Review Article

Biosynthesis, Composition and Sources of Floral Scent in Ornamental Crops: A Review

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Abstract

Fragrant flowers produce their perfume in glands on the petals known as "osmophores". Floral fragrance is typically a complex mixture of low molecular weight volatile compounds (100-200 Da) which gives the flower its unique, characteristic fragrance. Floral scents have vital function in plants reproductive process and possess substantial economic significance. Many floral scent volatiles fall into the category of terpenoid, phenylpropanoid/benzenoid, and aromatic amino acid. Flowers produce a great range of specific metabolites like fragrant volatiles to attract pollinators, hormones to stimulate or repress signalling cascades and fragrant volatiles for protection against herbivores or pathogens.

Keywords: Floral scent, Herbivores, Pollination, Terpenes

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Introduction

The ability of flowering plants to prosper throughout their long evolution has been strongly dependent on the constant development of strategies to lure pollinators. This has led to the creation of elaborate perianth forms, splendid colour patterns, and a broad spectrum of fragrances. Floral fragrance is an important trait of flower which plays an important role in the reproductive process and possesses substantial economic significance. It essentially improves aesthetic characteristics of ornamental plants. Together with shape and colour, it determines the pollination syndrome of the flower. Many floral scent volatiles fall into the category of terpenoid, phenylpropanoid/benzenoid, and aromatic amino acid [1]. Flowers produce a great range of specific metabolites like fragrant volatiles to attract pollinators, hormones to stimulate or repress signalling cascades and fragrant volatiles for protection against herbivores or pathogens [2, 3]. The array of particular metabolites synthesized by flowers of different plants is wide-ranging [4, 5]. Generally, the fragrance emission by the flowers is at maximal levels when the pollinator is active, and consists of volatile molecules derived from different biochemical pathways. Floral fragrance is typically a complex mixture of low molecular weight volatile compounds (100-200 Da) which gives the flower its unique, characteristic fragrance. A major part of the floral volatiles belong to the classes of terpenoids, benzenoids and phenylpropanoids, but there are also some fatty acid and carotenoid derivatives and nitrogen or sulphur containing compounds. Several enzymes producing the individual scent molecules have been identified, but there are still many steps unknown.

Biosynthesis of floral scent compounds

Terpenes, especially monoterpenes such as linalool, limonene, myrcene, and trans-b-ocimene, but also some sesquiterpenes such as farnesene, nerolidol, and caryophyllene, are common constituents of floral scent (**Figure 1**) [6]. They are also often found in vegetative tissues, where they serve mostly as defence compounds. In previous work done mostly with vegetative tissue, but also with daffodil petals, it was found that monoterpenes are synthesized in the plastid compartment. In this cellular compartment, isopentenyl pyrophosphate (IPP) is derived from the mevalonate independent "Rohmer" pathway [7]. IPP can be isomerized to dimethylallyl diphosphate (DMAPP), and one molecule of IPP is condensed with one molecule of DMAPP in a reaction catalyzed by the enzyme geranyl pyrophosphate synthase (GPPS) to form GPP, the universal precursor of all the monoterpenes. Similar research with vegetative tissue has revealed that in the cytosol, IPP is derived from the mevalonic acid pathway [8], and two molecules of IPP and one molecule of DMAPP are condensed in a reaction catalyzed by the enzyme farnesyl pyrophosphate synthase (FPPS) to form FPP, the universal precursor of all the sesquiterpenes [9]. To date, only the enzyme that catalyzes the formation of the acyclic monoterpene linalool has been characterized in floral tissue. *Clarkia breweri* flowers emit copious amounts of *S*-linalool from the petals, stigma, and style (the stigma and style

also emit large amounts of linalool oxides), and it is demonstrated that linalool was synthesized from GPP in a one step reaction (Figure 1) catalyzed by a monomeric enzyme linalool synthase (LIS) [10]. LIS was also purified from *C. breweri* stigmata by employing several chromatographic techniques [11] and to obtain peptide sequences that allowed us to isolate a LIS cDNA clone from a *C. breweri* flower cDNA library [12]. The phenylpropanoids, which are derived from *Phenylalanine*, constitute a large class of secondary metabolites in plants. Many are intermediates in the synthesis of structural cell components (e.g. lignin), pigments (e.g. anthocyanins), and defence compounds. These are not usually volatile. However, several phenylpropanoids whose carboxyl group at C9 is reduced (to the aldehyde, alcohol, or alkane/ alkene) and/or which contain alkyl additions to the hydroxyl groups of the benzyl ring or to the carboxyl group (i.e. ethers and esters) are volatiles (**Figure 2**). *Clarkia breweri* flowers has now resulted in the identification and characterization of three enzymes that catalyze the formation of floral volatiles from this group: (iso)methyleugenol, benzylacetate, and methylsalicylate. The enzymes are, respectively, *S*-adenosyl-l-Met:(iso) eugenol *O*-methyltransferase (IEMT), acetyl-CoA:benzylalcohol acethyltransferase (BEAT), and *S*-adenosyl-l-Met:salicylic acid carboxyl methyltransferase (SAMT) [13-17]. In addition, they have identified and characterized the enzyme *S*-adenosyl-l-Met:benzoic acid carboxyl methyltransferase (BAMT), which catalyzes the formation of methylbenzoate in snapdragon flowers [18]. cDNAs encoding all of these enzymes have also been characterized.

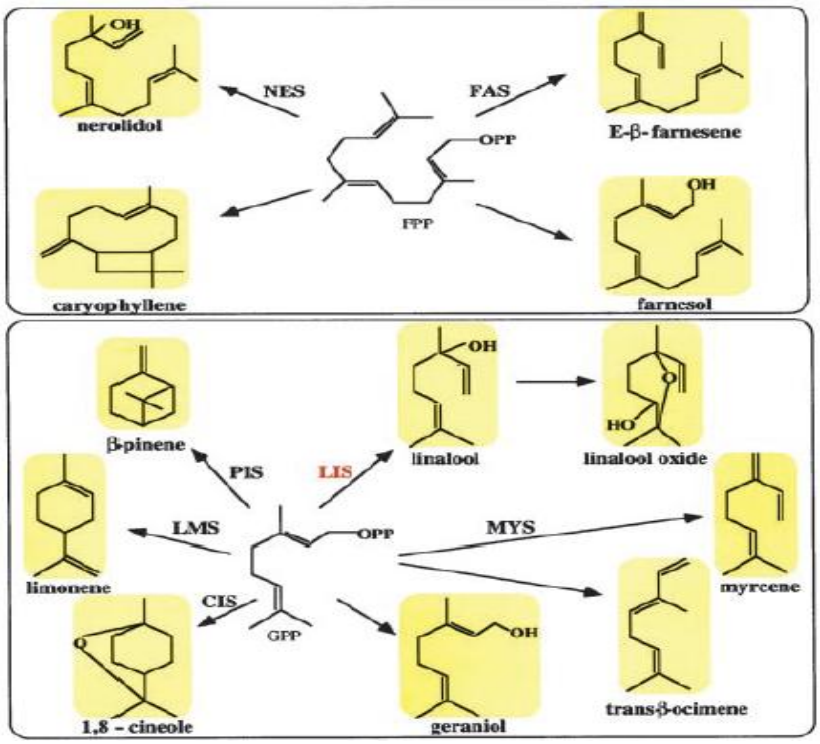

Figure 1 Pathways that lead to floral scent volatiles. Volatile compounds are shown with a yellow background; enzymes that have been identified in the synthesis of volatile compounds in vegetative tissues are shown in black; enzymes identified in floral tissues are shown in red. Not all reactions or enzymes have been identified. Sesquiterpenes (top) are synthesized in the cytosol. Biosynthesis of monoterpene (bottom) occurs in the plastids, although the location of the reactions leading to further modifications (e.g. linalool oxide) is not yet clears [6].

Floral fragrance is important for plant fitness

Many plants emit floral scents, and such scents can attract a variety of pollinators, mostly insects. When present, scent is often the dominant means of long distance attraction, particularly in moth-pollinated flowers, which are searched out and visited at night. Floral fragrances vary widely among species in terms of the number, identity, and relative amounts of constituent volatile compounds. Although little is known about how insects respond to individual components found in floral scents, it is clear that insects are able to distinguish between complex floral scent mixtures, and that discriminatory visitation based on floral scent has important implications for plant reproductive success [19]. Since floral scent can be crucial in ensuring fertilization, and therefore in determining seed or fruit set, the presence or absence of a scent attractive to the locally available insect pollinators may have a substantial impact on the yield of agronomically important crops. Plants did not naturally evolve to produce their scent for the benefit of

humans; nevertheless, it is clear that humans find an aesthetic value in certain types of floral scents, and the presence of floral scent may have contributed to the decision by humans to cultivate and propagate specific plant species. While there is certainly a wide variation in human taste, most people prefer the scents of bee pollinated and, especially, moth-pollinated flowers, which they often describe as "sweet-smelling" [20]. Unfortunately, very few plants are currently cultivated primarily for their scent. Moreover, a large number of commercial flower varieties have lost their scent during the selection and breeding processes due to, on the one hand, a focus on maximizing post-harvest shelf-life, shipping characteristics, and visual aesthetic values (i.e. colour, shape), and on the other hand, to the lack of selection for the scent trait. Some volatile compounds found in floral scent have important functions in vegetative processes as well. They may function as attractants for the natural predators of herbivores or as airborne signals that activate disease resistance via the expression of defence related genes in neighbouring plants and in the healthy tissues of infected plants. They may also serve as repellents against herbivores.

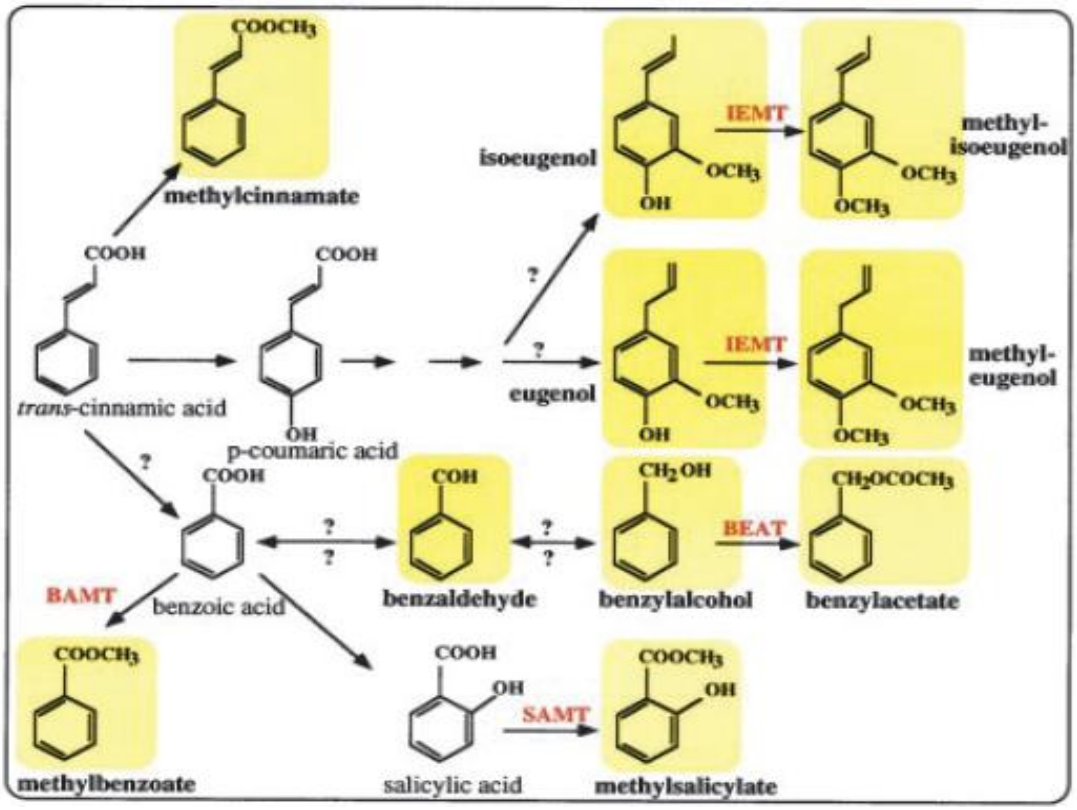

Figure 2 The location of synthesis of most phenolpropanoids/ benzenoids is not yet known, but is likely to be the cytosol and possibly the peroxisomes. IEMT, SAMT, and BAMT are methyltransferases that use SAM (not shown) as the methyl donor. BEAT is an acetyltransferase that uses acetyl-CoA (not shown) as the acetyl donor [6].

Floral scent composition

Until recently, investigations concerning floral scent have concentrated mainly on determining the chemical composition of floral fragrances. For this purpose, the "headspace" collection method was developed. In this procedure, a flower that is still connected to the rest of the plant is placed inside a glass chamber and its emitted volatiles are collected by continually purging the air inside the chamber through a polymer mesh that binds these volatiles. After a fixed period of time, the volatiles bound to the polymer are extracted with an organic solvent (a variation of this procedure, the highly sensitive solid phase micro extraction method, allows for "instant" sampling of headspace volatiles [21]. The solution is then injected into a gas chromatograph, which separates the different volatiles, and each volatile is identified by mass spectrometry. These investigations have determined that floral scents are almost always a complex mixture of small (approximately 100–250 D) volatile molecules and are dominated by monoterpenoid and sesquiterpenoid, phenylpropanoid, and benzenoid compounds (**Figure 1**). Fatty acid derivatives and a range of other chemicals, especially those containing nitrogen or sulphur, are also sometimes present [22].

Temporal and physiological variations in floral scent emission

There are many reasons why plants need to, and often do, vary the floral scent they emit during the lifespan of the flower, both in total output and in specific composition. It is to the advantage of the plant to have its scent output at maximal levels only when its potential pollinator is active. Thus, flowers that are pollinated by nocturnal insects such as moths tend to have maximal scent output in early evening [23], although this is not always the case [10]. Aside from the obvious consideration of conservation of energy, it is also to the advantage of the plant not to attract more general pollinators, who might disperse its pollen non-productively. However, a certain amount of visitation by generalist pollinators might have some benefit to the plant as "insurance," in case its specific pollinator is rare or absent. It has been suggested that specific compounds in floral bouquets are designed to attract specific pollinators, and that some flowers can change their floral scent composition over time to attract more general pollinators if the flower has not yet been pollinated. In addition, it has been hypothesized that some flowers emit certain chemicals designed to repel insects that are non-beneficial to the plant (e.g. the so called pollen or nectar "thieves," or generally destructive insects). Although specific changes in floral scents that follow diurnal, nocturnal, or circadian rhythms (and separate patterns may apply to different compounds in the same flower) or some other specific program over the lifespan of the flower have been well documented [24], knowledge of how insect pollinators respond to specific floral volatiles is so elementary that it is not yet possible to assign specific adaptive values to such changes. It should also be remembered that insects are capable of associative learning, and that the interests of the insect pollinators and those of the plants are not completely complementary, so there is a certain amount of "cheating" going on in these relationships. Sometimes the plants have the upper hand, as in the case of the *Ophrys* genus, where the insects are lured into visiting and pollinating the plants with the ruse of pheromone mimicry by floral scent (as well as morphological mimicry) [25], but often the plants are on the losing end.

Regulation of scent biosynthesis

In both *Clarkia breweri* and *Antirrhinum* majus flowers, emission of the bulk of the volatiles occurs from the petals. Identification of enzymes responsible for the formation of these volatile compounds allowed us to determine how the levels of enzymatic activities are distributed in different floral parts and how they vary during flower development. When activity levels are calculated per total weight of each organ, the highest levels of activity of all scent biosynthetic enzymes are found in the petals [24]. Other parts of the flower, however, also contain detectable levels of activity, and the stigma actually contains higher levels of LIS specific activity (but because the mass of the stigma of *C. breweri* is so small compared with the mass of the petals, LIS in the petal still comprises the majority of activity present in the flower). The specific types of cells expressing the genes encoding LIS and IEMT were determined by *in situ* hybridization. The results indicated that in *C. breweri* flowers, these scent genes are expressed uniformly and almost exclusively in cells of the epidermal layer of petals and other floral parts. Volatile compounds produced in epidermal cells can apparently escape directly into the atmosphere after being synthesized. *C. breweri* flowers, despite being moth-pollinated, do not show marked differences in emission between day and night. Snapdragon flowers, on the other hand, are bee pollinated and have a marked peak of emission during the day. Both types of flowers follow a long-term pattern in which emission peaks within a few days of anthesis and then declines gradually. In *Clarkia breweri*, the activities of scent enzymes follow two different patterns. The activities of the first group of enzymes, represented by LIS and SAMT, increase in maturing buds and young flowers, peaking about 12 to 24 h ahead of peak volatile emission. LIS and SAMT activities then decline in old (5 days) *C. breweri* flowers, but remain relatively high (40%–50% from the maximum level) even though emission of linalool and methylsalicylate has practically ceased. The causes and consequences of appreciable levels of activity of biosynthetic enzymes in old flowers, without concomitant emission of the volatile products, are unknown. Although it is possible that the biosynthetic pathways in which these enzymes participate are blocked elsewhere, another possibility that remains to be investigated is that the products of the reactions catalyzed by these enzymes are required for processes other than scent emission in the flowers. Indeed, it has been found that the flowers of many species accumulate glycosides of scent compounds as they age [26]. Such non-volatile glycosides are also sometimes found in buds, and were therefore originally hypothesized to be obligatory "scent precursors." However, closer examination has shown that, in most cases, an increase in emission of a particular volatile is not accompanied by a corresponding decrease in levels of the glycoside of this volatile, as would be predicted by this hypothesis [26]. The increased synthesis of such glycosides as the flowers age may account for the cessation of scent emission, although the specific roles of such glycosides in the flower remain to be determined. Expression of genes encoding scent-biosynthetic enzymes in the *C. breweri* flower is temporally and spatially regulated during flower development. The mRNAs encoding LIS, IEMT, and BEAT are first detected in

petal cells just before the flower opens, and their levels increase until they peak at or around anthesis and then begin to decline [12-14]. For all of these three genes, peak levels of the mRNAs occur 1 to 2 day ahead of the peaks of enzyme activity and emission of the corresponding compound. Similar results were found for these mRNAs in other parts of the flower.

On the evolutionary scale, it would be instructive to examine the molecular processes that bring about the variability in floral scent characteristics among different species, whether they are on the level of gene regulation, post-transcriptional regulation, or protein evolution. Finally, the contribution of specific scent compounds in attracting specific pollinators needs to be rigorously examined. The availability of scent genes should allow us to create transgenic lines whose floral bouquets differ by a single component.

Table 1 Chemical constituents of floral scent

Serial No.	Flower crops	Chemical constituents
1	Rose	Geraniol, Eugenol, Rhodinol, Citronellol (40-65 %), Linolool, Phenyl Ethyl Alcohol, Rhodinyl acetate
2	Jasmine	Benzyl Acetate, Linalool, Benzyl Alcohol, Indole, Benzyl Benzoate, Cis-Jasmone, Geraniol, Methyl Anthranilate and trace amounts of p. Cresol, Farnesol, Cis-3-Hexenyl Benzoate, Eugenol, Nerol, Ceosol, Benzoic Acid, Benzaldehyde, Y-terpineol, Nerolidol, Isohytol, Phytol
3	Tuberose	Geraniol, Methyl Benzoate, Methyl Anthranilate, Benzyl Alcohol, Butyric Acid, Eugenol, Nerol, Farnesol,Methyl Salicylate, Benzyl Benzoate
4	Marigold	Tagetone, Limonene, Valeric Acid, Ocimene, Dihydrotagetone, Allo Ocimene, Terpinen-4-Ol, Caryophyllene Oxide, Cymene
5	Geranium	Geraniol, Geranial, Imonene, Benzene Acetaldehyde,Myrcene, Linalool, Citronellol, Eugenol, Agarofuran, Gernyl Propanoate, Germacrene, Menthol, Menthone, B- Caryophyllene, Geranyl Tiglate, Hinesol, Piperitone,A-Guaine
6	Gardenia	Benzyl Acetate, Styroyl Acetate, Linalool, Linalyl Acetate, Terpeneol, Methyl Anthranilate
7	Carnation	Hexanal, (2E)- Hexanal, 1-Hexanol, 2-Hexanol, 3-Hexen-1-ol, Nonanal, Benzaldehyde, Benzyl Alcohol, Benzyl Benzoate, Caryophyllene
8	Lavender	Linanyl Acetate, Linalool, Borneol
9	Vanillin orchid	Eugenol, Caproic Acid, Acetaldehyde, Acetic Acid, Furan-2-Carbaldehyde, Hexanoic Acid, 4-Hydroxybenzaldehyde, 2-Methoxy-4-(Prop-2-En-1-Yl)Phenol, Methyl 3-Phenylprop-2-Enoate, 2-Methylpropanoic Acid
10	Vanda Mimi Palmer	Ocimene, Linalool Oxide, Linalool, Nerolidol, Methylbenzoate Benzyl Acetate, Phenylethanol, Phenylethyl Acetate, Indole, Formanilide
11	Snapdragon	Methylbenzoate, (E)-β-Ocimene and Myrcene
12	Petunia	Methylbenzoate, Benzaldehyde, Phenylacetaldehyde and Benzyl Benzoate

Fragrant varieties of flower crops

Rose

Nurjehan, Best Friend, Double Delight, Fragrance Cloud, Freedom, Red Sensation, Memorial Day, Mr. Lincoln, Scentimental, Papa Miellland, Blue Moon, Rose Sherbet, Sugandha, Raktima, Jawahar, Fragrant Delight

Geranium

Bourbon, CIM-Pawan, Kelkar, Algerian

Gardenia

August Beauty, Little Gem, Heaven Scent, Golden, White Gem

Table 2 List of few fragrant flowers of India

Sr. No	Common Name	Scientific Name	Family
1.	Champa or Joy perfume tree	*Magnolia champaca* or *Michelia champaca*	*Magnoliaceae*
2.	Dwarf magnolia	*Magnolia coco*	*Magnoliaceae*
3.	Southern magnolia	*Magnolia grandiflora*	*Magnoliaceae*
4.	Kewda, fragrant screw pine, umbrella tree, Screw pine, Screw tree	*Pandanus odorifer*	*Pandanaceae*
5.	Leafless Dendrobium	*Dendrobium aphyllum*	*Orchidaceae*
6.	Himalayan fragrant orchid	*Gymnadenia orchidis*	*Orchidaceae*
7.	Freesia	*Freesia* sp.	*Iridaceae*
8.	Milk and wine lily	*Crinum latifolium*	*Amaryllidaceae*
9.	Cape lily	*Crinum powellii*	*Amaryllidaceae*
10.	Spider lily	*Hymenocallis litt*	*Amaryllidaceae*
11.	Daffodil, Narcissus	*Narcissus tazetta*	*Amaryllidaceae*
12.	Corn plant	*Dracaena fragrans*	*Agavaceae*
13.	Mexican tuberose	*Polianthes tuberosa*	*Agavaceae*
14.	Dutch hyacinth	*Hyacinthus orientalis*	*Asparagaceae*
15.	Grape hyacinth	*Muscari armeniacum*	*Asparagaceae*
16.	Red ginger lily	*Hedychium marginatum*	*Zingiberaceae*
17.	Fragrant virgin's Bower	*Clematis flammula*	*Ranunculaceae*
18.	Fragrant acacia	*Acacia farnesiana*	*Mimosaceae*
19.	Amaltas	*Cassia fistula*	*Caesalpiniaceae*
20.	Chinese wisteria	*Wisteria sinensis*	*Fabaceae*
21.	Wild-Tea rose	*Rosa gigantea macrocarpa*	*Rosaceae*
22.	Hiptage	*Hiptage benghalensis*	*Malpighiaceae*
23.	Perfumed passion flower	*Passiflora vitifolia*	*Passifloraceae*
24.	Indian rose chestnut	*Messua ferrea*	*Clusiaceae*
25.	Rangoon creeper	Quisqualis indica	*Combretaceae*
26.	Sweet orange	*Citrus sinensis*	*Rutaceae*
27.	Orange jasmine	*Murraya exotica*	*Rutaceae*
28.	Sweet alyssum	*Lobularia maritima*	*Brassicaceae*
29.	Four O'clock	*Mirabilis jalapa*	*Nyctaginaceae*
30.	Spanish cherry	*Mimusops elengi*	*Sapotaceae*
31.	Gardenia	*Gardenia jasminoides*	*Rubiaceae*
32.	Kadam	*Neolamarckia cadamba*	*Rubiaceae*
33.	Indian pellet shrub	*Pavetta indica*	*Rubiaceae*
34.	Wax flower	*Hoya carnosa*	*Asclepiadaceae*
35.	Lady of the night	*Brunfelsia americana*	*Solanaceae*
36.	Night-blooming cestrum	*Cestrum nocturnum*	*Solanaceae*
37.	Juhi	*Jasminum auriculatum*	*Oleaceae*
38.	Rose	*Rosa damascene*	*Rosaceae*
39.	Lemon grass	*Cymbopogon citrates*	*Poaceae*
40.	Calendula	*Calendula officinalis*	*Asteraceae*

Conclusion

This article provides better understanding of biosynthesis of scent based on morphological and biochemical aspects. Further modification of metabolic pathway will help in production of novel plant products. The transgenics can be generated producing scented varieties without losing the commercial traits like vase life in flowers. Floral scent also helps in attracting pollinators thereby increasing productivity of many crops. Further value addition through

preparation of varied scent products is also commercial niche. Nowadays more research is oriented towards the evaluation of pesticidal properties of these scent compounds.

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