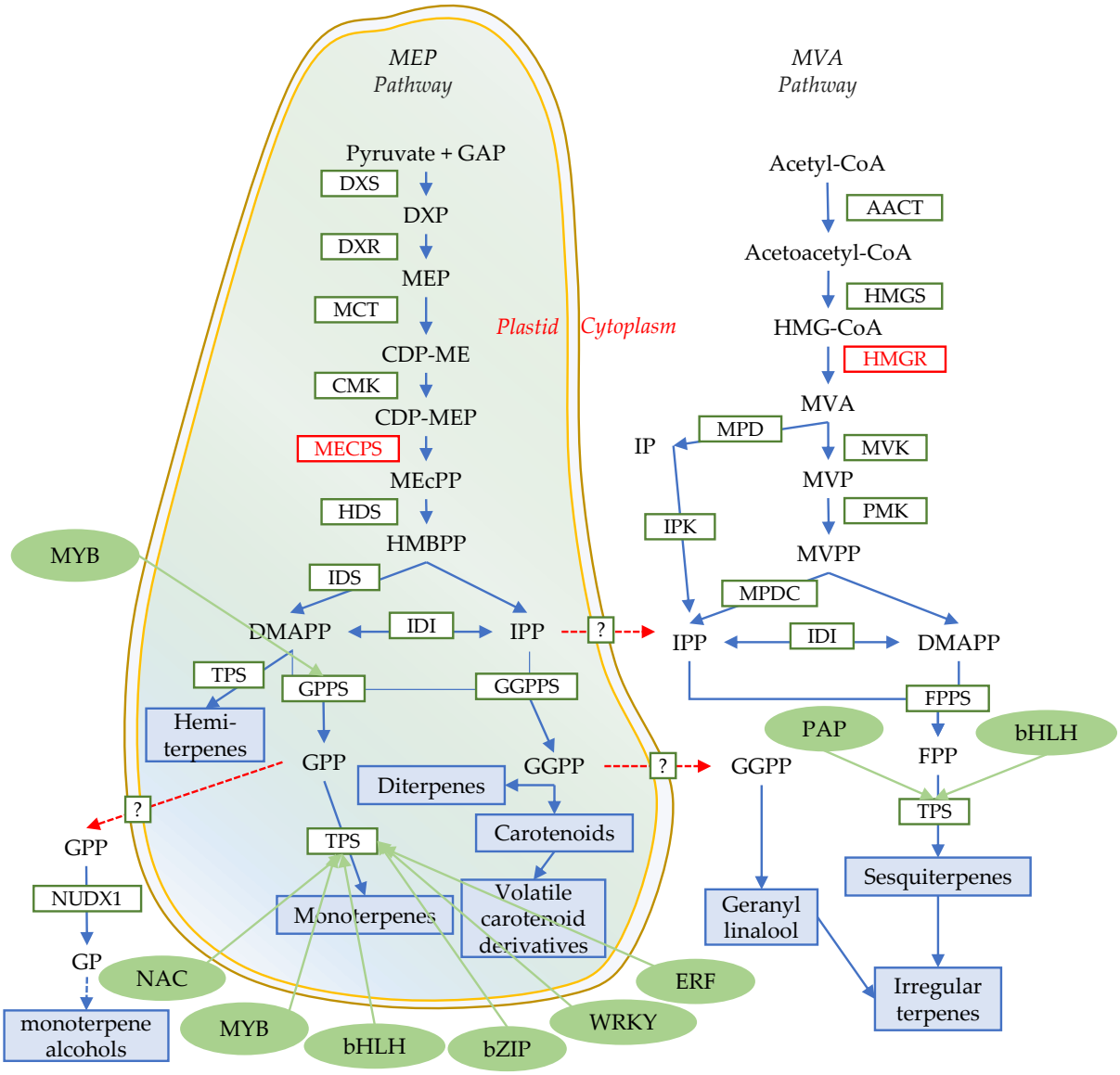

Figure 1. Biosynthesis and regulation of FVT production (adapted from [113,176]). Enzymes are placed in the green frame. Specialized terpenoids are in the blue frame. Dashed lines indicate multiple enzymatic steps and the transport of metabolites between cell compartments. Metabolites acting as signaling molecules are indicated in red. Unidentified transporters are indicated with question marks. Some transcription factors that interact with enzymes in the biosynthetic pathways are indicated with green boxes and arrows. The location of transcription factors in this illustration does not represent their subcellular location. Abbreviations: AACT, acetyl-CoA acetyltransferase; CDP-ME, 4-diphosphocytidyl-2-C-methyl-d-erythritol; CDP-MEP, 2-phospho-4-(cytidine 5′-diphospho)-2-C-methyl-d-erythritol; CMK, 4-(cytidine 5′-diphospho)-2-C-methyl-d-erythritol kinase; DMAPP, dimethylallyl pyrophosphate; DXP, 1-deoxy-d-xylulose 5-phosphate; DXR, 1-deoxy-D-xylulose 5-phosphate reductoisomerase; DXS, DXP synthase; FPP, farnesyl diphosphate; FPPS, farnesyl diphosphate synthase; GAP, D-glyceraldehyde 3-phosphate; GGPP, geranylgeranyl diphosphate (C20); GGPPS, GGPP synthase; GPP, geranyl diphosphate; GPPS, geranyl diphosphate synthase; HDS, 4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase; HMBPP, 4-hydroxy-3-methylbut-2-enyldiphosphate; HMBPP, 4-hydroxy-3-methylbut-2-enyldiphosphate; HMG-CoA, 3-hydroxy-3-methylglutaryl-CoA; HMGR, HMG-CoA reductase; HMGS, HMG-CoA synthase; IDI, IPP isomerase; IDS, isoprenyl diphosphate synthase; IP, isopentenyl phosphate; IPK, IP kinase; IPP, isopentenyl diphosphate; MCT, 2-C-methyl-D-erythritol 4-phosphate cytidylyltransferase; MDS, 2-C-methyl-d-erythritol 2,4-cyclodiphosphate synthase; MEcPP, 2-C-methyl-d-erythritol-2,4-cyclodiphosphate; MECPS, ME-CDP synthase; MEP, methylerythritol phosphate; MPD, mevalonate phosphate decarboxylase; MPDC, mevalonate-5-diphosphate decarboxylase; MVA, mevalonic acid; MVK, mevalonate kinase; NUDX, Nudix hydrolase; PMK, phosphomevalonate kinase; TPS, terpene synthase.

Numerous studies have focused on the upstream genes that encode the enzymes of the MEP and MVA pathways. In the MEP pathway, the expression of the *DXS* and *DXR* genes is positively correlated with the emission of volatile terpenoids throughout the flowering period in *S. oblata* and rose [15,57]. The Nudix hydrolase (RhNUDX1) in the cytosol hydrolyzes GPP to GP, which is converted to geraniol and is part of the biosynthetic pathway that produces the free monoterpene alcohols that contribute to fragrance in roses [51]. In *Litsea cubeba* (Lour.), the products of the MEP pathway are primarily utilized by GGPPS, and thus, more GGPP-derived products are produced relative to GPP-derived products. Recent studies have shown that both homodimeric and heterodimeric GPPSs contribute to the production of monoterpenes in flowering plants, such as *A. majus* and *C. breweri* [171], *C. praecox* L. [23], *L.* × *intermedia* [172] and *A. thaliana* [173]. The heterodimeric GPPS is composed of one large subunit (LSU) and one small subunit (SSU). The activity, function and regulatory mechanisms associated with the subunits of FVT biosynthetic enzymes are being investigated. The metabolic flux flows mainly from the plastic MEP pathway to the cytoplastic MVA pathway [14,174]. MEcPP is a possible rheostat that influences the abundance of upstream enzymes and is instrumental in fine-tuning the flux of the MEP pathway [175,176]. HMGR is the main rate-determining enzyme of the MVA pathway [177]. During flower development in *L. angustifolia*, the expression of most MEP pathway-associated genes was upregulated, especially genes that encode the synthases that contribute to the biosynthesis of monoterpenes and sesquiterpenes. In contrast, most genes in the MVA pathway were downregulated [178]. In *A. thaliana*, in both seedlings and mature plants, the expression of MVA pathway genes is more strongly expressed in the radicle, hypocotyl, roots, flowers and seeds relative to MEP pathway genes [179]. HMGS plays an important role in the yield of monoterpenes and sesquiterpenes and the communication between the MEP and MVA pathways. Overexpressing the *LcHMGS* gene is shown to significantly increase the types and quantities of FVTs and induce early flowering. In contrast, silencing this gene significantly delays flowering in *Litsea cubeba* (Lour.) [14]. Some of the transporters required for the subcellular transport of IPP and GPP remain unknown [180]. The MEP and MVA pathways ultimately control the availability of substrates for terpene synthases (TPS) and the interactions between the different substrate pools [14].

By catalyzing complex carbocation-driven cyclization, rearrangement and elimination reactions, TPSs have played a major role in converting a few acyclic prenyl diphosphate substrates into the vast chemical library of terpenoids. Plant *TPS* genes are widely distributed in flower tissues including buds, pistils, petals, stamens, tubes, corollas, sepals, stigmas and pollen [36,181]. Approximately 1000 monoterpenes and more than 7000 sesquiterpenes have been reported [182]. To date, more than 2000 *TPS* genes are responsible for the biosynthesis of monoterpenes, while sesquiterpenes have been identified in more than 40 species [182,183]. Table 1 lists some of the *TPS* genes that have been identified in flowering plants recently.

Three major mechanisms are generally thought to be responsible for the high structural diversity of terpenoids: (1) many TPSs utilize multiple substrates or convert one substrate into multiple products [3,87,184]; (2) single amino acid changes in a TPSs can lead to elementary changes in biosynthetic properties and thus, to the production of completely different mixtures of terpenoids [142]; (3) many modifying enzymes (e.g., oxidoreductases, isomerases, acylases, etc.) convert basic terpene skeletons into diverse products [142].

TPS is a superfamily in higher plants, making *TPS* gene function diverse. The TPS family is generally divided into three classes and seven sub-families. Class I consists of TPS-c, TPS-e/f and TPS-h. Class II consists of TPS-d. Class III consists of TPS-a, TPS-b and TPS-g [54,97]. The specific functions of particular classes of TPSs can vary from plant to plant. In angiosperms, subfamily TPS-b is typically comprised of mono-TPSs. The TPS-a subclass contributes to sesquiterpene synthases. TPS-e/f is responsible for the biosynthesis of particular mono- and sesquiterpenes, such as linalool synthase in *C. breweri* and *C. florida* cv. 'Kaiser' [76,78], geranyllinalool synthase in *A. thaliana* and farnesene synthase in

kiwifruit [15]. The angiosperm-specific TPS-g is responsible for the biosynthesis of acyclic monoterpenes and sesquiterpenes [3,36,97,183]. The TPS-f subfamily may be peculiar to dicotyledonous plants [122]. An updated phylogeny of the *CsTPS* gene family from *C. sativa* has shown three cannabis-specific clades, including a clade of sesquiterpene synthases within the TPS-b subfamily that typically contains mostly monoterpene synthases [72]. In *L. odoratus* (sweet pea), *LoTPS4* and *LoTPS7* belong to the TPS-b clade but catalyze the formation of monoterpenes and sesquiterpenes. *LoTPS3* and *LoTPS8* from the TPS-a clade also produce monoterpenes and sesquiterpenes [97]. Both TPS-b and TPS-e/f contribute to floral monoterpene biosynthesis in *P. bellina* [122]. However, in *N. attenuata*, *TPS38* belongs to the TPS-b clade and synthesizes sesquiterpenes, despite being expected to synthesize monoterpenes [112]. The substantial evolution and expansion of mono- and sesqui-TPS families [183] has enabled flowers to produce a surprisingly large variety of FVTs.

5. Transcriptional Regulation and Modification of Terpene Skeletons

5.1. Transcriptional Regulation

Transcription factors regulate gene expression by binding *cis*-acting elements (i.e., they inhibit or enhance the transcription initiation). Although terpenoids are widely used, their content is low. Transcription factors can regulate gene transcriptions that encode enzymes that contribute to the biosynthesis of secondary metabolites. FVT biosynthesis is regulated by transcription factors (TFs). To date, six TF families have been reported to be involved in the biosynthesis of FVTs in various plants, including MYB- [89,185,186], basic helix-loop-helix (bHLH)- [89,121,187,188], WRKY- [189], ethylene response factor (ERF/AP2)- [190], basic leucine zipper (bZIP)- and NAC-type [185] transcription factors. In the biosynthesis of FVTs, certain TFs work independently, while others work cooperatively. Transcription factors have been thoroughly studied in aromatic plants with small, scentless or inconspicuous flowers, such as *Cinnamomum Camphora* [191], and in less volatile terpenes, such as artemisinin [192].

5.1.1. MYB

MYB transcription factors are ubiquitous in plants and animals. In plants, the MYB transcription factor family consists of four subclasses: 1R-MYB, R2R3-MYB, R1-R2R3-MYB and 4R-MYB. R2R3-MYB is the largest subclass [186]. Evidence suggests that members of the R2R3-MYB subclass may control the biosynthesis of volatile terpenoids during the full flowering stages in *H. coronarium*, the bud stages in *S. oblata* [57,93] and flowers from *O. fragrans* [193]. The production of anthocyanin pigment-1 (PAP1) is an R2R3-MYB transcription factor that contributes to the biosynthesis of phenylpropanoids, benzenoids and anthocyanins in Arabidopsis, tobacco and petunia flowers [194], and regulates the biosynthesis of the phenylpropanoid and terpenoid scent compounds in rose flowers [195]. PAP1 enhances the emission levels of the sesquiterpene germacrene D in rose flowers [195]. HcMYB directly binds the promoters of genes that contribute to volatile terpenoid biosynthesis (*HcTPS1*, *HcTPS3* and *HcTPS10*) in *H. coronarium* [94]. In the same plant, a flower-specific HcMYB2 activates the expression of the linalool synthase gene *HcTPS5*. The expression of *HcMYB2* is induced by auxin [95]. However, in *M. spicata*, a MYB transcription factor is a novel negative regulator of monoterpene biosynthesis that perturbs the production of sesquiterpene- and diterpene-derived metabolites by binding *cis*-elements in the gene encoding the large subunit of MsGPPS (MsGPPS.LSU) and suppressing its expression [109].

5.1.2. bHLH

The basic helix-loop-helix type (bHLH) transcription factor family is the second-largest transcription factor family found in plants, and it is divided into 26 subfamilies [196]. Recently, MYC2, a member of the bHLH transcription factor family, was found to activate the expression of two sesquiterpene synthase genes, *TPS21* and *TPS11*, in *Lilium* 'Siberia' [197], after they were found to influence both gibberellic acid (GA) and jasmonic acid (JA) signaling in the inflorescence of Arabidopsis [69]. Meanwhile, both MYB21 and MYC2 were

confirmed to upregulate the expression of a monoterpene (linalool) synthase gene in *F. hybrida* [89]. In *C. praecox* L., the MYC2 and bHLH13 transcription factors possibly contribute to the biosynthesis of monoterpene (linalool) and sesquiterpene (β-caryophyllene) biosynthesis [21,24].

5.1.3. WRKY

The WRKY family consists of three major groups (I, II and III) that are distinguished based on the number of WRKY domains and the type of zinc-finger-like motifs [198]. Members of group I contain two WRKY domains. Members of groups II and III have a single WRKY domain [199]. In *O. fragrans* flowers, WRKY transcription factors play important roles in regulating the biosynthesis of secondary metabolites. The expression of OfWRKY19/36/84/139 positively correlates with the biosynthesis of volatile monoterpenes; in contrast, the expression of OfWRKY7 negatively correlates with the biosynthesis of volatile monoterpenes [46]. In addition, the OfWRKYs regulate volatile monoterpene biosynthesis in *O. fragrans* by binding plant zinc cluster domains [45].

5.1.4. Others

The specificity of transcription factors is versatile in different plants. Additionally, different types of transcription factors may work together for a particular purpose in a particular plant. To date, the following types of transcription factors have been found to work together to regulate FVT biosynthesis in flowering plants: bZIP, bHLH, ERF, MYB and NAC. The NAC genes are specific to plants [200] and contain five subdomains: A, B, C, D and E. Among them, A, C and D are highly conserved, while B and E are relatively less conserved [201]. The bZIP transcription factors are widely distributed and highly conserved in eukaryotes. In plants, the bZIP transcription factors usually contribute to stress responses and the regulation of secondary metabolism [202]. In *P. bellina*, five TFs (PbbHLH4, PbbHLH6, PbbZIP4, PbERF1 and PbNAC1) have been found to transactivate several structural genes involved in monoterpene biosynthesis [121]. The genes encoding geraniol and linalool synthetase, *PbTPS5* and *PbTPS10*, are regulated by several transcription factors (TFs), including PbbHLH4, PbbHLH6, PbbZIP4, PbERF1, PbERF9 and PbNAC1 [123]. PbNAC1 might be regulated by HY5, a bZIP-type transcription factor. In addition, *cis*-acting elements in the promoters of PbNAC1, structural genes and TFs associated with monoterpene biosynthesis have been identified that are responsive to light signaling and the circadian clock [123].

Some TFs can collaboratively activate a number of genes in particular secondary metabolic pathways and thus contribute to a comprehensive regulatory network. For instance, in *L.* × *intermedia*, LiMYB, LibZIP, LiGeBP, LiSBP-2, LiERF-1 and LiERF-2 possibly activate the transcription of genes that encode monoterpene synthases [185]. LiMYB, LibZIP and LiGeBP activate transcription from both the linalool and linalool synthase promoters, while LiNAC activates transcription only from the 1,8-cineole synthase promoter [185]. In *P. bellina*, PbbHLH4 may interact with PbbZIP4 and/or PbNAC1 to regulate monoterpene biosynthesis to varying degrees, and PbbHLH4 can regulate the expression of PbTPS7 [121].

5.2. Modification of Terpene Skeletons

In addition to a wide range of volatile terpenoids formed directly through the catalytic activities of TPS enzymes, there are a large number of modifying enzymes, such as cytochrome P450 monooxygenases (P450s) and glycosyl- and acyltransferases, that modify the volatile terpenes produced by TPSs. These modifying enzymes often add functional groups to the volatile terpenes using methylation, acylation or oxidation [203,204]. Modifying enzymes helps to produce more than 80,000 distinct natural products and, thus, alter the olfactory properties of flowers [7,183].

The role of cytochrome P450 enzymes in the modification of FVTs has been widely studied. In flowers, cytochrome P450 enzymes are able to perform highly regio- and stereoselective irreversible oxidations of terpenes, and hence contribute to the structural diversity

of terpenes [205,206]. Cytochrome P450 enzymes oxidize more than 20 small and highly hydrophobic natural compounds [207]. For instance, they turn volatile terpenes into soluble compounds stored in floral organs, which prevent the invasion of pests and pathogens [119]. The irregular acyclic C11 and C16 homoterpenes, such as 4,8-dimethylnona-1,3,7-triene (DMNT) and 4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT), are usually synthesized in leaves and flowers by a pathway that includes an oxidative degradation step catalyzed by a cytochrome P450 monooxygenase and that utilizes the C15 and C20 tertiary alcohols, (*E*)-nerolidol and (*E*, *E*)-geranyl linalool as the substrates [208,209]. DMNT and TMTT are common constituents of floral volatile blends, as well as of herbivore- and pathogen-induced volatile blends in angiosperms. They contribute to the deterrence or attraction of insect pests and the parasites or predators [208,209] in orchids [210] and Arabidopsis [209]. Based on existing research, members of the CYP70, CYP71 and CYP76 clans, including CYP706A3, CYP76C1, CYP71D13, CYP71A, CYP76AH1 and CYP102A1, oxidize limonene to perillyl alcohol, the anti-tumor compound, and have been co-expressed with genes related to volatile terpenoid biosynthesis [137,211–214].

Studies on cytochrome P450 enzymes in floral organs have mainly focused on their associations with *TPS* genes. There is sufficient evidence that cytochrome P450 enzymes are co-expressed with monoterpene synthases and involved in monoterpenoid metabolism. In Arabidopsis flowers, the TPS10 and TPS14 are the terpene synthases that synthesize the two different enantiomers of linalool, (−)-(*R*)-linalool and (+)-(*S*)-linalool, respectively. *TPS10* and *TPS14* are co-expressed with two genes that encode cytochrome P450s (*CYP71B*31 and *CYP76C3*) at anthesis, mainly in the upper anther filaments and in petals. CYP71B31 and CYP76C3 produce different but overlapping sets of hydroxylated or epoxidized products [211]. TPS enzymes colocalize in vesicular structures associated with the plastid surface. In contrast, cytochrome P450 enzymes are typically found in the endoplasmic reticulum [211]. These oxygenated products are not emitted into the floral headspace but accumulate in floral tissues as conjugated metabolites [206,211]. CYP76C1 is the most abundant and active linalool-metabolizing enzyme in the flowers of Arabidopsis [213]. In the same flowers, the expression of *CYP76C1* is tightly coregulated with *TPS10* and *TPS14*. These genes are expressed in the petals and anthers at anthesis. They facilitate and modulate the emission of linalool and the production of soluble carboxylinalool in opening flowers. They also contribute to reductions in floral attractiveness and flavor, thus protecting flowers against florivorous insects [213]. Moreover, in Arabidopsis, TPS11 produces a blend of sesquiterpenes. *TPS11* and *CYP706A3* are tightly co-expressed in floral tissues during anthesis and floral bud development. Sesquiterpene and most monoterpene emissions from opening flowers are largely suppressed by CYP706A3-mediated metabolism, which produces terpene oxides retained in floral tissues and soluble sesquiterpene oxides in flower buds. These terpenes effectively protect against insect larvae feeding [119,207]. Mutations in *CYP706A3* suppress sesquiterpene and monoterpene emissions from *Arabidopsis* flowers and change the floral microbial operational taxonomic units (OTUs) in the genus *Pseudomonas* [119]. In addition, it has also been reported that several members of the CYP76 family in *Catharanthus roseus* and *Grapevine* catalyzed different oxidation reactions with monoterpenes, including sequential reactions and conversion of different related compounds [12,211,215].

6. Intersection of Synthetic Pathways That Influence Flower Fragrance and Color

Usually, flowering plants use both fragrance and color to attract pollinators by stimulating the sensory systems of flower-visiting animals [216]. A study on *Phrygana*, a natural Mediterranean scrubland flower, displayed integrated patterns of scent composition (including monoterpenes and sesquiterpenes) and color consistent with the sensory abilities and perceptual biases of bees [216]. Bee visitation rates are associated with color hue and are positively related to terpenoid emissions from flowers, especially the emission of sesquiterpenes [217]. This is consistent with the integration of phenotypes potentially facilitating pollination. Some scientists hypothesized that if particular plant species emit

elevated levels of sesquiterpenes, they would appear more vividly colored to bees. However, neither shared metabolic pathways nor a direct pleiotropy between anthocyanins and sesquiterpenes are known [218]. In addition, in the flowers of *Ionopsis utricularioides* (Sw.) Lindl., no association between color and fragrance has been observed [218].

Studies of phenotypic characteristics propose an association between FVTs and flower color. The pale-colored *R. damascena* flowers with their low anthocyanin content appear to produce higher levels of carotenoids and monoterpenes during flower development [219]. Although the gene encoding GGPPS contributes to monoterpene biosynthesis and is probably responsible for both the production of volatile terpenes and floral coloration, further research is needed to establish this connection [219]. In wild roses, the early blooming flowers accumulate low levels of geraniol, developing white petals. The petals of geraniol-rich roses are bigger and have longer shelf lives compared to small, monoterpene-poor roses [55]. As for *Cymbidium* 'Sael Bit', small green and light-yellow colored flowers are highly fragrant relative to brightly colored flowers [220].

From a biosynthesis and transcriptional regulation perspective, there are interactive and competitive relationships between flower fragrance and flower color. TFs that influence different biosynthetic pathways in *N. tazetta* constitute a complex flower scent–color competition-regulatory network. Potential competition exists between biosynthetic pathways that contributes to the production of floral pigments and fragrance during the growth, development and reproduction of *N. tazetta*. Coronas MYB12, MYB1, AP2-ERF, bZIP, NAC and MYB are associated with a metabolite flux through the: phenylpropanoid pathway that produces flavonols/anthocyanins; the phenylpropanoid pathway that produces volatile benzenoid/phenylpropanoids in the tepal; and the biosynthetic pathways that produce FVTs and carotenoids/carotene derivatives [111]. During flower development, different enzymes are responsible for directing the carbon flux through different biosynthetic pathways. The levels of transcripts that encode ENT-COPALYL DIPHOSPHATE SYNTHASE/TPS, phenylalanine ammonia-lyase (PAL) and PHYTOENE SYNTHASE/GERANYL-GERANYL REDUCTASE impact the metabolite flux through the terpene biosynthetic pathway and, therefore, influence the benzenoid/phenylpropanoid and carotenoid biosynthetic pathways. Branches of the carotenoid biosynthetic pathway produce the yellow color and increases in indole, (*E*)-β-ocimene and the benzyl acetate scent in the corona of narcissus [111].

In common angiosperm flowers, biochemical connections between the production of compounds that contribute to color and scent are known from early studies on the phenylpropanoid and terpenoid pathways. One such connection is the shared transcription factor PAP1 [194,195]. Our understanding of the relationship between FVTs and the biosynthesis of pigments is still limited due to the complexity of the two biosynthetic pathways. Nonetheless, the whole genome sequences of model plants and common aromatic flowering plants, such as Arabidopsis, petunia, rose and snapdragon, and the reconstruction of the regulation that controls secondary metabolism, will give researchers a better understanding of the interactions between flower fragrance and color [54].

7. Conclusions and Perspectives

The availability of whole genome sequences for many plants and the recent progress in -omics technology has led to a new genomics and -omics era in plant biology research that has contributed to a novel understanding of regulatory mechanisms involved in the biosynthesis of FVTs. The progress achieved in our understanding of VOCs and FVTs highlights the importance of floral volatile terpenes in natural ecosystems, plant reproduction, plant defense, pollination and signal transduction. Recent breakthroughs in the identification of *TPS* genes, associated TFs, the supplementation of terpene biosynthetic pathways and its derivatives demonstrate that we have reliable genetic techniques and methods that can be used to improve floral fragrance, such as modifying the emissions of FVTs, to greatly facilitate the recruitment of pollinators and control pests and improve the production of targeted FVTs and essential oils. Moreover, growing metabolically and

genetically engineered plants in different natural conditions will allow us to determine the species-specific functions of different FVTs.

Generally speaking, the study of flower fragrance has seen considerable progress in recent years, but there are still many gaps in our knowledge. There is a connection between the biosynthetic pathways that produce FVTs and pigments, but the details of the connection remain unclear. Although our knowledge of FVT biosynthesis is substantial, the transcriptional and post-translational regulation of these pathways requires further study. Meanwhile, our understanding of the influence of hormones, such as auxin, ABA and GA, on FVTs is still limited. In addition, the transport of FVTs remains to be explored. To date, the transmembrane transporters of FVTs and their biosynthetic precursors remain unknown. However, we can speculate that ATP-binding cassette (ABC) transporters transport FVTs across membranes because previous research indicates that an ABC transporter transports phenylpropanoid/benzenoid volatiles across the plasma membrane [221,222].

Moreover, extraction and isolation methods of FVTs, especially specific volatile terpenoids, remain ambiguous. There are significant prospects in investigating the extraction technology of specific terpenes due to the chemical and physical properties of FVTs and their promising applications.

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