

Floral Volatile Terpenoids

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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.

floral volatile terpenoids

function

regulation

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][6][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.

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

Latin Name	Family	Main FVT compounds	Genes	Ref.
<i>Actinidia deliciosa</i> ‘Hayward’	Actinidiaceae	(<i>E,E</i>)- α -farnesene, (<i>E</i>)- β -ocimene, (+)-		^[9]

Latin Name	Family	Main FVT compounds	Genes	Ref.
		germacrene D		
<i>Albizia julibrissin</i>	Leguminosae	α -farnesene, (Z, E)- β -farnesene	<i>AjTPS2, AjTPS5, AjTPS7, AjTPS9, AjTPS10</i>	[10]
<i>Camellia</i> spp.	Theaceae	linalool and its oxides, geraniol, α -farnesene, hedycaryol	<i>CbTPS1, ChTPS1, CbTPS18, CbTPS25, CbTPS28, CbTPS33, CbTPS35 CsTPS29, CbTPS47, CbTPS48, CbTPS51, CbTPS52</i>	[11] [12] [13]
<i>Cananga odorata</i> var. <i>fruticosa</i>	Annonaceae	linalool	<i>CoTPS1, CoTPS2, CoTPS3, CoTPS4</i>	[14]
<i>Chimonanthus praecox</i> L.	Calycanthaceae	linalool, trans- β -ocimene, β -caryophyllene	<i>CpTPS1, CpTPS9, CpTPS10, CpTPS14, CpTPS16, CpTPS4, CpTPS9, CpTPS42</i>	[15] [16] [17] [18]
<i>Datura wrightii</i>	Solanaceae	linalool and its enantiomers		[19]
<i>Eurya japonica</i> Thunb	Theaceae	α -pinene, linalool		[20]
<i>Gardenia jasminoides</i>	Rubiaceae	farnesene, Z-3-hexenyl tiglate, indole		[21]
<i>Gelsemium sempervirens</i> (L.) J. St.-Hil.	Gelsemiaceae	(Z)- α -ocimene, α -farnesene		[22]
<i>Gossypium hirsutum</i>	Malvaceae	(3S)-linalool	<i>GhTPS12</i>	[23] [24]
<i>Jasminum</i> spp.	Oleaceae	?-farnesene, linalool, β -ocimene, germacrene-D		[25] [26] [27] [28] [29]
<i>Laurus nobilis</i>	Lauraceae	sesquiterpenes, γ -cadinene, δ -cadinene		[30]
<i>Lonicera japonica</i>	Caprifoliaceae	linalool		[31]
<i>Magnolia champaca</i>	Magnoliaceae	(R)-linalool, linalool and its oxides		[32]
<i>Malus domestica</i>	Rosaceae	(E)-linalool oxide		[33]

Latin Name	Family	Main FVT compounds	Genes	Ref.
<i>Murraya paniculata</i>	Rutaceae	<i>E</i> - β -ocimene, linalool, α -cubebene		[34] [35]
<i>Myrtus communis</i> L.	Myrtaceae	α -pinene, linalool, 1,8-cineole		[36]
<i>Osmanthus fragrans</i>	Oleaceae	linalool and its derivatives, α -ionone, β -ionone	<i>OfTPS1</i> , <i>OfTPS2</i> , <i>OfTPS3</i>	[37] [38] [39] [40]
<i>Paeonia</i> spp.	Paeoniaceae	β -caryophyllene, linalool		[41] [42]
<i>Psidium guajava</i>	Myrtaceae	α -cadinol, β -caryophyllene, nerolidol		[43]
<i>Rosa</i> spp.	Rosaceae	geraniol, linalool, nerolidol, myrcene, ocimene, citronellol	<i>NEROLIDOL SYNTHASE (NES)</i> , <i>RcLIN-NERS1</i> , <i>RcLIN-NERS2</i>	[44] [45] [46] [47] [48] [49]
<i>Styrax japonicas</i> spp.	Styracaceae	linalool, α -pincnc, gcrmacrcnc D		[50]
<i>Syringa oblata</i> Lindl.	Oleaceae	<i>D</i> -limonene		[51] [52]
<i>Penstemon digitalis</i>	Plantaginaceae	linalool and its enantiomers, <i>cis</i> - and <i>trans</i> - β -ocimene		[53] [54] [55]
<i>Alstroemeria</i> spp.	Alstroemeriaceae	(<i>E</i>)-caryophyllene, α -caryophyllene		[56]
<i>Anthurium 'Mystral'</i>	Araceae	eucalyptol, β / α -pinene, β -phellandrene, β -Myrcene		[57]
<i>Antirrhinum majus</i>	Plantaginaceae	nerolidol, linalool, (<i>E</i>)- β -ocimene, myrcene		[58] [59]
<i>Arabidopsis thaliana</i>	Brassicaceae	α -copaene, α -caryophyllene, β -elemene	<i>AtTPS21</i> , <i>AtTPS11</i> , and other 40 terpenoid synthase genes	[60] [61] [62] [63] [64]

Latin Name	Family	Main FVT compounds	Genes	Ref.
<i>Aristolochia gigantea</i>	Aristolochiaceae	linalool, (Z,E)- α -farnesene, geraniol		[65]
<i>Caladenia plicata</i>	Orchidaceae	β -citronellol		[66]
<i>Cannabis sativa</i>	Cannabaceae	(+)- α -pinene, (-)-limonene, β -caryophyllene		[67]
<i>Chrysanthemum indicum</i>	Asteraceae	1,8-cineole, germacrene D, camphor		[68] [69]
<i>Citrus</i> L.	Rutaceae	linalool, β -myrcene, α -myrcene, limonene		[70]
<i>Clarkia breweri</i>	Onagraceae	S-linalool, Linalool, linalool oxide	<i>linalool synthase (LIS)</i> gene	[71] [72]
<i>Clematis florida</i> cv. 'Kaiser'	Ranunculaceae	linalool, linalool oxide, nerolidol	<i>CfTPS1, CfTPS2, CfTPS3</i>	[73]
<i>Cymbidium</i> spp.	Orchidaceae	(E)- β -farnesene, nerolidol, linalool	<i>CgTPS7</i>	[74] [75]
<i>Dendrobium officinale</i>	Orchidaceae	α -thujene, linalool, α -terpineol	<i>DoTPS10</i>	[76] [77] [78]
<i>Dianthus caryophyllus</i> L.	Caryophyllaceae	caryophyllene, caryophyllene oxide, linalool		[79] [80] [81]
<i>Freesia hybrida</i> . "Shiny Gold"	Iridaceae	linalool, β -ocimene, D-limonene	<i>FhTPS1, FhTPS2, FhTPS3, FhTPS4, FhTPS5, FhTPS6, FhTPS7, FhTPS8</i>	[82] [83] [84]
<i>Gymnadenia conopsea</i> (L.) R. Br.	Orchidaceae	β -myrcene, α -terpineol, (+)-cyclosativene, α -santalene, trans- α -bergamotene, (Z,E)- α -farnesene, (E,E)- α -farnesene		[85]
<i>Hedychium coronarium</i>	Zingiberaceae	β -ocimene, 1,8-cineole, linalool	<i>HcTPS1, HcTPS3, HcTPS5, HcTPS6, HcTPS7, HcTPS8, HcTPS10, HcTPS11, HcTPS21</i>	[86] [87] [88] [89] [90]
<i>Hippeastrum</i> spp.	Amaryllidaceae	eucalyptol, (Z)- β -		[91]

Latin Name	Family	Main FVT compounds	Genes	Ref.
		ocimene		
<i>Lathyrus odoratus</i>	Leguminosae	α -bergamotene, linalool, (-)- α -cubebene		[92]
<i>Lavandula</i> spp.	Lamiaceae	linalool acetate, linalool, lavandulyl acetate, α/β -Pinene	<i>LaLIMS</i> , <i>LaLINS</i>	[92] [93] [94] [95] [96]
<i>Lilium</i> spp.	Liliaceae	linalool, myrcene, (<i>E</i>)- β -ocimene, α -pinene, limonene	<i>LoTPS1</i> , <i>LoTPS2</i> , <i>LoTPS3</i> , <i>LoTPS4</i>	[97] [98] [99]
<i>Maxillaria tenuifolia</i>	Orchidaceae	β -caryophyllene, α -copaene, delta-decalacton		[100]
<i>Mentha citrata</i>	Lamiaceae	linalool and its enantiomers		[101]
<i>Mimulus</i> spp.	Phrymaceae	(<i>E</i>)- β -ocimene, d-limonene, β -myrcene	<i>OCIMENE SYNTHASE</i> (OS) gene	[102] [103] [104]
<i>Narcissus</i> spp.	Amaryllidaceae	myrcene, eucalyptol, linalool		[105] [106]
<i>Nicotiana</i> spp.	Solanaceae	(<i>E</i>)- α -bergamotene, (<i>E</i>)- β -ocimene, 1,8-cineole	<i>NaTPS25</i> , <i>NaTPS38</i>	[107] [108] [109] [110] [111]
<i>Nymphaea subg. Hydrocallis</i>	Nymphaeaceae	linalool, farnesene, nerolidol		[112]
<i>Ocimum basilicum</i> L.	Lamiaceae	linalool		[113]
<i>Petunia hybrida</i>	Solanaceae	germacrene D, β -cadinene	<i>PhTPS1</i> , <i>PhTPS2</i> , <i>PhTPS3</i> , <i>PhTPS4</i>	[114]
<i>Passiflora edulis</i> Sims	Passifloraceae	linalool	<i>PeTPS2</i> , <i>PeTPS3</i> , <i>PeTPS4</i> , <i>PeTPS24</i>	[115]
<i>Phalaenopsis</i> spp.	Orchidaceae	α -pinene, trans- β -ocimene, linalool, geraniol and their derivatives	<i>PbTPS5</i> , <i>PbTPS7</i> , <i>PbTPS9</i> , <i>PbTPS10</i> , <i>PbTPS3</i> , <i>PbTPS4</i>	[116] [117] [118]

Latin Name	Family	Main FVT compounds	Genes	Ref.
<i>Plectranthus amboinicus</i> (Lour.) Spreng	Lamiaceae	linalool, nerolidol		[119]
<i>Polianthes tuberosa</i> L.	Amaryllidaceae	germacrene D, 1, 8-cineole, α -terpineol		[120] [121] [122] [123]
<i>Rheum nobile</i>	Polygonaceae	α -pinene		[124]
<i>Salvia officinalis</i>	Labiatae	myrcene, (+)-neomenthol, 1,8-cineole		[125]
<i>Tanacetum vulgare</i>	Asteraceae	α -pinene, 3-hexen-1-ol-acetate		[126]

2. 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 [\[79\]](#)[\[104\]](#). The mechanisms that influence the biosynthesis and emission of FVTs in response to specific environmental factors are still to be studied [\[80\]](#).

2.1. 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 [\[64\]](#)[\[84\]](#)[\[127\]](#)[\[128\]](#). 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 [\[128\]](#)[\[129\]](#). 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 [\[40\]](#). 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 [\[84\]](#). 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 [\[130\]](#), lemon basil (*O. citriodorum* Vis) [\[131\]](#), roses [\[48\]](#), *J. auriculatum* [\[25\]](#), *J. grandiflorum* flowers [\[27\]](#), styrax flowers [\[49\]](#), *M. tenuifolia* [\[99\]](#), *C. sativa* [\[66\]](#) and *C. goeringii* [\[73\]](#). Moreover, the circadian rhythm strongly influences the release of FVTs including (*Z*)- β -ocimene and (+/–)-linalool from *lilium* ‘Siberia’ [\[98\]](#), myrcene and (*E*)- β -ocimene from snapdragon flowers, 1,8-cineole from *N. suaveolens* [\[110\]](#) and linalool and its enantiomers from *Jasminum* spp. (*J. auriculatum*, *J. grandiflorum*, *J. multiflorum* and *J.*

malabaricum) [132]. 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 [113]. In *Lilium* 'Siberia' flowers, the expression of the *TPS* genes was prominent in flowering parts, especially in sepals and petals [98]. Specifically, *LoTPS1* and *LoTPS3* were localized to plastids and mitochondria, respectively [98]. 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 senesce. In contrast, the emissions from females and hermaphrodites do not change significantly during senescence [19].

2.2. 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 [133], *P. bellina*, *P. violacea* and *Phalaenopsis* hybrid flowers [118], *Narcissus* sp. cut flowers [104] and *C. sinensis* leaves [134]. 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 [135].

2.3. Radiation

Gamma 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 [24]. 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 [136]. These data provide evidence that UV-B light affects FVT biosynthesis.

2.4. 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 [137][138]. Moreover, elevated levels of O_3 , carbon dioxide (CO_2), diesel exhaust and nitrogen inputs (e.g., atmospheric NO_x , N deposition and soil N enrichment) contribute to the production of O_3 —and have recently been reported to rapidly degrade floral volatiles [138][139][140]. Thus, these environmental factors decrease the distance of scent trails and negatively affect the orientation of pollinators toward floral sources [138].

2.5. 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 [25][140][141][142][143]. The enhancement of temperature and humidity have a significant effect on the amounts of floral scent components, especially FVTs from the *O. fragrans* cultivars [37], *P. axillaris* [144], *J. auriculatum* [25], *Lilium* 'Siberia' [145] and seven common Mediterranean species [146]. 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 [143][147][148][149].

3. 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 [150][151].

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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