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REVIEW

Genetic Aspects of Floral Fragrance in Plants

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Abstract—It is generally assumed that compounds are emitted from flowers in order to attract and guide pollinators. Due to the invisibility and the highly variable nature of floral scent, no efficient and reliable methods to screen for genetic variation have been developed. Moreover, no convenient plant model systems are available for flower scent studies. In the past decade, several floral fragrance-related genes have been cloned; the biosynthesis and metabolic engineering of floral volatiles have been studied with the development of biotechnology. This review summarizes the reported floral fragrance-related genes and the biosynthesis of floral scent compounds, introduces the origin of new modification enzymes for flower scent, compares different methods for floral fragrance-related gene cloning, and discusses the metabolic engineering of floral scent. Finally, the perspectives and prospects of research on floral fragrance are presented.

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Key words: biosynthesis, floral scent compound, gene cloning, evolution, genetic manipulation, metabolic engineering

Flowers of many plants emit scent, a composite character determined by a complex mixture of low-molecular-weight volatile molecules. It is generally assumed that compounds are emitted from flowers in order to attract and guide pollinators [1]. Some volatile compounds found in floral scent play important roles in vegetative processes. They may function as chemical signals that attract natural enemies of herbivores [2] or as airborne signals that activate defense responses in the healthy tissues of infected plants [3, 4]. In addition, volatile compounds emitted from flowers and vegetative parts may repel herbivores [5]. Moreover, the compositions of floral scents have been widely applied to the perfume, cosmetic, and fragrance industries.

Though floral volatiles play important roles in plant propagation and vegetative processes, no simple, efficient, and reliable methods to screen for genetic variation have been developed [6]. The difficulties in investigations of the biochemical and genetic basis of scent production are due to the invisibility of floral scent, the highly variable nature of the trait, and the shortcomings of humans' sense of smell. Moreover, very few plants are currently cultivated primarily for their scent, so a large number of commercial flower varieties have lost their scent during the selection and breeding processes.

For many years, research into flower fragrance has focused mainly on its chemical analysis coupled with chemical synthesis because of the commercial value of floral volatiles in perfumery, and several thousands of volatiles have been identified [7], whereas until the last few years there have been few studies concerning the bio-

Abbreviations: AAT) alcohol acetyltransferase; BAMT) S-adenosyl-L-methionine:benzoic acid carboxyl methyltransferase; BEAT) acetyl CoA:benzylalcohol acetyltransferase; BEBT) benzoyl CoA:benzyl alcohol benzoyl transferase; BPBT) benzoyl-CoA:benzyl alcohol/phenylethanol benzoyltransferase; BSMT) S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase; CaMV35S) cauliflower mosaic virus 35S; CST) *p*-coumaroyl-CoA:shikimic acid *p*-coumaroyl transferase; DMT) 3,5-dimethoxytoluene; DMAPP) dimethylallyl diphosphate; DXR) 1-deoxy-D-xylulose-5-phosphate reductoisomerase; EST) expressed sequence tag; FaNES1) *S*-linalool/(3*S*)-*E*-nerolidol synthase 1; FPP) farnesyl pyrophosphate; GPP) geranyl pyrophosphate; IEMT) S-adenosyl-L-methionine:(iso)eugenol O-methyltransferase; IPP) isopentenyl pyrophosphate; LIS) linalool synthase; OOMT) orcinol *O*-methyltransferases; POMT) phloroglucinol *O*-methyltransferase; RACE) rapid amplification of cDNA end; SAM) S-adenosyl-L-methionine; SAMT) S-adenosyl-L-methionine:salicylic acid carboxyl methyltransferase.

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chemical synthesis of floral scent compounds and the enzymes and genes that control these processes. Although the number of genes involved in the biosynthesis of floral scent compounds that have been cloned is steadily increasing, biochemical and molecular knowledge of the biosynthesis of scent compounds is still limited [8]. Just because of the complexity of biochemical and genetic processes involved in the biosynthesis of floral volatiles, traditional breeding technologies fail to solve the problem of fragrance absence in plants, whereas it may be obtained by means of metabolic engineering that bring new ideas and methods. So far, several floral fragrance-related genes have been isolated and characterized, and their cDNA have been cloned. Furthermore, some genes have been introduced to fragrance-lacking plants.

In this paper, we review the floral fragrance-related genes that have been cloned, compare different methods of floral fragrance-related gene cloning, and discuss the metabolic engineering of floral scent. Finally, the perspectives and prospects of research on floral fragrance are presented.

CLONING OF FLORAL SCENT GENES

Biosynthesis of floral scent compounds. Many flowers emit a mass of volatile compounds, but these compounds are often biosynthesized by only a few overlapping metabolic pathways (figure, panel (a)) [6]. Generally, floral fragrances are dominated by terpenoids, phenylpropanoids, and benzenoids. Fatty acid derivatives and other chemicals, especially those containing nitrogen or sulfur, are also sometimes present [9]. Terpenoids, divided into monoterpenoids and sesquiterpenoids, are the largest group of natural volatile products known [10]. The monoterpenoids and sesquiterpenoids derive from the mevalonic acid pathway via geranyl pyrophosphate (GPP) and farnesyl pyrophosphate (FPP), respectively [8, 11]. In the cellular compartment, isopentenyl pyrophosphate (IPP) can be isomerized to dimethylallyl diphosphate (DMAPP), and one molecule of IPP is condensed with one molecule of DMAPP in a reaction to form GPP; two molecules of IPP and one molecule of DMAPP are condensed in a reaction to form FPP. Then different mono- or sesquiterpene synthases catalyze the formation of GPP or FPP to form monoterpenes or sesquiterpenes [11].

Phenylpropanoids including benzenoids derive from shikimic acid via phenylanaline, cinnamic acid, and further decarboxylation and ring oxidation (figure, panel (b)) [9]. Fatty acid derivatives are products of the malonic acid pathway [12]. Other volatile compounds, such as short-chain alcohols and aldehydes, originate from membrane lipids and are the products of the lipoxygenase pathway [13].

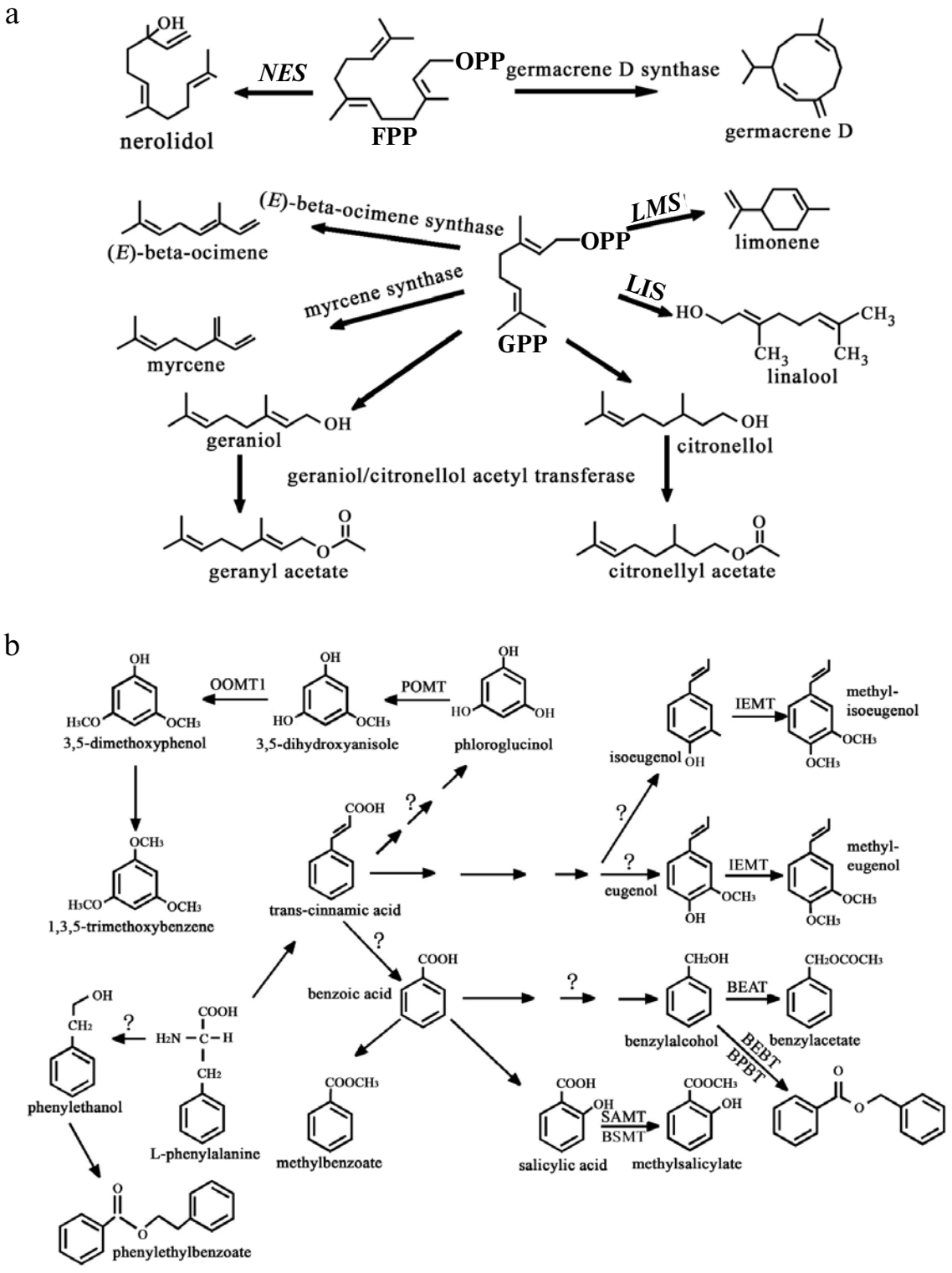
Genes involved in floral scent production. Methods of their cloning. Biochemical processes involved in the synthesis of the aforementioned floral scent compound classes are catalyzed by many vital enzymes. Recently, some genes that encode these enzymes have been isolated and characterized, and their cDNA have been cloned from several model plants.

The first floral scent biosynthetic gene that was isolated and characterized was the linalool synthase (LIS) gene from *Clarkia breweri*. The enzyme catalyzes the formation of an acyclic alcohol, monoterpene linalool [14]. The LIS protein was purified to homogeneity from stigmata of *C. breweri*, and its cDNA was cloned [15, 16]. The floral fragrance-related genes characterized and cloned to date are shown in the table.

Among the enzymes encoded by those genes, LIS, β-ocimene synthase, myrcene synthases, geraniol/citronellol acetyl transferase, and germacrene D synthase catalyze the production of terpenoids. (Iso)eugenol O-methyltransferase (IEMT), benzylalcohol acetyltransferase (BEAT), salicylic acid carboxyl methyltransferase (SAMT), benzyl alcohol benzoyl transferase (BEBT), benzoic acid/salicylic acid carboxyl methyltransferase (BSMT), benzyl alcohol/phenylethanol benzoyltransferase (BPBT), benzoic acid carboxyl methyltransferase (BAMT), phloroglucinol *O*-methyltransferase (POMT), and orcinol *O*-methyltransferases (OOMT) 1 and 2 catalyze the production of phenylpropanoids and benzenoids. The processes of floral scent compound synthesis catalyzed by those enzymes are shown in the figure. To date, no enzymes that are involved in the fatty acid derivatives production have been isolated and characterized from scented plant.

The aforementioned floral scent genes were isolated mainly via three approaches. The genes coding for LIS, BEAT, SAMT (from *C. breweri*), IEMT, BAMT, and POMT, were isolated via classical biochemical approaches. The method uses reverse genetics approaches to screen targeted cDNA library with probes obtained from purified enzymes sequences. Genes encoding POMT have been cloned by the method of rapid amplification of cDNA end (RACE) with degenerate primers designed based on amino acid sequence of purified enzyme. In general, the floral scent genes could be isolated accurately by this classical biochemical method, but the step of purification of enzymes is often very difficult [30].

In the recent years, a similarity-based cloning technique based on the use of conserved sequence elements for design of degenerate primers for PCR amplification was developed [30]. This method has been used to clone the genes coding taxadiene synthase from *Taxus brevifolia* and myrcene synthase from *Abies grandis* [31, 32]. In addition, the BSMT and SAMT (from *Stephanotis floribunda*) genes involved in floral scent formation were also isolated by RT-PCR and RACE based on sequence information available from previously identified scent-related genes [20, 22]. This method can isolate target genes efficiently, but as for most floral scent genes, it is difficult to



Pathways leading to floral scent volatiles (by [8]). Enzymes that have been identified in the synthesis of volatile compounds in vegetative tissues are shown in italic letters; enzymes identified in floral tissues are shown in normal letters. a) The biosynthesis of sesquiterpenes (top) and the biosynthesis of monoterpenes (bottom). Geraniol/citronellol acetyl transferase catalyzes the formation of geranyl acetate and citronellyl acetate from geraniol and citronellol, respectively. b) The biosynthesis of phenylpropanoids/benzenoids. IEMT, SAMT, BAMT, and BSMT are methyltransferases that use S-adenosyl-L-methionine (SAM) (not shown) as the methyl donor. BEAT and geraniol/citronellol acetyl transferase are acetyltransferases that use acetyl-CoA (not shown) as the acetyl donor. BEBT and BPBT are benzoyltransferases that use benzoyl-CoA (not shown) as the acetyl donor

List of cloned floral fragrance-related genes

Name of gene or gene product	Coded enzyme	Source	Product of the reaction catalyzed by encoded enzyme	GenBank accession No.	References
LIS	LIS	*Clarkia breweri*	linalool	U58314	[15]
IEMT	IEMT	*C. breweri*	methyleugenol and isomethyleugenol	U86760	[17]
BEAT	BEAT	*C. breweri*	benzyl acetate	AF043464	[18]
SAMT	SAMT	*C. breweri* *Stephanotis floribunda*	methyl salicylate	AF133053 AJ308570	[19] [20]
BEBT	BEBT	*C. breweri*	benzyl benzoate	AF500200	[21]
BSMT	BSMT	*Nicotiana suaveolens*	methyl benzoate and methyl salicylate	AJ628349	[22]
BPBT	BPBT	*Petunia x hybrida*	benzyl benzoate and phenylethyl benzoate	AY611496	[23]
BAMT	BAMT	*Antirrhinum majus*	methyl benzoate	AF198492	[24]
β-Ocimene synthase	β-ocimene synthase	*A. majus*	β-ocimene	AY195607	[25]
Myrcene synthase	myrcene synthase	*A. majus*	myrcene	AY195608 AY195609	[25]
Germacrene D synthase	germacrene D synthase	*Rosa x hybrida*	germacrene D	FC0592	[26]
Geraniol/citronellol acetyl transferase	geraniol/citronellol acetyl transferase	*R. hybrida*	geranyl acetate/ citronellyl acetate	AY850287	[27]
OOMT1 and OOMT2	OOMT1 and OOMT2	*R. hybrida*	(3-methoxy,5-hydroxy-toluene and 3,5-dimethoxytoluene) or (3,5-dimethoxyphenol and 1,3,5-trimethoxybezene)	AF502433 AF502434	[28]
POMT	POMT	*R. chinensis*	3,5-dihydroxyanisole	AB121046	[29]

design primers because available information is still extremely poor.

Another method is the genomics approach. The method is high-throughput technology, which applies expressed sequence tag (EST) database, metabolic profiling, microarray expression analyses, proteomics, and serial analysis of gene expression (SAGE) to identify new genes [33]. The germacrene D synthase gene was obtained by combining EST database mining with metabolic profiling and microarray expression analyses. The genes coding for BEBT, β-ocimene synthase, and myrcene synthase were cloned by combining RACE with the EST database. The OOMT1 and OOMT2 were identified in EST database by homology search (BLAST) with other O-methyltransferases, and in the same way, the BPBT gene was isolated. The geraniol/citronellol acetyl transferase gene was also identified with other alcohol acetyltransferases and then cloned. Generally, this method is informative, but it needs advanced equipment and abundant funds. So, it does not suit the common laboratory.

Overall, the studied fragrance-related genes come mainly from four model plants, namely *C. breweri*, *Antirrhinum majus*, *Nicotiana suaveolens*, *Petunia x hybrida*, and *Rosa x hybrida*, because most biochemical and biological researches have been performed in these plants. With the development of biotechnology and its cost reduction, more plants that are fragrant can be used as floral scent research materials, and the genomic approaches may be widely applied to cloning of fragrance-related genes. In addition, the similarity-based cloning technique may be also widely applied to the clones of fragrance-related genes in the future.

ORIGIN OF NEW MODIFICATION ENZYMES FOR FLOWER SCENT

It is believed that plants possess several families of modifying enzymes that catalyze similar reactions but use distinct substrates [34]. Moreover, clear patterns in the evolution of these families could be discerned [35]. An enzyme can be defined as new when: (i) the gene encodes an enzyme that catalyzes a chemically similar reaction but on a different substrate than the enzyme encoded by its progenitor gene; or (ii) the enzyme carries out a different chemical reaction on the same substrate.

One way that new volatiles are produced is because of the evolution of new enzymatic functions. First, gene duplication followed by divergence retains the original enzymatic function in the plant, while the duplicate gene can then accumulate mutations until it has acquired a new function and might then become fixed in the population [36]. OOMT1 and OOMT2 from *R. hybrida* illustrate the processes of gene duplication followed by divergence, with OOMT1 and OOMT2 performing the last two O-methylation steps to form dimethoxytoluene and trimethoxybenzene [28]. Furthermore, convergent evolution, where new functions arise independently multiple times, occurs in this process of gene duplication and divergence. Though the BEAT [18, 37] and the BEBT [21] from *C. breweri* both utilize the same substrate (benzyl alcohol) as the most efficient acyl acceptor, they belong to two very divergent clusters in the family tree. This is an example of convergent evolution. A special case of convergent evolution, termed repeated evolution, where a new and identical (or very similar) genetic function arises independently in the same gene family from two or more orthologous or paralogous genes that did not share the same function [35]. The LIS from *C. breweri* catalyze the production of (+)-3S-linalool from GPP [16]. Nevertheless, the LIS [38] from *Mentha aquatica* catalyze the production of (–)-3R-linalool. Moreover, molecules of 3R-linalool and 3S-linalool are not the same; they are enantiomers. This is a perfect example of repeated evolution.

Furthermore, a new enzyme is likely to be a variation of an existing enzyme that uses a similar substrate and catalyzes the formation of a similar product. This will result in a new enzymatic function, but also leads to concomitant loss of the prior function. This way will result in an enzyme that can carry out the same type of reaction on a new substrate, or carry out a different reaction on an old substrate [35]. For example, the IEMT from *C. breweri* has been shown to have arisen from the caffeic acid *O*-methyltransferase (which methylates caffeic acid to give ferulic acid and is involved in lignin biosynthesis).

New volatiles may also arise due to absence of enzymatic activity that is caused by loss of gene expression. This would occur due to hybrid formation and accompanying chromosomal rearrangements or when it is damaged by point mutations [39]. The transposons or other factors may disrupt the coding region of the gene or silence gene expression [40]. Changes in regulatory protein expression may also lead to changes in gene expression [41]. Basil varieties that produce eugenol and methyleugenol actively express *p*-coumaroyl-CoA: shikimic acid *p*-coumaroyl transferase (CST) in the glandular trichomes [42]. However, other basil varieties that produce high levels of methylchavicol without methyleugenol or eugenol do not have detectable CST activity in the glandular trichomes. So, differential production of volatiles in basil varieties (eugenol/methyleugenol versus methylchavicol) is due to differential expression of the branch point CST in the pathway. This is an example of the evolution of gene expression that is probably caused by a change in a regulatory protein.

GENETIC MANIPULATION OF FLORAL SCENT

For many years, research on ornamental plants focused on maximizing post-harvest shelf life, color, shape, and disease resistance of flowers. Traditional breeding of ornamentals has led to a scent reduction of many floricultural varieties due to a negative correlation between flower longevity and fragrance [6]. Absence of scent had been recognized as one of main problems in floriculture, and recent progress in the molecular biology of floral scents offers tools for modification of fragrance in flowering plants.

Metabolic engineering is a science that combines systematic analysis of metabolic pathways with molecular biology techniques to improve the production of existing compounds or mediate their degradation [43]. In recent years, metabolic engineering has been also applied to modify the scent of flowering plants. In general, it involves two methods: the introduction of exogenous fragrance-related genes and the regulation of endogenous gene expression.

The first approach is based on the introduction of new genes encoding enzymes that produce novel products not normally found in the target plant; this would offer new ideas for genetic improvement of flower fragrance. Moreover, an increasing number of cloned genes encoding scent biosynthetic enzymes may be used in transgenic plants to modify volatile composition.

The difficulties of this method derive from the fact that as far as the plant is concerned, the introduction of foreign genes or the enhancement of an existing genes' activities may be insufficient to modulate flower scent, for instance because of no substrate is availability in the same cell that is one of the main limitations in volatile production. It was recently shown that the level of methyl benzoate produced from snapdragon flowers was limited by the level of the precursor, namely benzoic acid [24]. The gene encoding rose alcohol acetyltransferase (RhAAT)

was introduced into *Petunia hybrida* cv. Mitchell under the control of a constitutive enhanced cauliflower mosaic virus 35S (CaMV35S) promoter. Although the preferred substrate of RhAAT *in vitro* is geraniol, transgenic petunia flowers expressing RhAAT emitted a higher level of benzyl acetate and phenylethyl acetate, indicating that in plants availability of substrates and biochemical properties of the enzyme determine the spectrum of emitted volatiles [44]. In addition, this approach was already accepted in the ornamental industry, but a hazard was still existent when the end products were used directly for cosmetic products or human dietary consumption.

For the past few years, different groups have reported genetic manipulation of plant volatile composition [45]. The LIS cDNA from *C. breweri* was introduced into *P. hybrida* under the control of the CaMV35S promoter. An appropriate enzymatic activity was detected in petals and leaves of the transgenic plant. However, only a trace of S-linalool was detected in flowers; instead, the non-volatile linalool glycoside largely accumulated in the transgenic plants [46].

On the other hand, the same gene was introduced into the carnation that normally produces benzoic acid derivatives and sesquiterpenes but not monoterpenes. The transformation led to the emission of linalool from petals and leaves. Moreover, linalool derivatives *cis*- and *trans*-linalool oxides were also detected from transgenic carnation petals. However, the changes of floral scent were not sufficient for olfactory detection by humans even though linalool and its derivatives (*cis*- and *trans*-linalool oxide) constituted almost 10% of the total volatiles emitted by the petals [47].

LIS cDNA from *C. breweri* has also been expressed in tomato fruit under the control of the tomato late-ripening-specific *E8* promoter and enough S-linalool and 8-hydroxylinalool were produced in ripening fruits to enable detection by the human subjects [45]. In addition, the gene coding S-linalool/(3*S*)-E-nerolidol synthase 1 from *Fragaria anannasa* (FaNES1) was overexpressed in *Arabidopsis* plants. Leaves of transgenic plants emitted linalool and its glycosylated and hydroxylated derivatives and at the same time, low level nerolidol was also detected [48].

Nicotiana tabacum was transformed with three different monoterpene synthases genes from lemon. The leaves and flowers of transgenic tobacco plant produced β-pinene, limonene, γ-terpinene, and a number of side products of the introduced monoterpene synthases, which resulted in drastic changes in fragrance [49]. The transformation of the lemon-scented geranium (*Pelargonium graveolens*) with T-DNA of *Agrobacterium rhizogenes* led to the enhancement of fragrance, the possible reason being that the introduction of the foreign gene changed the metabolic flux [50].

These reports indicate that fragrance modification by introducing foreign genes encoding scent biosynthetic enzymes is possible, but sufficient levels of precursors (such as GPP and FPP) are necessary. In addition, two other problems occurred in the genetic engineering of flower fragrance: (i) the volatile compounds from transgenic plants may be modified into non-volatile form, e.g. by glycosylation and hydroxylation; or some non-volatile derivations occur as concomitant with the aimed production; (ii) the emitted amount of modified scent compounds from transgenic plants may be insufficient for olfactory detection by humans.

The second approach to metabolic engineering is based on down- or up-regulating the expression of endogenous genes to increase the production of desirable volatiles or alternatively blocking the production of an undesirable compound can change the metabolic flow, leading to modification of the fragrance composition.

Up-regulation is based on increasing the amount of precursor through transformation with the genes encoding upstream enzymes in metabolic pathway to enhance the production of target volatiles. In this route, precursor for the volatile composition is a key factor. Methyl benzoate, the most abundant compound in snapdragon (*Antirrhinum majus*), was reported to be regulated by the amount of its precursor, benzoic acid [24]. Peppermint (*Mentha piperita*) was transformed with a homologous sense version of the 1-deoxy-D-xylulose-5-phosphate reductoisomerase cDNA [51]. This upstream enzyme in a mevalonate-independent pathway catalyzes the production of methylerythritol phosphate, which is an intermediate for IPP and DMAPP biosynthesis. The resultant transgenic plants accumulated substantially more essential oil (about 50% yield increase) compared with wild type.

Down-regulation is based on increasing the desirable volatile components through transformation with genes encoding downstream enzymes in metabolic pathway to enhance the quality and commercial value of scent. Down-regulation of limonene hydroxylase using a constitutively expressed antisense transgene resulted in increased levels of limonene in the essential oil of peppermint, indicating the feasibility of pathway engineering to modify essential oil composition in trichomes [52]. In addition, down-regulation of an R2R3 MYB-type transcription factor, ODORANT1 (ODO1), in transgenic *Petunia hybrida* cv. Mitchell (W115) plant strongly reduced volatile benzenoid levels through decreased synthesis of precursors from the shikimate pathway. Suppression of ODO1 expression by RNA interference (RNAi) revealed that it specifically regulates the shikimate pathway in petals toward benzenoid production. This results in a strongly reduced emission of volatile benzenoids, the main compounds of the floral scent [53].

Therefore, the regulation could have an important application in controlling biosynthetic pathways for high-quality fragrance compounds.

Another way of regulation is based on blocking the production of an undesirable volatile that have same pre-

cursor with target compound to increase the level of the latter. This route was demonstrated in carnation, in which blocking the anthocyanin biosynthetic pathway by antisense suppression of the flavanone 3-hydroxylase gene — the critical enzyme catalyzing the formation of anthocyanin — led to increased methyl benzoate production [54]. The enhanced fragrance in the transgenic carnation plants was thus caused by redirection of metabolic flux from anthocyanin biosynthesis to benzoic acid (precursor of methyl benzoate) production, since both anthocyanin and methylbenzoate originate from the same phenylpropanoid pathway.

In general, changes in metabolic flow can increase the content of target volatiles, but it may have a deleterious effect on the plant because the normal levels of general precursors may be necessary for natural plant development. For example, transgenic *Arabidopsis* plants expressing FaNES1 were retarded in their growth compared with wild-type plants grown under identical greenhouse conditions [48]. The reason might be the reduction in the availability of substrates for other metabolites produced in the plastids or the toxic effect of the high levels of linalool produced, as several monoterpenes including linalool have been demonstrated to be harmful to plant cells [55].

The aforementioned examples suggest that the metabolic engineering of odor and flower fragrance is now feasible and has enormous potential. However, it is still in its infancy as different results have been obtained from researches on the emission of desirable volatile compound in modified plants. Like the manipulation of other plant traits, the metabolic engineering of floral scent will require considerable effort before it can become routine, predictable, efficient, and commercially viable. Modification of volatile composition and new aroma introduced into plants will not only increase the value of ornamentals, but may also enhance attraction of pollinators, increasing reproduction efficiency and the yield of important agricultural crops.

CONCLUSIONS AND PERSPECTIVES

The biochemical pathways of floral scent compounds have been elucidated to a certain extent. Several floral fragrance-related genes have been isolated and characterized, and metabolic engineering has been attempted to manipulate floral scent. On the whole, floral fragrance research is still in its infancy, and knowledge of the mechanism regulating fragrance production and emission remains sketchy. Furthermore, to date little information is available for the cellular localization of the substrates responsible for synthesis of scent compounds. Scalliet et al. reported that in the 3,5-dimethoxytoluene (DMT) producing rose (*Rosa x hybrida*) varieties, orcinol *O*-methyltransferases (OOMT) 1 and 2 were shown to be localized specifically in the petal, predominantly in the adaxial epidermal cells. In these cells, OOMTs become increasingly associated with membranes during petal development, suggesting that the scent biosynthesis pathway catalyzed by these enzymes may be directly linked to the cells' secretory machinery [56]. So, in the future the identification and characterization of enzymes and genes that control the synthesis of floral scent constituents should be studied continually, and the cellular location of biosynthesis of most scent compounds still needs to be determined. In addition, to achieve abundant production of new floral scent compounds, several genes active in epidermal cells and encoding the biosynthetic enzymes should be inserted into the plant genome. In such a way, we not only introduce a new scent gene, but may also increase the substrate concentration that is required for production of the corresponding scent compound. Finally, the contribution of specific scent compounds in attracting specific pollinators needs to be examined. The metabolic engineering of floral scent and cloning of floral fragrance-related genes should be constantly studied.

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