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Do we really know the scent of roses?

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Abstract

Roses have been admired ever since antiquity. They have followed all of the human history for reasons other than just medicine and food, mostly because of their beauty and their fragrance. They have always been used in perfumes, in gardens, and yet again in the cut flower market. Humans have listed more than 25,000 cultivars to this day, while there are only a little over a hundred species in the wild. In this review, we will present the domestication history of roses used for perfumes, and the selection of garden roses and cut rose cultivars. We will also compare the scent of modern roses and wild roses and give the chemical analysis of representative volatile compounds that have been characterized in roses. We will then summarize the biochemical pathways that have been studied in roses at the gene level. We will conclude that scent is not a trait in itself but a multitude of traits driven by many genes. Their alleles could perhaps be used as markers for the selection of new cultivars.

Key-words

Rose; scent; terpenes; essential oil; biosynthetic pathways; volatile compounds; chemical ecology; specialized metabolites

Introduction

Among flowers, roses have had a place of honor ever since antiquity (Krüssmann 1981). In ancient Greece, Aphrodite, the Goddess of Love, is said to have created red roses with her blood, and in ancient Persia and India, the bride of Vishnu was created from rose petals. The rose is mentioned in the oldest cuneiform texts known to mankind (approx. 1800-800 B.C.E. for different versions; (Azrié 2015). As far back as 600 B.C.E., Sappho, an Archaic Greek poet, named her the queen of flowers. This craze has never ceased to this day and has spread throughout the world. It is the most striking example of a plant that has followed history of Mediterranean civilizations on a large scale for aesthetic and symbolic reasons, and not strictly for food or medicine. It can be estimated that over 25,000 cultivars have been created by breeders (Cairns 2000; Young and Schorr 2007), most of them since the 18th century in Western countries. Fragrance has always been a criterion of choice for the

domestication of spontaneous mutations or crossings, and for the breeding of roses. The Romans and Persians already cultivated roses and used them to perfume objects, fabrics, oils, or water by maceration. This is not very different from what is being done today, with the exception that hydrodistillation and modern techniques are now used for the extraction of scent (Brun and Fernandez 2015). Nowadays, garden roses have a huge diversity of scents such as myrrh, tea, lemon, peach, or parsley for example. This is the result of a long history of domestication and breeding from wild briars of the genus *Rosa* to modern roses (Fig. 1), a process in which the scent was one of the major players. Unfortunately, some cultivars, such as those used for cut roses, are less fragrant. Indeed, during the 20th century and for the cut flower market, growers have paid more attention to the long vase life character rather than to the criteria of scent.

For the past 20 years, researchers have begun to decipher the biochemical pathways of volatile molecules that constitute the rose scent (Smulders et al. 2019). This allowed them to suspect that the scent is not a trait in itself but a multitude of traits driven by many genes (Spiller et al. 2010; Roccia et al. 2019; Schulz et al. 2021). Furthermore, they discovered that roses sometimes synthesize common volatile compounds with uncommon enzymes. Evolution's driving force may have played a major role in this phenomenon, or the domestication process may have created new biochemical functions (Magnard et al. 2015; Sun et al. 2016; Baudino et al. 2020).

In this review, we will describe the domestication of roses, in particular those which are used for the perfume market. We will also question whether the fragrance of wild roses is different from that of modern roses. This aspect will allow us to discuss the chemical composition of the fragrance of roses, the biosynthesis of their volatile compounds and the corresponding genes that have been studied. We will conclude on the possibility of understanding the inheritance of fragrant molecules to drive crossbreeding more efficiently.

History of the domestication of roses used for perfumes

The domestication of roses certainly dates back more than 2,000 years in the Mediterranean area, the Middle East, and China (Krüssmann 1981; Touw 1982; Wang 2007). Earliest Western record of a wild rose drawing was found on the murals of Knossos palace (approx. 1700-1500 B.C.E.; Fig. 2), but one of the oldest types of evidence (approx. 1200 B.C.E.) for the use of roses was discovered on a tablet in the palace of Nestor in Greece, which reported the composition of an anointment. Furthermore, Homer, the Greek poet, narrated the anointing of the corpse of Hector by Aphrodite with rose oil as a divine oil, before 8th century B.C.E. After that, ancient authors described the importance of the scent of roses in religious ceremonies, in pharmacopoeia, in banquets, in thermal baths, or even for seduction (Brun 1998; Brun and Monteix 2009). Concrete evidence of the domestication of roses were provided by recipe descriptions of rose perfumes, named *rhodinon*, by depiction on murals, and by texts describing cultivation of ever-blooming roses with hundreds of petals (Krüssmann 1981; Brun and Monteix 2009; Fernandez and Levasseur 2013). *Rhodinon* was obtained by maceration of petals in hot oil. Indeed, semi-double roses are painted on murals of Villa de Livia in Rome (55 to 29 B.C.E), and in Casa del Bracciale d'Oro in Pompei (79 C.E.). Double roses are represented in mosaics (100-200 C.E.) of the Museum of Vatican, and fields of ever-blooming roses were described by Virgil (37 to 30 B.C.E.) and Martial (101 to 102 C.E.). Semi-double, double and ever-blooming characteristics can be interpreted as domestication traits. Numerous authors tried to identify these roses and it is very common to give the name *R. × damascena* 'Bifera' to ever-blooming roses of the Roman Empire, and *R. gallica* 'Officinalis' or *R. × centifolia*, to roses found on antic murals and mosaics. Nevertheless, the exact identification of these species is impossible, as the notion of species and variety did not exist at that time. For example, the mention of the term 'biferous rose' in

an ancient text could very well correspond to a mixture of roses in the same field, some flowering early and the others later.

In reaction to Romans, early Christians denounced the use of perfumes, assimilated to lust, around the year 100 C.E. (Touw 1982). In the Middle Ages, rose perfumes were only used in the Middle East. In Europe, roses were mainly used for their symbolism and rose cultivation for perfumes was neglected until around the years 700-800 C.E (Krüssmann 1981). In China, roses had also been cultivated ever since at least 200 B.C.E., but traits of domestication such as the ever-blooming character seem to have appeared later on, around 1000 C.E. (Wang 2007). The use of rose water, thus hydrodistillation, is attested by a written debt of 30,000 bottles to the Caliphate of Bagdad circa 810-817 C.E. (Widrechner 1981). The separation of water and oil during the distillation process was described in the Middle East around the year 900 C.E. The essential oil was called “attar of roses” (Touw 1982). Europeans reintroduced the use of roses for medicine and for hygiene by bringing back cultivated roses during the Crusades and afterwards. From this period, only two main roses were used for the extraction of perfumes: *R. gallica* ‘Officinalis’ and *R. × damascena* ‘Trigintipetala’. According to some authors, the first cultivar had been known since Antiquity; for others it was brought back from the region of Damask in 1238 C.E. by Thibault IV of Champagne, or by “Le Bon Roi René” in the 15th century (Joyaux 1998). *Rosa gallica* ‘Officinalis’ was largely cultivated in Provins (France), firstly for its medicinal properties but rapidly for its beauty and perfume. It quickly became the rose of apothecaries, called the Rose of Provins. At this period (Champier 1512) wrote a book on plants used for nutrition and health, and named it *R. gallica*. Unfortunately, there are lots of confusions in the literature regarding *R. gallica*, *R. gallica* ‘Officinalis’, Rose of Provins, Apothecary Rose, Gallic Roses, and their hybrids. It is very difficult to identify synonyms or varieties among these names. The second cultivar, *R. × damascena* ‘Trigintipetala’, is a Damask rose commonly equated with *R. × damascena* ‘Kazanlik’. Indeed, this is probably the same cultivar as the one which had been cultivated in Kazanlik in Bulgaria since the 16th century. In an ordinance, Sultan Murad III (1574-1574 C.E.) gave the order to cultivate *R. × damascena* in the old palace of Constantinople for its essential oil (Joyaux 2005; Roques 2021). Today, *R. × damascena* ‘Kazanlik’ is the most widely used rose cultivar for essential oil extraction all around the Mediterranean basin and the Middle East (Rusanov et al. 2009). The oil production is mostly localized in Bulgaria, Turkey, and Morocco thanks to the use of this cultivar. Some local productions are also using this cultivar alongside others, as in Iran or India for example. According to genetic markers, all the Damask roses could be originating from a single natural cross between *R. moschata* and *R. gallica*, itself crossed with *R. fedtshenkoana* (Iwata et al. 2000). In any case, the genetic diversity of these oil producing cultivars is particularly low (Baydar et al. 2004; Rusanov et al. 2005; Rusanov et al. 2009; Smulders et al. 2011), with the exception of some cultivars from Iran, which could thus be, together with Turkey, the geographical origin of *R. × damascena*’s biodiversity (Widrechner 1981; Babaei et al. 2007).

At the end of the 19th century, attempts to obtain new cultivars for scent extraction were successful, but unfortunately their usage did not last long. This is for example the case for *R. rugosa* hybrids and for Crimean roses. ‘Roseaie de l’Haÿ’ and ‘Rose à Parfum de l’Haÿ’ were two famous cultivars obtained in 1901 C.E. by Jules Gravereaux and Cochet-Cochet to respond to a request from the Ministry of Agriculture for French essential oil production. The first one was a seedling of *R. rugosa* ‘Rubra’, and the second one a progeny of (*R. × damascena* ‘Bifera’ × *R. ‘Général Jacqueminot’*) × *R. rugosa* (Young and Schorr 2007). Unfortunately, growers were used to harvesting roses in May during a short blooming period, and then moving on to another plant production. They therefore never got used to working with staggered and extended blooming. Furthermore, these cultivars were not easy to acclimatize for production in Grasse, the major production center in France at that time. Crimean roses have also been selected in the Soviet Union since 1877 C.E. after an order of

the Ministry of State Property to cultivate *R. × damascena* in Crimea (Marko et al. 2020). The first cultivar adapted to cold conditions was 'Krymskaya Krasnaya', a seedling of *R. gallica* obtained in 1926 C.E. Numerous cultivars were then obtained for local culture, such as 'Festivalnaya' for example (Widrechner 1981; Marko et al. 2020). They came from different crossings involving *R. gallica* and *R. × damascena*. Unfortunately, despite the great success for this oil in the U.S.S.R., production was stopped at the end of the 20th century. Other cultivars were sometimes used for oil production at the end of the 19th century, such as 'Ulrich Brünner fils' in France (Rolet 1918), and *R. alba* in Bulgaria (Rolet 1918; Verma et al. 2020), but *R. × damascena* 'Kazanlik' has never been dethroned. Nevertheless, some countries, such as China for example, are still developing new cultivars and trying to obtain quality certificates for their rose extracts. Nowadays, hydrodistillation is the most common process for obtaining essential oil. Petals are immersed in water heated to 100°C. The vapor condenses after cooling in a coil. Through decantation, a layer of rose water is obtained, surmounted by essential oil, essence, or attar of rose. The production of 1 kg of distilled essential oil requires 3 to 5 tons of roses, the equivalent of about 200 million petals. Consequently, the price of essential oil is quite high, from 5000 to 7000 € kg⁻¹ depending on the sources and the year. A field of *R. × damascena* 'Kazanlik' produces about 1.5 tons ha⁻¹ of flowers from the third year of planting and then up to 5 tons ha⁻¹ in subsequent years. The flowers are collected by hand, one by one, between 5 a.m. and 9 a.m., when the concentration of scent is at its maximum.

At the end of the 19th century, a new technique of extraction was set up for industrial purposes. In this process, petals are washed in hexane until saturation. The solution is then decanted, concentrated and partially distilled to obtain a dough named concrete, which is mixed with alcohol, filtrated, refrigerated at -15°C, then filtrated again to remove plant waxes. The pure extract is named absolute. The Chiris Company developed this process on a large scale in Grasse in 1894 C.E. (Cocoual 2016), and Gilbert Nabonnand, a French breeder, introduced the famous "Rose de Mai" in 1895 C.E. (Jean 1937), a new cultivar created specifically for hexane extraction. Nowadays, this cultivar is still cultivated in France and in several other countries. It is sometimes extracted by supercritical CO₂. It is often named *R. × centifolia*, but is in fact a hybrid of *R. × centifolia* with other unknown species or cultivars. It should therefore be designated as *R. × centifolia* 'Nabonnand'. Its absolute is a highly concentrated and very expensive product (1200 to 2000 € kg⁻¹). Approximately 400 kg of roses are extracted to obtain 1 kg of concrete and 0.5 kg of absolute.

Nowadays, the world production of rose essential oil and concrete is estimated at around 15 tons per year, of which about 5 tons are essential oil. Turkey and Bulgaria are the main two producers (80% of total production). Iran, China, Egypt, France, India, and Morocco are also important contributors in this perfume sector. Both products, essential oil and absolute, which have different scent characteristics, are mostly used in perfumery and cosmetic industries.

Roses for gardens and the cut flower market

During the 18th and 19th centuries, gardeners, breeders and rose lovers discovered wild roses and ancient varieties from all over the world and cultivated them in their gardens. At first, they used spontaneous mutations, called sports, and natural random crosses. At the end of the 19th century, they succeeded in making crosses by manually transferring pollen from the stamens of one rose to the pistil of another one (Oghina-Pavie 2016). During this period, many horticultural traits concerning scent, colors, number of petals and blooming characters for example were sought. Some of these traits, such as the yellow color and the recurrent blooming for example, were very rare and difficult to obtain. For crossings, breeders extensively used roses coming from the Middle East and Asia: the yellow roses *R. × odorata* 'Parks' Yellow Tea-scented China', and *R. foetida* 'Persian Yellow', and the ever-

blooming roses *R. × damascena* 'Bifera', *R. chinensis* 'Old Blush', *R. × odorata* 'Hume's Blush Tea-scented China', and *R. chinensis* 'Semperflorens' for example (Krüssmann 1981). All these crosses gave rise to numerous horticultural groups, with a huge diversity of scents. Following these multiple crossings, there is some confusion in the nomenclature of groups of horticultural roses. Two classifications are unfortunately mixed: the Rheder's classification, and the horticultural classification of the World Federation of Rose Societies (Rehder 1940; Cairns 2003; Oghina-Pavie 2015). For example, the common name "Gallic rose" can designate different roses: *i/* the wild species, *R. gallica*, *ii/* the very old cultivated rose of Provins, *R. gallica* 'Officinalis', which seems to be a semi-double variety of *R. gallica*, or *iii/* even sometimes one of the unidentified *R. gallica* hybrids of the "Gallica Group" (Joyaux 2005). In addition to this confusion on rose names, the so-called "hybrids" in rose catalogs may be crosses between species according to the botanical nomenclature, or crosses between horticultural groups, themselves hybrids. As an evidence, rose nomenclature relies more heavily on historical events and famous breeders' names than on identified genetic groups.

Studying genetic diversity of garden roses bred during the 19th and the beginning of the 20th centuries, (Liorzou et al. 2016) has allowed the description of 16 genetic groups. These groups formed a continuous series mostly driven by crosses with roses of four ancestors from China (*R. chinensis* 'Old Blush', *R. chinensis* 'Slater's Crimson China', *R. × odorata* 'Parks' Yellow Tea-scented China', and *R. × odorata* 'Hume's Blush Tea-scented China'). Varieties from the beginning of the 19th century have a European genetic background, close to that of ancient European roses. Varieties from the middle of the 20th century have a Chinese genetic background. This is completely in line with the history of rose breeding, as growers introgressed these varieties to obtain ever-blooming roses during the 18th and 19th centuries. Horticultural groups such as "Bourbon Group", "Damask Group" and "Noisette Group", for example, were very famous because blooming occurred twice during the year, in spring and in autumn. To obtain continuous blooms from spring to fall, Chinese roses were extensively used during this period. Their hybrids did not have the typical rose scent but a tea scent. They were then crossed with other fragrant roses to obtain ever-blooming roses with a typical scent, giving rise to the "Hybrid Tea Group" at the end of the 19th century. It is commonly accepted that the first rose of the "Hybrid Tea Group" was the cultivar 'La France' obtained in 1867.

Among these garden roses, some breeders had the idea to produce them in winter, forcing the plants to bloom by different processes of culture: arcuate culture, cut at ground level after the first bloom, greenhouses... For this purpose, roses of the "Hybrid Tea Group" were perfect, and several centers of production began to select varieties for the cut flower market: the French Mediterranean and Brie areas, as well as the Netherlands (Maumenè 1935; Nicol 1996; Joyaux 2005; Leus et al. 2018). Unfortunately, during the 20th century, the selection of rose cultivars specifically for the cut-flower market has led to the loss of scent in these cultivars. The cause of the absence of typical rose scent in these varieties is not known. Some authors hypothesize a genetic link between lack of scent and agronomic traits such as resistance to Botrytis or to black spot disease, as well as vase life. However, an anise scent is present in some varieties for cut flowers. Moreover, some experiments failed to demonstrate any relationship between the amounts of volatile compounds emitted and vase life, when fragrant and non-fragrant rose cultivars were compared (Borda et al. 2011). Breeders today are redoubling their efforts to obtain cultivars with a long vase life and scent at the same time. Several genes encoding enzymes involved in the biosynthesis of rose scent have been identified in the past few years, which should shed light on the genetic determinism of this major trait.

Is the scent of wild roses different from that of modern roses?

When speaking about rose scent, people often think of the typical rose scent, similar to the one of roses used for the perfume industry, or the one of some garden roses such as *R. 'Papa Meilland'* for example. However, lots of rose species and varieties have very different scents, and sometimes no scent, as some recent bush roses and cut roses.

Wild roses have a wide variety of scents. For example, *R. arvensis* have a sweet smell of myrrh, *R. bracteata*, a fruity smell, *R. foetida*, an unpleasant smell of old attic, *R. moschata*, a smell of musk or clove, and *R. roxburghii*, no scent at all. In modern roses or “Hybrid Tea Group”, scents sometimes also deviate from what is considered as the typical rose scent. Breeders are actively working to find original fragrances in cultivars such as 'Paul Ricard' (anise scent), 'Constance Spry' (myrrh scent), 'Gloire de Dijon' (“tea scent”), 'Prestige de Lyon' (raspberry) and 'Souvenir de Marcel Proust' (lemongrass), among others. The scent of roses is extraordinarily complex, with hundreds of different molecules in some species and varieties. For over 30 years, these molecules have been isolated, purified and studied by chemists. From a chemical point of view, it is interesting to focus on some specific compounds which have a typical odor, and which were mixed when roses were hybridized (Table 1). *Rosa chinensis* f. *spontanea* and *R. gigantea* are supposed to be wild ancestors of Chinese roses, and *R. gallica* 'Officinalis', a putative ancestor of roses used for perfumes, *R. × centifolia* 'Nabonnand' and *R. × damascena* 'Trigintipetala'. *R. 'Papa Meilland'* is one of the most famous scented garden roses, and *R. 'Rouge Meilland'*, an unscented parent. Roses with a tea scent have several μg of 3,5-dimethoxytoluene (DMT), and roses with a typical rose scent have huge amounts of 2-phenylethanol, which smells powdery rose (Table 1). The most fragrant cultivars also produce acyclic monoterpenes (geraniol, nerol, β -citronellol), which smell of essential oil of rose, and their aldehydes (geranial, neral, β -citronellal), which smell like sweet lemon. Some trace compounds are sometimes very appreciated by perfumers, as for example Z-3-hexenol for the green note, or ionones for the violet note. Their biochemical pathways are thus also investigated.

Modern garden roses have therefore inherited their olfactory characteristics from multiple roses involved in the history of breeding during the 19th century, olfactory characteristics which they themselves had inherited from wild roses. As a consequence, breeders should consider fragrance not as a single phenotypic trait but rather as a multitude of traits or molecules. Furthermore, inheritance of scent traits may depend on the genetic background of the cultivars. This is the case for 2-phenylethanol for example, which inheritance was shown to be distinct in two different breeding populations (Spiller et al. 2010; Rocchia et al. 2019).

To facilitate fragrant rose breeding, a possible approach would be to use the genes involved in volatile compound biosynthesis as markers during selection. This strategy supposes an in-depth knowledge of the biochemical pathways and a focus on genes which encode flux-limiting enzymes, and/or alleles which encode the most efficient enzymes.

Biochemical pathways involved in scent compound production

In roses, emitted volatiles may be organized into several main classes associated with their biosynthesis pathways: fatty acid derivatives, phenyl methyl ethers, phenylpropanoids/benzenoids, and terpenoids. Some of them have been particularly studied during the last two decades because they include major compounds of rose fragrance (see Table 1 for the list of these volatiles), but trace compounds have also been studied.

Phenylpropanoids and benzenoids have a benzene ring in their skeleton and are found in many flower odors (Knudsen et al. 2006; Widhalm and Dudareva 2015). Some of these compounds are major constituents of the scent of roses, such as 2-phenylethanol, with the

typical odor of rose water. Other more minor compounds such as eugenol and methyleugenol, with a pronounced odor of clove, add spicy notes to the fragrance of certain varieties. These compounds are mostly derived from L-phenylalanine (Fig. 3). The genes and enzymes responsible for the biosynthesis of 2-phenylethanol have been identified in several plant species. Interestingly, plants have developed different pathways to convert L-phenylalanine to 2-phenylethanol. In roses, two main pathways have been identified: the PAAS pathway and the AAAT pathway. The phenylacetaldehyde synthase gene (*RhPAAS*) was cloned from *R.* 'Fragrant Cloud' (Kaminaga et al. 2006), and from *R.* 'H190' (Roccia et al. 2019). It is a bifunctional enzyme that catalyzes the efficient coupling of L-phenylalanine decarboxylation to oxidation, generating phenylacetaldehyde. The second step is performed by a phenylacetaldehyde reductase (RdPAR) characterized in *R. x damascena* (Chen et al. 2011b). Surprisingly, another pathway also exists in roses, and was discovered in *R.* 'Yves Piaget' (Hirata et al. 2012). In this alternative pathway, L-phenylalanine is first converted into phenylpyruvate by an aromatic amino acid aminotransferase (RyAAAT3) which then undergoes decarboxylation to form phenylacetaldehyde by RyPPDC (phenylpyruvic acid decarboxylase), and then 2-phenylethanol by RyPAR. This alternative pathway identified for the production of 2-phenylethanol seems to be activated in response to seasonal changes in temperature (Hirata et al. 2016).

Other phenylpropanoid compounds are also present in the rose flower, such as eugenol and methyleugenol. These phenylpropenes are important constituents of many plants in which they are supposed to play a role in pathogen defense due to their antibacterial and antifungal effects. Some phenylpropenes are also floral attractants for pollinators (Koeduka 2014). In some rose cultivars, they are present in high quantities in stamens and, to a lesser extent, in petals, giving a clove scent. Methyleugenol has recently drawn much attention because of its carcinogenic activity in rodents (Bouhleb et al. 2012). Eugenol is synthesized from coniferyl acetate, by eugenol synthase (Fig. 3). In roses, a eugenol synthase gene, *RdEGS1*, has been isolated, although the functional characterization of the protein in vitro is still missing (Yan et al. 2012; Yan et al. 2018). An *O*-methyl transferase, encoded by *RcOMT1*, a gene highly expressed in flowers of *R. chinensis* f. *spontanea*, was shown to produce the methylated derivative methyleugenol, which is a potential floral attractant for pollination (Wu et al. 2003).

Despite their benzene skeleton, phenolic methyl ethers are not derived from aromatic amino acids, and can be classified in a specific class of biosynthetic compounds. DMT is responsible for the characteristic "tea scent" of some rose cultivars which, in reality, is not the scent of tea. It is commonly explained that this semantic ambiguity could come from a phonetic deformation of "Fa-Ti roses", Fa-Ti being a famous Chinese plant nursery near Beijing. Anyway, this compound is biosynthesized in two Chinese species, *R. gigantea* and *R. chinensis* f. *spontanea* (Table 1). Many modern "Hybrid Tea Group" roses contain only small amounts of DMT, which are generally not strongly perceived by the human nose. DMT is synthesized by two specific enzymes, orcinol-*O*-methyl transferases 1 and 2 (*RcOOMT1* and *RcOOMT2*), that catalyze the methylations of orcinol as substrate (Fig. 4) (Lavid et al. 2002; Scalliet et al. 2002; Scalliet et al. 2006). *RcOOMT1* and *RcOOMT2* are very similar enzymes. They exhibit different substrate specificities that are consistent with their operating sequentially in DMT biosynthesis. It has been shown that these substrate specificities are mostly due to a single amino acid polymorphism in their phenolic substrate binding site. An analysis of the *OOMT* gene family in 18 species representing the diversity of the genus *Rosa* indicated that if all wild rose species have *OOMT2* genes, only Chinese roses also have *OOMT1* genes. In addition, research provided evidence that the Chinese-rose-specific *OOMT1* genes most probably evolved from an *OOMT2*-like gene that has homologs in the genomes of all extant roses. It was proposed that the emergence of the *OOMT1* gene may have been a critical step in the evolution of scent production in Chinese roses (Scalliet et al. 2008). This gene, and thus the

“tea scent”, were transmitted during the process of creation of modern roses and are found today in thousands of rose cultivars.

Terpenoids constitute a class of very important fragrant molecules, responsible for the scent of many flowers and aromatic plants (Tholl 2015). In many roses, terpenoids represent the most abundant scent compounds, in particular the monoterpene alcohols such as geraniol, β -citronellol, nerol and their derivatives. These terpenoids are generally responsible for the floral and fruity notes typical of the perfume of roses. In addition to these major terpenoids, trace compounds such as the norisoprenoid ionones also make a great contribution to the scent of these roses because of their low odor threshold in humans (Ohloff 1978). Pathways leading to the biosynthesis of terpenoids are well documented in dozens of plants. Precursors of all terpenes, isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP) are supplied by the methylerythritol 4-phosphate pathway for the monoterpene synthesis which generally takes place in plastids (Rodriguez-Concepcion and Boronat 2002). On the contrary, IPP and DMAPP for the biosynthesis of sesquiterpenes are synthesized in the cytosol by the mevalonate pathway (Hemmerlin et al. 2012). These precursors are transformed to allylic diphosphates, geranyl diphosphate (GPP) for the monoterpenes and farnesyl diphosphate (FPP) for the sesquiterpene biosynthesis by prenyltransferases. GPP and FPP are then used as substrates by various terpene synthases for monoterpene and sesquiterpene production respectively (Chen et al. 2011a). Finally, several enzymes such as P450 cytochromes or acetyltransferases are able to modify these terpenes and perform oxidation or acetylation reactions on the terpene skeletons (Shalit et al. 2003; Boachon et al. 2015). In roses, only few genes have been isolated so far (Fig. 5). A sesquiterpene synthase, *RhGDS*, responsible for the biosynthesis of germacrene D has been characterized in *R.* ‘Fragrant Cloud’ (Guterman et al. 2002). Data mining of ESTs databases in the same cultivar also led to the characterization of an alcohol acetyltransferase, *RhAAT1*, involved in the formation of geranyl acetate (Shalit et al. 2003; Guterman et al. 2006). RCLINS is the first monoterpene synthase that was functionally characterized in *R. chinensis* ‘Old Blush’. It was shown that it is responsible for the production of the minor compound, (-)-3*R*-linalool (Magnard et al. 2018).

Concerning major terpenes involved in the typical rose scent, a key gene was discovered, the expression of which is strongly correlated with the presence of terpenoids in different rose cultivars (Magnard et al. 2015). For this work, the transcriptomes of two rose cultivars that have very different scents were compared: highly fragrant *R.* ‘Papa Meilland’ and unscented rose *R.* ‘Rouge Meilland’ (see Table 1). The gene with the highest differential expression was found to encode a nudix hydrolase, specifically expressed in petals. In modern rose cultivars, its expression was correlated with the presence of the monoterpene geraniol. It was demonstrated by complementary approaches that rose flowers use an alternative route to produce geraniol by employing a completely unexpected diphosphohydrolase enzyme of the Nudix family. RhNUDX1 is responsible for the dephosphorylation of GPP, a precursor of monoterpenes, into geranyl phosphate (Fig. 5). It is localized in the cytosol, although in other plants, monoterpenes are synthesized principally into plastids, thus raising the question of the origin of the cytosolic GPP in roses. Nudix hydrolases belong to a superfamily of pyrophosphatases found in animals, plants and bacteria (Srouji et al. 2017). They generally catalyze the hydrolysis of nucleoside diphosphates linked to other moieties (X) and contain the Nudix domain defined by (Bessman et al. 1996) as G(X5)E(X7)REUXEEXX. In plants, Nudix hydrolases are poorly characterized, although up to 29 genes have been identified in the *Arabidopsis* genome (Kraszewska 2008). Based on sequence similarities, several functional groups have been defined. These enzymes can act as diphosphoinositol polyphosphate phosphohydrolases, coenzyme A pyrophosphatases, ADP-ribose pyrophosphatases, ApnA hydrolases and mRNA decapping enzymes. In *Arabidopsis*, few Nudix hydrolases have been linked to a specific function *in vivo*. RhNUDX1 shows the closest similarity to AtNUDX1 from

Arabidopsis. This protein was proposed to have a similar function to *Escherichia coli* mutator protein MutT, which acts to eliminate harmful compounds such as 8-oxo-dGTP which may be misincorporated into DNA during replication (Maki and Sekiguchi 1992; Yoshimura et al. 2007). Nevertheless, in *A. thaliana*, it has been recently shown that it can be involved in the regulation of IPP concentration in leaves (Henry et al. 2015; Henry et al. 2018). The discovery that a nudix hydrolase is involved in scent production adds to an increasing line of evidence that shows that although many plants produce similar, or even exactly the same scent compounds, they independently evolved the enzymes needed to do this (Sun et al. 2016). It has recently been shown that *NUDX1* genes were highly duplicated in *Rosa* species. From one to more than 10 copies were found in the rose genome and four clades numbered Nudx1-1 to Nudx1-4 could be defined. It was showed that the *RwNUDX1-2c* gene was involved in *E,E*-farnesol production in a hybrid of *R. wichurana* (Sun et al. 2020), and that a Nudx1-1a subclade contained the genes involved in geraniol biosynthesis in the more recent wild species of roses (Conart et al. 2022). Since this discovery, *NUDX1* genes have been found to be involved in terpene biosynthesis in other plants. For example, in *Tanacetum cinerariifolium*, a plastidial Nudix hydrolase catalyzes the formation of chrysanthemol which is the precursor of pyrethrins (Li et al. 2020). In *Pelargonium* species, both terpene synthases and nudix hydrolases could be involved in the production of geraniol (Blerot et al. 2018; Bergman et al. 2021). This could be similar to a situation in *R. x damascena*, where (Önder et al. 2021) have cloned a putative geraniol synthase. The Nudix family is thus more implicated in terpene production than it was previously thought (Bessman 2019).

Other key terpenoid compounds in rose essential oil are norisoprenoids, such as β -damascenone, β -damascone, and β -ionone, which are derived from carotenoid degradation. Ionones have a low concentration in petals but it is enough to give a violet note to the scent. Their odor thresholds are very low, which explains their importance in the olfactory characteristics of rose essential oil. However, β -damascenone and β -damascone are not produced by roses but come from the degradation of norisoprenoid precursors during the distillation of essential oil (Suzuki et al. 2002). Nevertheless, some genes responsible for the cleavage of carotenoids, the carotenoid cleavage (di-) oxygenase (CCD), were isolated from rose tissues and functionally characterized (Fig. 5). One particular protein, RdCCD1, which efficiently forms C13-norisoprenoids *in vivo* and is expressed in *R. x damascena* flowers, is probably involved in formation of ionones (Huang et al. 2009).

Conclusions

All these researches on the biosynthesis of rose fragrance will no doubt lead to a better knowledge of rose scent. These investigations will hopefully help rose breeders in their difficult task of breeding, to provide a beautiful, fragrant rose with a long vase life.

Understanding the molecular mechanisms that control scent traits may allow the identification of molecular and genetic markers to assist selection. This technique has not been applied to the rose, although it is widely used in animals and crops. Towards this aim, correlating scent volatiles and molecular markers is a powerful tool that has already been used to find QTLs influencing the amounts of rose volatiles compounds (Spiller et al. 2010; Rocca et al. 2019). These genome-wide association studies will certainly help to study the inheritance of scent in roses, as was already done for other traits (Schulz et al. 2016; Cheng et al. 2021).

Moreover, these studies could also be used to establish a link between fragrance and other parameters of flower quality, such as color and vase life (Smulders et al. 2019). For example, precursors of red to violets pigments (anthocyanins) are also precursors of

phenylpropanoids/benzenoid compounds and some yellow to orange pigments (carotenoids) are terpenoids, the degradation of which produces scent compounds (norisoprenoids). This pigment/scent relationship has already been demonstrated in another fragrant flower: the carnation (Zuker et al. 2002). Besides, in roses, the overexpression of the *Arabidopsis* gene *PAP1* that encodes a transcription factor activating the phenylpropanoid pathway led to an enhancement of the production of both phenylpropanoid (color and scent) and terpenoid (scent) compounds (Ben Zvi et al. 2012). Moreover, a few recent studies have tried to correlate scent and color in rose petals, although no direct link was demonstrated (Feng et al. 2021). The role of phytohormones such as gibberellins in the activation of the different branches of the biosynthesis pathways has also recently been demonstrated (Ravid et al. 2017). In the model plant *Arabidopsis thaliana* L. (Heynh. 1842), key regulators of flower maturation have been recently isolated and have been shown to synchronize petal expansion and volatile terpenoid emission (Liu et al. 2015). Identifying such regulators in roses is an important goal of future research. The breeding of rose cultivars would certainly benefit from a better understanding of the complex relationships between scent and other flower traits, even the vase life trait. Finally, a major challenge for rose research is to understand the subcellular trafficking and secretion of scent. Indeed, the subcellular localization, storage in the cellular compartments, and transport out of the cell of the volatile compounds remain largely unknown (Widhalm et al. 2015).

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Author contributions

J.C.C and S.B. wrote the paper. I.A., C.C. and S.N.P. made the sampling and GC analyses of Table 1.

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Table 1: Main compounds extracted by hexane in rose petals from different varieties ($\mu\text{g g}^{-1}$ FW)

Rose name	<i>Chinensis</i> ¹	<i>Gigantea</i> ²	<i>Provins rose</i> ³	<i>Damask rose</i> ⁴	<i>Provence rose</i> ⁵	Papa Meilland ⁶	Rouge Meilland ⁷
Fragrance	Unscented	Tea scent	Strong rose scent	Strong rose scent	Strong rose scent	Rose scent	Unscented
PE ⁸	1.41 ± 0.80	-	483.55 ± 44.22	570.53 ± 94.51	436.29 ± 49.92	48.77 ± 8.90	-

Geraniol	-	-	192.08 ± 42.46	112.20 ± 39.51	45.30 ± 17.24	53.49 ± 11.29	0.32 ± 0.04
Nerol	-	-	49.23 ± 19.12	34.50 ± 22.05	24.36 ± 7.75	5.39 ± 1.75	-
β-citronellol	-	-	24.30 ± 13.34	63.38 ± 42.40	39.22 ± 4.33	-	-
Geranial	-	-	8.48 ± 2.36	22.12 ± 19.18	7.72 ± 0.90	10.91 ± 1.01	-
Neral	-	-	2.30 ± 0.94	9.31 ± 7.87	3.65 ± 0.33	2.03 ± 2.04	-
β-citronellal	-	-	-	1.80 ± 2.01	0.27 ± 0.24	-	-
DMT ⁹	0.24 ± 0.27	6.32 ± 0.44	-	-	-	2.25 ± 2.25	1.93 ± 0.47

1. *R. chinensis* 'Spontanea', Asian wild rose,
2. *R. gigantea*, Asian wild rose,
3. *R. gallica* 'Officinalis', Eastern and European botanical rose,
4. *R. × damascena* 'Trigintipetala', rose used for essential oil,
5. *R. × centifolia* 'Nabonnand', rose used for concrete and absolute,
6. *R.* 'Papa Meilland', famous garden rose,
7. *R.* 'Rouge Meilland', rose for garden and for cut-flower market,
8. 2-phenylethanol,
9. 3,5-dimethoxytoluene.

Figures:

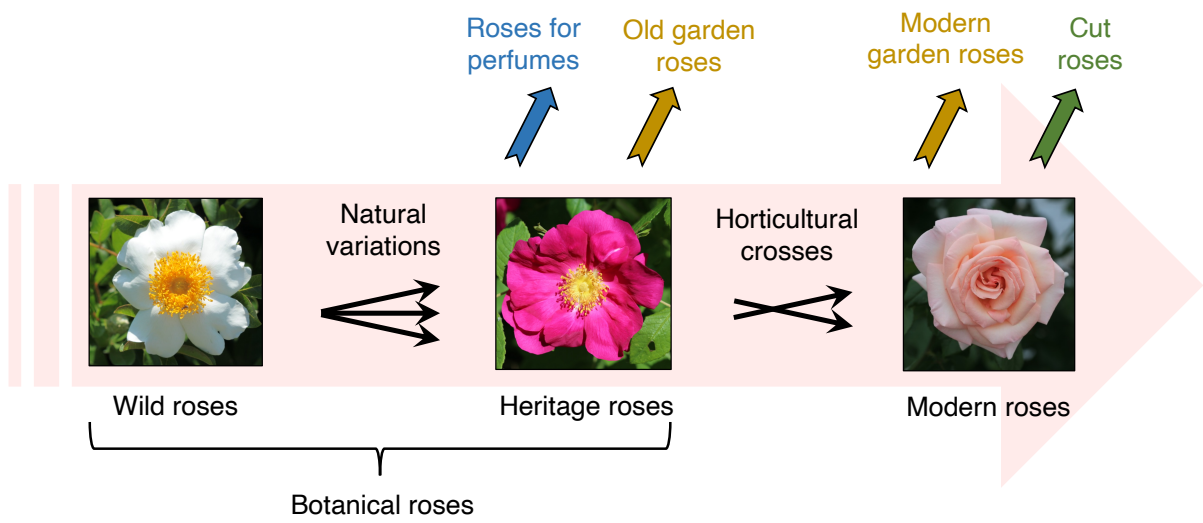


Fig. 1: Schematic representation of historical stages of rose domestication.



Fig. 2: The blue bird fresco in Knossos (approx. 1700-1500 B.C.E.).
The arrow points to the only original drawing of a wild rose. Personal photography.

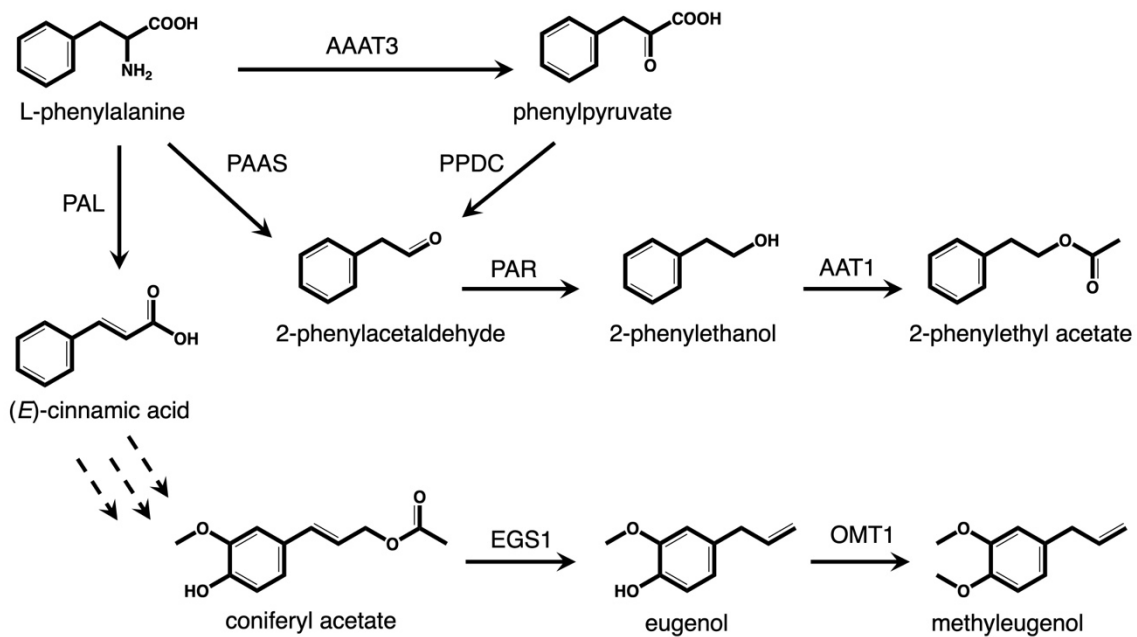


Fig. 3: Biosynthesis pathway of phenylpropanoids in roses.

Only the enzymatic steps whose genes have been cloned in roses are indicated by a full arrow. Dashed arrows indicate several enzymatic steps not studied in roses.

AAAT, aromatic amino acid transferase; AAT, alcohol acyl transferase; EGS, eugenol synthase; OMT, *O*-methyl transferase; PAAS, phenylacetaldehyde synthase; PAL, phenylalanine ammonia lyase; PAR, phenylacetaldehyde reductase; PPDC, phenylpyruvic acid decarboxylase.

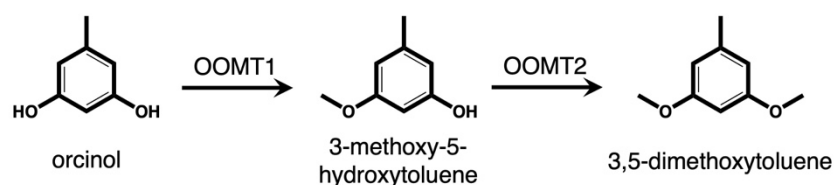


Fig. 4: Biosynthesis pathway of phenolic methyl ethers in roses.

Only the enzymatic steps whose genes have been cloned in roses are indicated by a full arrow. OOMT, orcinol *O*-methyl transferases.

Fig. 5: Biosynthesis pathway of terpenes in roses.

Only the enzymatic steps whose genes have been cloned in roses are indicated by a full arrow. Dashed arrows indicate several enzymatic steps not studied in roses. Single dashed arrows indicate putative single enzymatic steps.

(1), in this step there is a polymerization of one unit of isopentenyl diphosphate and one unit of dimethylallyl diphosphate; (2), in this step there is a polymerization of two units of isopentenyl diphosphate and one unit of dimethylallyl diphosphate; (3), in this step there is a polymerization of three units of isopentenyl diphosphate and one unit of dimethylallyl diphosphate; AAT, alcohol acyl transferase; CCD, carotenoid cleavage dioxygenase; GDS, germacrene D synthase; LINS, (-)-3*R*-linalool synthase; NUDX, nucleoside diphosphate linked to some moiety X.

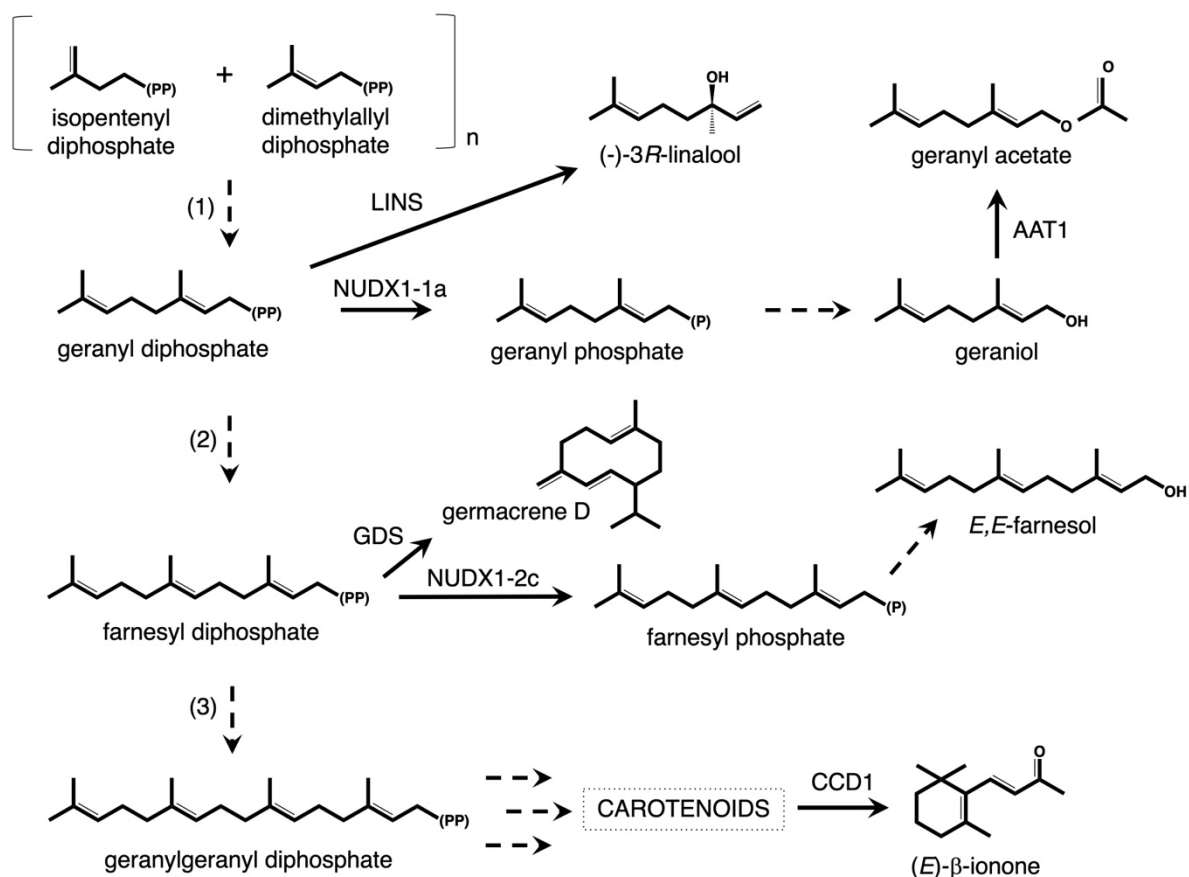


Fig. 5: Biosynthesis pathway of terpenes in roses.

Only the enzymatic steps whose genes have been cloned in roses are indicated by a full arrow. Dashed arrows indicate several enzymatic steps not studied in roses. Single dashed arrows indicate putative single enzymatic steps.

(1), in this step there is a polymerization of one unit of isopentenyl diphosphate and one unit of dimethylallyl diphosphate; (2), in this step there is a polymerization of two units of isopentenyl diphosphate and one unit of dimethylallyl diphosphate; (3), in this step there is a polymerization of three units of isopentenyl diphosphate and one unit of dimethylallyl diphosphate; AAT, alcohol acyl transferase; CCD, carotenoid cleavage dioxygenase; GDS, germacrene D synthase; LINS, (-)-3*R*-linalool synthase; NUDX, nucleoside diphosphate linked to some moiety X.