

REVIEW

Open Access



Molecular mechanisms regulating ornamental traits and scent production in snapdragon (*Antirrhinum majus* L.)

Zhenglin Qiao^{1,2}, Xiaohui Song^{1,2}, Yulai Kong^{1,2}, Senbao Shi^{1,2}, Bo Yan^{1,2}, Marcos Egea-Cortines³ and Longqing Chen^{1,2*}

Abstract

Snapdragon (*Antirrhinum majus* L.) is a widely cultivated and economically important cut flower and bedding plant worldwide due to its high ornamental value. At the same time, owing to its herbaceous features, ease of growth and cultivation, short life cycle, diploid inheritance, diverse morphological variation, and self-incompatibility, it has also been used as a model plant for studies on molecular biology, biochemistry, and plant developmental genetics. Over the past few decades, hundreds of plant genetics and physiology studies have been published on snapdragon. This review aims to summarize the advances in the characterization of snapdragon ornamental characters associated with floral organ size, shape, scent, color, and plant appearance. A broad spectrum of genes and their action mechanisms were explored and discussed, including comprehensive investigations at the genome-wide level and unraveling the functions of structural genes and master regulators and their interactions. In addition, the biosynthetic pathway involved in floral volatile scent production was summarized. Finally, the TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTORS (TCP) family in snapdragon was investigated using the latest whole-genome data. This review will lay the foundation for future molecular genetics and genomics research and applications on snapdragon. It further contributes to improve our knowledge of the mechanisms regulating morphogenesis and ornamental qualities in snapdragon.

Keywords Snapdragon, Flower development, Ornamental traits, Volatile organic compounds, Floral pigments

Introduction

Our pursuit of beauty has propelled the ornamental plant and flower industry to become one of the most dynamic industries worldwide. With the current economic development and prosperity, ornamental flower quality characteristics, such as plant type, floral color, floral fragrance, flower shape, and flowering length, play an increasingly prominent role in the embodiment of commodity value. This is the main driving force behind the economic growth and robustness of the flower market. Studies on functional genes and their mechanisms

related to flower quality formation have undoubtedly laid the foundation for ornamental plant molecular breeding and have far-reaching significance for the application of modern biotechnologies to enhance competitiveness in the flower industry. In recent years, the exploitation and utilization of ornamental flowering herbs in horticulture, forest reconstitution projects, fragrance, and the cosmetics industry have received increasing attention. Additionally, they offer significant economic advantages in landscape seasonal transformations. Currently, roses, lilies, orchids, and other cut flowers are widely used for these purposes; new, unique plant and flower combinations have become a popular trend to meet people's broader aesthetic needs.

*Correspondence:

Longqing Chen
chenlq@swfu.edu.cn

Full list of author information is available at the end of the article

Snapdragon (*Antirrhinum majus* L.), a member of the Plantago family (Plantaginaceae) based on APG IV (2016), is renowned worldwide not only as an ornamental cut and bedding flower but also as a model plant for research on the regulatory mechanisms of ornamental traits (Fig. 1). The original *Antirrhinum* genus includes approximately 20 diverse species (Hudson et al. 2008; Gorospe et al. 2020) that are native to regions in Europe. They are broadly naturally distributed in southwestern Europe, especially along the Mediterranean coast (Gorospe et al. 2020). *A. majus*, commonly known as the garden snapdragon, has been extensively utilized as a prominent model plant in molecular biology, biochemistry, plant developmental genetics and self-incompatibility due to its well-established research protocols, herbaceous characteristics that facilitate cultivation, short life cycle allowing for efficient experimentation, diploid inheritance enabling genetic analyses, and broad and prominent morphological variations (Hudson et al. 2008). Laboratory lines of *Antirrhinum* have been generated carrying mutations that result in a wide range of phenotypic traits. These laboratory lines were used to screen mutations that disrupted various traits, including floral shape and size, color, plant type, and changes in the density of glandular trichomes. Additionally, they were used to identify mutations affecting physiological, biochemical, and metabolic properties.

Snapdragon is often used to study biotic stress and the interactions among plants, pollinators, predators, and fungi (Guzmán et al. 2015; El-Nashar 2017; Guzmán

et al. 2017; Wei et al. 2023), and the response to various types of abiotic stresses, such as temperature extremes, heavy metals, and water deficiency (Asrar et al. 2012; Zhi et al. 2020; Wei et al. 2023; Alcantud et al. 2023). Furthermore, snapdragon serves as an excellent model system for identifying the associations between genes and significant ornamental characteristics through genetic and transcriptome profiling approaches.

The garden snapdragon has a long history of cultivation as an ornamental flower and is cultivated worldwide. The Vilmorin company, founded in 1743 by Claude Geoffrey, a key supplier of seeds to the French King Louis XV, began breeding and distributing *Antirrhinum* varieties at that time. The mutant *nana* was first described in the Vilmorin catalog in the early 18th century (Stubbe 1966). Plants carrying this mutation are semidwarf and used for bedding (Fig. 1). In the early 20th century, *Antirrhinum* was adopted as a genetic model by the followers of William Bateson at the John Innes Centre and by the German researchers led by Erwin Baur (Baur 1911). Their works initiated a strong interest in plant color and morphology (Wheldale and Bateson 1907, 1909). Many mutant lines were identified and are preserved to date at the Leibniz-Institut (IPK) Gatersleben collection.

Snapdragons produce multicolored tubular flowers that emit a pleasant fragrance, which has made them popular as cut or bed flowers in recent decades (Guzmán et al. 2017). Interestingly, snapdragon flowers contain a diverse range of organic and inorganic metabolites and nutrients that are beneficial to human health, including mineral elements, anthocyanins, carotenoids, flavonoids, phenolics, alkaloids, fatty acids, nitrogen-containing compounds, organosulfur compounds (Rop et al. 2012; Lu et al. 2016; Fernandes et al. 2017; González-Barrio et al. 2018; Jingyun et al. 2019). Thus, snapdragon has gradually been adopted both for its edible flowers (petal and seed oil) and as an ornamental plant (González-Barrio et al. 2018; Pires et al. 2019; Kumari and Bhargava 2021; Pires et al. 2021). Although snapdragon has a long history of use as a traditional Chinese medicine, recent research has provided further evidence of its medical values and properties. For example, the iridoid glucoside antirrhinoside is accumulated in high concentrations and was reported to account for 2 to 9% of the total dry weight in several common cultivars of ornamental snapdragons (Kries et al. 2017; Fernandes et al. 2017; Sokornova and Matveeva 2022). The health-promoting properties of snapdragon may be explained by the anti-inflammatory, antimicrobial, antioxidant, and anticancer properties of iridoids (Xiong et al. 2014; Fernandes et al. 2017; Kries et al. 2017; Kumari and Bhargava 2021). Further research on the specialized metabolites of snapdragon may result

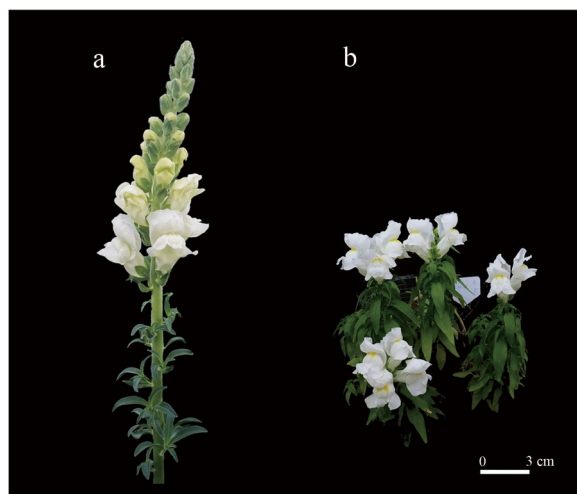


Fig. 1 The typical snapdragon (*Antirrhinum majus* L.). (a) The tall cultivars are often used for cut flower production. (b) The short cultivars are widely used in flower beds, windowsill decoration, planting troughs, and indoor arrangements

in its reclassification and characterization as a medicinal plant, additionally increasing its economic value.

This review comprehensively elucidated the biological functions of relevant genes and regulatory factors in snapdragon to enhance our understanding of the current research findings and contribute to future scientific investigations, breeding strategies, and utilization prospects. It is specifically focused on the genetic characterization of floral and ornamental traits, including flower morphology development, regulation of flower types and organ size, and floral fragrance biosynthesis and emission. Additionally, we discuss current research trends and the future prospects of utilizing snapdragon as a model for ornamental horticulture research in the upcoming decades (Manchado-Rojo et al. 2014).

Genes and molecular mechanisms of flower development and formation in *Antirrhinum*

Establishment of the ABC model and its regulatory interactions in flower development

The flower is an important plant organ highly attractive to humans and other animals, playing a crucial role in plant reproduction. Therefore, its biological and ecological values are immeasurable, and its formation mechanisms and development have long been a key research focus. A significant breakthrough in our understanding of flower development was achieved by analyzing floral homeotic mutants from *Arabidopsis thaliana* and *A. majus* during the 1990s (Schwarz-Sommer et al. 1990). Based on these findings, the ABC model proposes that three classes of genes (class A, B, and C) regulate flower development. It has been demonstrated that each group of genes controls organ identity in two adjacent whorls. This widely popularized model served as the fundamental basis for the subsequent ABCDE model after identifying additional genes affecting flower structure and development (Theissen 2000; Hu et al. 2021).

Snapdragon has a unique flower morphology. Its flowers consist of four organ types arranged in a coaxial manner on the central axis: sepals in whorl 1, petals in whorl 2, stamens in whorl 3, and carpels in whorl 4. Ideally, a typical class-A mutant has carpels instead of sepals in the first whorl and stamens instead of petals in the second whorl. On the other hand, class-B mutants have sepals instead of petals in the second whorl and carpels instead of stamens in the third whorl. Furthermore, class-C mutants have petals instead of stamens in the third whorl, and sepals replace carpels in the fourth whorl. Therefore, organ identity is determined by flower identity genes that occur as combinations of A, AB, BC, and C genes across whorls 1–4 (Mizzotti et al. 2014). The above is the basis of the ABC model, also known as the homologous gene

model for flower development, and serves as a guide for experimental models in studying the molecular genetics of flower development (Fig. 2a, b).

Studies at the molecular level have identified key genes underlying each snapdragon flower morphology mutants (Table 1). The class-A function was postulated initially based on a semi-dominant mutation that causes reproductive organs to grow to replace sepals and petals. The class-B function results from the action of the *DEFICIENS* (*DEF*) and *GLOBOSA* (*GLO*) genes. The class-C function is provided by *PLENA* (*PLE*). *LIPLESS* (*LIP*) genes that play a role in establishing sepal and petal development. Suppression of class C depends on *FISTULATA* (*FIS*), *FLORICAULA* (*FLO*), *CHORIPETALA* (*CHO*), and *STYLOSA* (*STY*) (Keck et al. 2003). Cloning and characterization of these genes during the 1990s indicated that they encode putative transcription factors (TFs) (Bradley et al. 1993; Jofuku et al. 1994). The functionally redundant *LIPLESS* (*LIP1*) and *LIP2* in snapdragon are two apparent AP2 orthologs (Keck et al. 2003). Over the past 30 years, although class A genes have been well characterized in *A. thaliana* (Mizzotti et al. 2014), unfortunately, no class A mutants have been described in snapdragon to date.

The *DEF* gene, the first plant MADS-box gene cloned in snapdragon, plays a crucial role in the genetic regulation of flower development in *A. majus* (Schwarz-Sommer et al. 1990). Mutations in this gene transform petals into sepals and the stamens into carpels (Schwarz-Sommer et al. 1990). The *APETALA1* (*AP1*) (Alejandra et al. 1992; Yamaguchi 2021) and AP2 genes may encode similar functions essential for specifying the floral organ initiation pattern and determining floral meristem development. It is proposed that the products of the AP1 and AP2 genes and those of the *AGAMOUS* locus collaborate to establish a determinate floral meristem. In contrast, other homeotic gene products are crucial in proper cell differentiation based on positional information (Durfee et al. 2003). These findings further enhance our understanding of the involvement of homeotic genes in floral development and propose novel models for floral pattern establishment.

The original model of *DEF* and *GLO* molecular functions suggested that *DEF* and *GLO* proteins form a heterodimer with specific DNA binding capacity. This heterodimer would then activate petal and stamen formation *via* an autoregulatory feedforward loop based on the *DEF* and *GLO* capacity to bind their own promoters (Schwarz-Sommer et al. 1992). Yeast two-hybrid assays further demonstrated that *DEF* and *GLO* indeed form stable heterodimers (Davies et al. 1996). Moreover, the formation of ternary complexes between

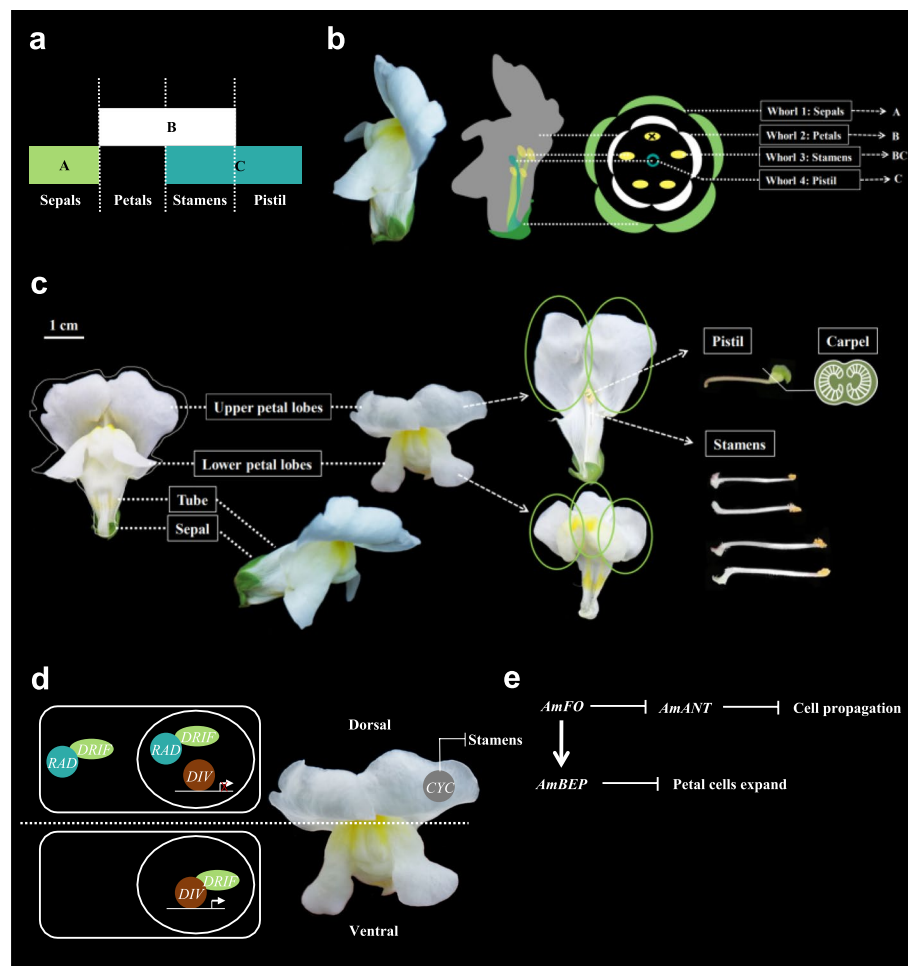


Fig. 2 Snapdragon flower morphology and genes involved in flower development. **(a)** Working model of snapdragon class-A, -B, and -C genes (Mizzotti et al. 2014). **(b)** The relationship of snapdragon flower morphology and class-A, -B and -C genes. The four whorls and their components (Coen and Meyerowitz 1991). **(c)** The symmetrical structure of snapdragon flowers. **(d)** Proposed model for the regulation of petal morphology (Raimundo et al. 2013). **(e)** Regulation of flower organ size by *AmFORMOSA* (*AmFO*) and *AmBIGPETAL* (*AmBPE*) genes. *AmFO* inhibits cell division by negatively regulating *AmAINTÉGUMENTA* (*AmANT*) and regulates *AmBPE*, which inhibits petal cell elongation and expansion and thus modulates floral organ size

snapdragon MADS-box proteins was verified using a newly developed ternary factor trap technology in yeast (Egea-Cortines et al. 1999). This work showed that MADS proteins form stable tetrameric complexes, providing a plausible molecular explanation for the ABC model (Gutierrez-Cortines and Davies 2000; Theissen and Saedler 2001).

While a model based on coexpression and autoregulation coupled to protein complex formation may indicate similar DEF and GLO expression levels, a differential expression has been observed at the late stages of flower development. Indeed, transcriptional analysis at late stages of flower development indicates differing DEF and GLO transcript levels, suggesting yet unidentified functions of these genes during flower opening and later stages (Manchado-Rojo et al. 2012).

Molecular regulatory mechanisms underlying flower shape and size regulation

During the pollination process, the recruitment of pollinators by the flowers is crucial. Some pollinators are attracted only by symmetrical flowers (Guzmán et al. 2015; Vargas et al. 2017). Moreover, bilaterally symmetrical corollas increase the approach of pollinators from one orientation (Vargas et al. 2017). Although the specialized structure of the personate snapdragon flower has been assumed to be one of the most sophisticated and potent physical barriers for physically restricting access to some pollinators, this structure accommodates specific pollinators, such as bees and bumblebees, to enter the flower and receive nectar and pollen (Vargas et al. 2017). This is a very efficient strategy for snapdragon, which increases pollination activity and reduces unnecessary resource wasting.

Table 1 Related genes and their functions in the ABC model of the snapdragon flower

ABC model	Organs	Genes	Gene fuctions	References
A	Sepals	<i>LIP</i>	Sepal development establishment	Keck et al. 2003
B	Petals, Stamens	<i>FO, BPE, ANT</i>	Cell propagation inhibition by negatively regulating <i>AmANT</i> and regulates the <i>AmBPE</i> , which inhibits the expansion of petal cells and thus, modulates floral organ size	Kim et al. 2011; Delgado-Benarroch et al. 2009a, b
		<i>DEF, GLO</i>	Class-B functions in flower morphology	Keck et al. 2003
		<i>CYC, DICH</i>	The <i>CYC</i> gene and the paralogous gene <i>DICH</i> inhibit petal and stamen growth	Luo et al. 1996; Theissen 2000
		<i>RAD, DIV</i>	<i>RAD</i> primarily acts downstream of <i>CYC</i> and <i>DICH</i> , and is activated by <i>CYC</i> in the dorsal domain of floral meristems where it antagonizes <i>DIV</i> , expressed throughout the meristem. <i>DIV</i> determines the ventral identity of petals observed in the radial flowers of the <i>cyc-dich</i> double mutant	Luo et al. 1999; Costa et al. 2005; Corley et al. 2005; Galego and Almeida 2002; Almeida and Galego 2005
C	Pistil, Stamens	<i>PLE</i>	Class-C functions in flower morphology	Keck et al. 2003
		<i>FIS, FLO, CHO, STY</i>	Suppression of class-C functions	Keck et al. 2003

LIP LIPLESS, *FO* FORMOSA, *BPE* BIGPETAL, *ANT* AINTEGUMENTA, *DEF* DEFICIENS, *GLO* GLOBOSA, *CYC* CYCLOIDEA, *DICH* DICHOTOMA, *RAD* RADIALIS, *DIV* DIVARICATA, *PLE* PLENA, *FIS* FISTULATA, *FLO* FLORICAULA, *CHO* CHORIPETALA, *STY* STYLOSA

Broadly speaking, flower morphology broadly comprises terms such as flower organ morphology, including flower branch morphology inflorescence type. Here, we mainly discuss the flower organ shape. The snapdragon flower is a typical bilaterally pentamerous and zygomorphic flower with a basic five-organ per whorl structure and is formed in the axil of a small leafy-like organ, which is a tubular corolla (Theissen 2000; Hileman et al. 2003). Four mature stamens per flower are produced during flower development, and the fifth adaxial stamen primordium is aborted. This phenomenon is regulated by the interaction of four genes from two transcription factor families (Luo et al. 1996; Corley et al. 2005). The adjacent regions of snapdragon petals are fused to form a corolla tube. More distant regions include lobes that are partially joined together to form lips. There are two dorsal petals, two lateral petals, and one ventral petal (Fig. 2c). The petals vary in size and shape along the dorsal–ventral flower axis. The number and location of the sepal and petal primordia are determined by the downregulation of regulatory genes across the dorsal-to-ventral axis and the size of the floral stem cell region, known as the meristem tissue (Nakagawa et al. 2020). The complex morphology of snapdragon petals is considered to have evolved to promote insect pollination (Keck et al. 2003).

The growth of petals and stamen is dynamically regulated. The *CYCLOIDEA* (*CYC*) gene and the paralogous gene *DICHOTOMA* (*DICH*) inhibit petal and stamen growth (Luo et al. 1996; Theissen 2000). *CYC* is expressed throughout the dorsal domain and promotes petal lobe growth while suppressing the stamen development in whorl 3 (Luo et al. 1996; Theissen 2000).

RADIALIS (*RAD*) largely acts downstream of *CYC* and *DICH* (Luo et al. 1999; Corley et al. 2005; Costa et al. 2005) and is activated by *CYC* in the dorsal domain of floral meristems, where it antagonizes *DIVARICATA* (*DIV*), expressed throughout the meristem. *DIV* determines the ventral identity of petals, as indicated by the formation of radial flowers in the *cyc dich* double mutant (Galego and Almeida 2002; Almeida and Galego 2005). Both *RAD* and *DIV* are members of the MYB transcription factor family (Fig. 2d). *RAD* belongs to the SANT/MYB subfamily and has one MYB domain that is highly similar to the N-terminal domain of *DIV*, which has two MYB-like domains and belongs to the R2R3-MYB subfamily (Stracke et al. 2001; Galego and Almeida 2002; Baxter et al. 2007). *RAD*-like genes form a small family in both *A. majus* and *A. thaliana* (Baxter et al. 2007). Both *CYC* and *DICH* possess a conserved basic helix-loop-helix (bHLH) domain unique to plants that belong to the TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTORS (TCP) gene family, influencing flower shape (Cubas et al. 1999a; Cubas et al. 1999b; Navaud et al. 2007). The TCP protein family was originally defined by its originally identified members, such as TEOSINTE BRANCHED 1 (TB1) in *Zea mays*, *CYC* in snapdragon, and proliferating cell factor in *Oryza sativa* (Navaud et al. 2007).

The TCP transcription factor family has become the focus of current research focusing on plant development at the cellular, tissue, and organ levels. The snapdragon TCP class I proteins with NAC TF family members, including CUPULIFORMIS (CUP), contribute to the formation of organ boundaries (Manassero et al. 2013).

Boundary domain genes are often expressed around or within organ primordia and are pivotal to the shape, formation, and subdivision of planar organs, such as petals and leaves. The boundary domain gene *CUP* contributes to the development of the exquisite snapdragon flower morphology through its functions in the establishment of the lip and palate domains (Rebocho et al. 2017).

We identified the *TCP* gene family members based on the whole genome data (WGD) from snapdragon (Li et al. 2019). Through comparisons with the sequences of *Arabidopsis TCP* genes, we identified a total of 35 *TCP* genes in snapdragon, congruent with the presence of 33 *TCP* genes in *Arabidopsis*. The two known genes *CYC* and *DICH* mentioned above (Luo et al. 1996; Theissen 2000) exhibited significant sequence similarity to the A and B gene sequences found in previously characterized family members (Fig. 3). Further analysis of the WGD revealed that these two genes carried nucleotide base mutations (Supplementary Figs. 1 and 2). Future investigations should focus on exploring their potential functional roles in snapdragon.

Apart from *TCP* proteins, MYB-like proteins are also involved in flower shape regulation. Three MYB-like proteins, *DIV*, *RAD*, and *DIV*-and-*RAD*-interacting-factor (*DRIF*), are characterized by molecular antagonistic relationships that regulate the snapdragon flower asymmetry. *DIV* and *RAD* proteins can both form a heterodimer with *DRIF*. The *DIV*-*DRIF* heterodimer binds to a consensus DNA sequence and potentially regulates the expression of target genes critical for ventral flower patterning. Nevertheless, in the dorsal region, *RAD* outcompetes *DIV* for *DRIF* binding. As a result, it inhibits and restricts *DIV* activity to the ventral organs of the flower where *RAD* is not expressed (Raimundo et al. 2013). *DIV* regulates *AmMYBML1* in combination with the B-function proteins *DEF* and *GLO* and contributes to the specific differentiation of particular cells within the ventral region of the petal. This will endow the corolla with special functions during pollination (Perez-Rodriguez et al. 2005) (Fig. 2d).

A relationship has been observed between genes controlling organ size and specialization. It has been demonstrated that organ size is regulated by the organ-specific expression of both general and local gene networks (Delgado-Benarroch et al. 2009b). The *AmFORMOSA* (*AmFO*) gene was shown to inhibit cell propagation by negatively regulating *AmAINTEGUMENTA* (*AmANT*) and acts upstream of *AmBIGPETAL* (*AmBPE*), which inhibits the petal cell elongation and expansion and thus modulates floral organ size (Delgado-Benarroch et al. 2009a; Kim et al. 2011). On the petal surface, pyramidal cells play a role in floral pigmentation accumulation and floral volatile organic compounds (FVOC) emission. Three snapdragon mutants with different macroscopic floral phenotypes exhibited significantly larger

pyramidal cells when the petal size decreased, which is a conceivable compensation mechanism related to petal development. This can guarantee normal function when the flower shape changes (Delgado-Benarroch et al. 2009b; Tabeta et al. 2022) (Fig. 2e).

Biosynthesis pathways and molecular mechanisms regulating floral scent compound production

More than 1700 VOCs have been identified in more than 90 diverse plant families (Knudsen et al. 2006), including volatile terpenoids, phenylpropanoids and benzenoids, fatty acid derivatives, amino acid derivatives, and a few genus-specific compounds (Dudareva et al. 2013; Boncan et al. 2020). Floral volatile terpenoids (FVTs) are the most abundant FVOCs, followed by particular floral volatile benzenoids and phenylpropanoids (FVBPs) (Dudareva et al. 2013; Farré-Armengol et al. 2020).

Antirrhinum is one of the first herbaceous plants to be studied for its floral scent. *Antirrhinum* species emit an extremely complex mixture of VOCs. To date, many of the *Antirrhinum* species and varieties used in scientific research and produced by the ornamental horticulture industry abundantly produce various VOCs. 63 floral VOCs were identified in the flowers of eight common wild species from Europe and two laboratory inbred lines, including FVBPs, FVTs, nitrogen-containing compounds, and aliphatic alcohols, that have also been identified in other plant species (Weiss et al. 2016b). The main FVTs were ocimene, linalool, and nerolidol, while the main FVBPs included methyl cinnamate, methyl benzoate, and acetophenone (Weiss et al. 2016b). In *A. majus* cv. Maryland True Pink, the volatile aromatic ester methyl benzoate and two monoterpenes, myrcene and ocimene, account for 60% of the total VOC content (Dudareva et al. 2000). The circadian clock was shown to control the release of these compounds (both FVTs and FVBPs) and apparently follows diurnal rhythms due to the regulation of the pertinent VOC synthases and the genes encoding the VOC synthases by the endogenous clock (Dudareva et al. 2005). Characteristic scent profiles change greatly during the diurnal cycle among *Antirrhinum* species and cultivars due to changes in the activities of different biosynthetic pathways (Weiss et al. 2016b). Thus, no single volatile but rather a combination of volatiles greatly influences olfactory perception. The ability of bees or bumblebees to discriminate among flowers may rely upon both the scent intensity and the ratios of FVOCs in a complex mixture of volatiles rather than upon the scent of only a few compounds (Wright et al. 2005). To further improve our understanding of the snapdragon aroma and to help future scientific research towards the generations of new snapdragon varieties

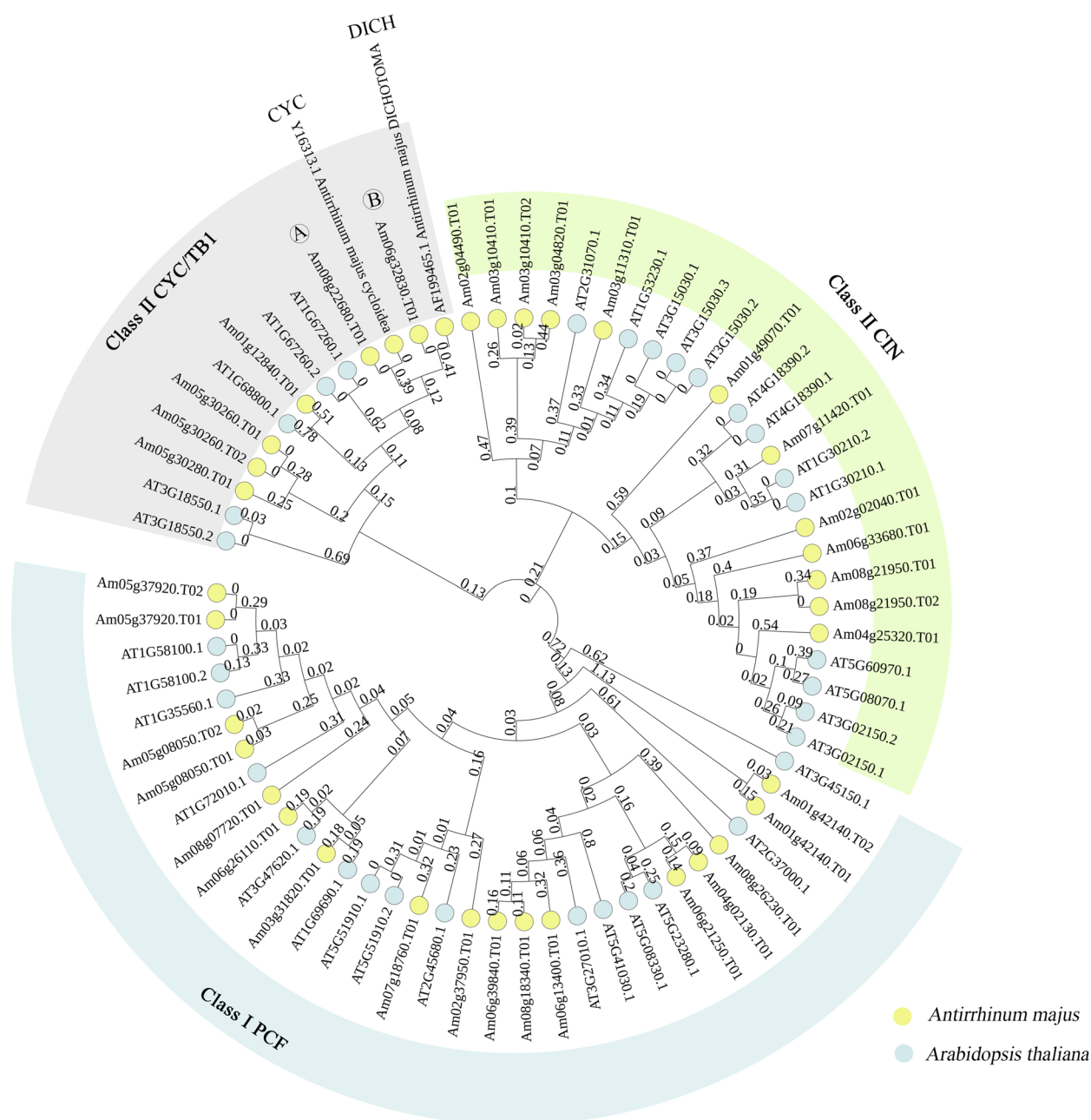


Fig. 3 Phylogenetic tree of TCP family members in snapdragon (*Antirrhinum majus*) and *Arabidopsis thaliana*. The circles labeled A and B represent the two candidate genes that exhibit the highest similarity to the known CYC and DICH genes on the phylogenetic tree. The outer circle corresponds to three classes (blue-Class I PCF, gray-Class II CYC/TB1, green-Class II CIN) in the TCP gene family. CYC, CYCLOIDEA; DICH, DICHOTOMA; TB1, teosinte branched 1; PCF, proliferating cell formation; CIN, CINCINNATA-like gene (Crawford et al. 2004; Manassero et al. 2013)

with different flowers, we comprehensively summarized the biosynthetic pathways involved in snapdragon flower fragrance below.

Biosynthesis of FVTs

FVTs are the main floral volatiles produced by snapdragon and are largely responsible for their characteristic

scent. FVTs include hemi-, mono-, sesqui-, and some diterpenoids (Yazaki et al. 2017). The five-carbon precursors of all terpenoids are produced from two distinct pathways: the plastidial 2-C-methylerythritol 4-phosphate (MEP) and cytosolic mevalonic acid (MVA) pathways. The MEP pathway provides precursors for the biosynthesis of hemiterpenes, monoterpenes, and diterpenes.

The MVA pathway is involved in the biosynthesis of sesquiterpenes (Qiao et al. 2021). However, in snapdragon flowers, sesquiterpenes are uniquely produced only by the MEP pathway (Dudareva et al. 2005; Qiao et al. 2021) (Fig. 4).

The homodimeric and heterodimeric forms of geranyl diphosphate synthase (GPPS) contribute to flower monoterpenes production. Partially conflicting with the above, only the heterodimeric GPPSs produce monoterpenes in snapdragon. The heterodimeric *GPPS* constitutes one large subunit (*LSU*) and one small subunit (*SSU*) (Orlova et al. 2009). In snapdragon and Fairy Fans (*Clarkia breweri*)—two species that produce VOCs rich in monoterpenes—a gene encoding a heterodimeric GPPS and an *SSU* gene may

serve as major regulators of monoterpene biosynthesis (Tholl et al. 2004; Orlova et al. 2009).

Terpene synthases (TPSs) contribute to plants' enormous diversity of FVTs due to their capacity to form multiple terpenoid products from a single substrate (Dudareva et al. 2013). The *TPS* gene family, identified and characterized in many plant species, commonly includes more than 100 members. Approximately one-third of these *TPS*s contribute to terpenoid production in flowers and fruits (Dudareva et al. 2013). The *TPS* gene family is divided into 7 subfamilies (designated *TPS-a* through *TPS-g*) based on functional properties, sequences, and gene structures (Dudareva et al. 2013). Snapdragon monoterpene synthases that are responsible for (*Z*)- β -ocimene and myrcene biosynthesis and

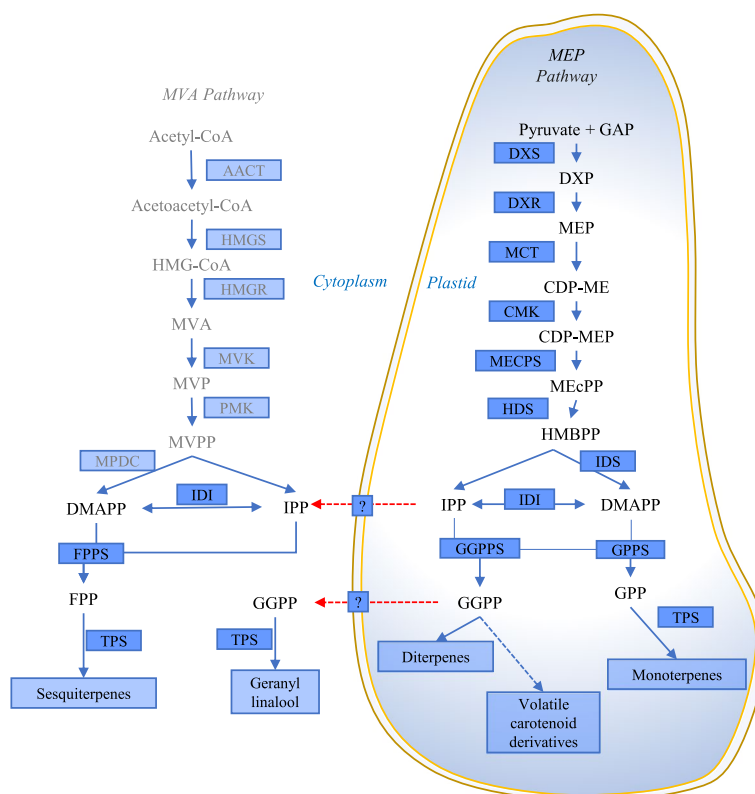


Fig. 4 Floral volatile terpenoids (FVT) metabolic pathway in *Antirrhinum*. Since the upstream module of the mevalonic-acid (MVA) pathway in snapdragon is not involved in FVT biosynthesis, it is illustrated in gray font. Geranyl diphosphate synthase (*GPPS*) and certain *Terpene synthases* (*TPS*) genes have been studied in snapdragon. Dashed lines indicate multiple enzymatic steps and the transport of metabolites between cell compartments. AACT, acetyl-CoA acetyltransferase; CDP-ME, 4-diphosphocytidyl-2-C-methyl-d-erythritol; CDP-MEP, 2-phospho-4-(cytidine 5'-diphospho)-2-C-methyl-d-erythritol; CMK, 4-(cytidine 5'-diphospho)-2-C-methyl-d-erythritol kinase; DMAPP, dimethylallyl pyrophosphate; DXP, 1-deoxy-d-xylulose 5-phosphate; DXR, 1-deoxy-D-xylulose 5-phosphate reductoisomerase; DXS, DXP synthase; FPP, farnesyl diphosphate; FPPS, farnesyl diphosphate synthase; GAP, D-glyceraldehyde 3-phosphate; GGPP, geranylgeranyl diphosphate (C20); GGPPS, GGPP synthase; GPP, geranyl diphosphate; GPPS, geranyl diphosphate synthase; HDS, 4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase; HMBPP, 4-hydroxy-3-methylbut-2-enyldiphosphate; HMG-CoA, 3-hydroxy-3-methylglutaryl-CoA; HMGR, HMG-CoA reductase; HMGS, HMG-CoA synthase; IDI, IPP isomerase; IDS, isoprenyl diphosphate synthase; IPP, isopentenyl diphosphate; MCT, 2-C-methyl-D-erythritol 4-phosphate cytidyltransferase; MEcPP, 2-C-methyl-d-erythritol-2,4-cyclodiphosphate; MECPS, CDP-ME synthase; MEP, methylerythritol phosphate; MPDC, mevalonate-5-diphosphate decarboxylase; MVA, mevalonic acid; MVK, mevalonate kinase; MVP, mevalonate 5-phosphate; MVPP, mevalonate 5-pyrophosphate; PMK, phosphomevalonate kinase; TPS, terpene synthase

Arabidopsis AtTPS14 constitute the *TPS-g* subfamily (Dudareva et al. 2003). Expression analysis of these monoterpene synthase genes in specific tissues during development and in response to the circadian rhythm has provided evidence for the coordinated regulation of FVT production in snapdragon flowers (Dudareva et al. 2003) (Fig. 5). Certain *TPS* genes were first cloned from snapdragon (e.g. the two nerolidol/linalool synthases) and other homologous *TPS* genes were cloned for functional verification.

Biosynthesis of FVBPs

FVBPs, which correspond to the second largest group in abundance and production of plant VOCs, include benzenoids (C6-C1), phenylpropanoids (C6-C2), and phenylpropenes (C6-C3). Most phenylpropanoids are derived directly from L-phenylalanine (L-Phe). First, phenylalanine ammonia-lyase (PAL) commits L-Phe to the phenylpropanoids (C6-C2) branch by catalyzing the deamination of L-Phe to *trans*-cinnamic acid (*t*-CA), an initial metabolite involved in the biosynthesis of precursors for both C6-C1 and C6-C3 compounds (Qualley et al. 2012) (Fig. 5). The benzenoid compounds are formed from *t*-CA via the β -oxidative pathway (Van Moerkercke et al. 2009; Qualley et al. 2012). The biosynthesis of volatile phenylpropenes includes some shared initial biosynthetic reaction steps with the lignin and flavonoid biosynthetic pathways all the way to the formation of coniferyl alcohol (Vanholme et al. 2019). In

their biosynthetic pathway, *t*-CA is hydroxylated to yield *p*-coumaric acid and then converted to 4-coumaryl-CoA, which is the branch point metabolite between anthocyanin and phenylpropene synthesis (Dudareva et al. 2013).

Benzoic acid (BA) is a crucial precursor for the biosynthesis of various compounds ranging from primary metabolites to natural products. BA biosynthesis from L-Phe occurs *via* two alternative pathways, the β -oxidative pathway and the non- β -oxidative pathway. Benzaldehyde is a key intermediate product in BA biosynthesis. Benzaldehyde dehydrogenase (BALDH) is necessary in the non- β -oxidative branch for the oxidation of benzaldehyde to BA. *AmBALDH* is involved in this function (Long et al. 2009). We believe some other dehydrogenases are involved in forming compounds in the FVBP biosynthesis pathway, but this needs to be further studied and explored.

In addition to dehydrogenases, methyltransferases are also involved in the FVBP biosynthesis pathway. Carboxyl methyltransferases, such as *S*-adenosyl-L-methionine:benzoic acid carboxyl methyltransferase (BAMT), *S*-adenosyl-L-methionine:jasmonic acid carboxyl methyltransferase (JMT) and *S*-adenosyl-L-methionine:salicylic acid carboxyl methyltransferase (SAMT), are crucially involved in the biosynthesis of FVBPs and are responsive to ethylene (Negre et al. 2003). All three genes have been cloned in snapdragon. *AmBAMT* is responsible for the formation of methyl benzoate (Fig. 5), *AmJMT* for methyl jasmonate, and

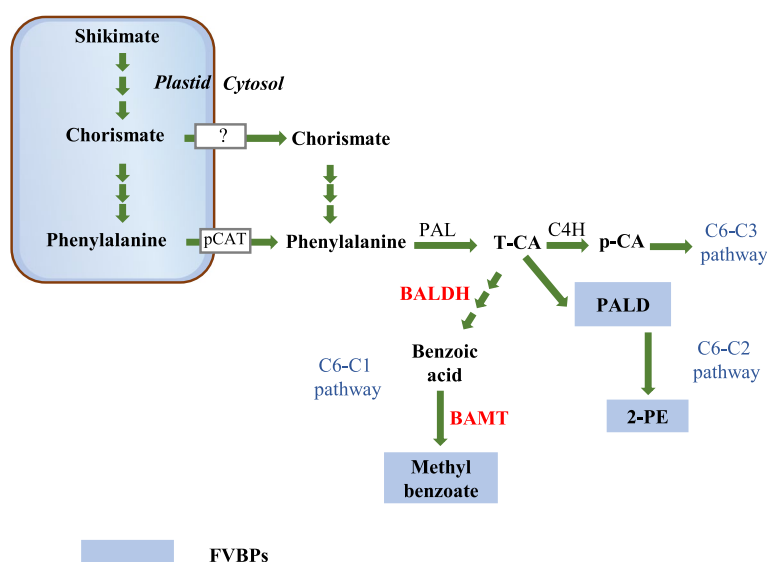


Fig. 5 A simplified schematic representation of the floral volatile benzenoids and phenylpropanoids (FVBP) metabolic pathway. The FVBP pathway is complex, and more efforts should be undertaken to study the involved genes and transcription factors. The blue box represents FVBPs (Dudareva et al. 2013). 2-PE, 2-phenylethanol; BALDH, benzaldehyde dehydrogenase; BAMT, benzoic acid carboxyl methyl transferase; C4H, cinnamate-4-hydroxylase; FVBPs, floral volatile benzenoids/phenylpropanoids; pCAT, plastidial cationic amino-acid transporter; PAL, phenylalanine ammonia lyase; PALD, phenylacetaldehyde; *p*-CA, *p*-Coumaric acid; *t*-CA, *t*-Cinnamic acid

SAMT for methyl salicylate. Among them, BAMT was cloned from the petal tissues of snapdragon flowers. SAMT, expressed in the flower petals of *Clarkia breweri*, shares 40% amino acid sequence similarity with *AmBAMT*, but there is no functional evidence to prove its contribution to floral scent production in snapdragon flowers (Negre et al. 2002).

The volatile ester methyl benzoate is an FVBP and one of the most abundant VOCs produced in snapdragon flowers. It is one of the crucial contributors to the particular odor of snapdragon flowers and has been found to have critical ecological functions. Methyl benzoate is synthesized and emitted only from the upper and lower lobes of the corolla (*i.e.* where pollinators, such as bumblebees, alight to access the snapdragon flowers) (Dudareva et al. 2000). Methyl benzoate release out of cells occurs rhythmically, with an emission maximum during the daytime and an emission minimum during the night (Dudareva et al. 2000). The timing of the maximum emission appears to coincide with the hours of maximum activity of particular snapdragon pollinators. The *AmBAMT* protein localized in the cytosol, was found to be present in the inner epidermis of the corolla tube, accumulated in small amounts in the outer epidermis of the corolla tube, and was also detected in the yellow trichomes that may serve as nectar guides for bees. These data indicate that the genes encoding for VOC biosynthetic enzymes are potentially explicitly expressed in the cuticular cells of floral organs (Dudareva et al. 2000; Murfitt et al. 2000). After a pollinator alights on a snapdragon flower, the cuticular cells facing the insect generate a concentrated scent that may improve pollination efficiency and minimize the costs of attracting more pollinators. Soon after the pollen tube reaches the ovary, methyl benzoate emissions are significantly reduced. This decrease results from reductions in the *AmBAMT* activity after pollination. Methyl benzoate is the main volatile substance responsible for this sensory effect (Horiuchi et al. 2007). Notably, nearby plants can perceive and respond to flower volatiles (Horiuchi et al. 2007).

Through FVOC determination in different natural *Antirrhinum* species, methyl benzoate was found to be emitted by *A. majus* but not by *A. linkianum*. This may be due to *A. linkianum* being homozygous for the naturally occurring null allele of *AmBAMT*. Based on these data, we suggest that natural variation in VOC emission in *Antirrhinum* species results from naturally occurring loss-of-function alleles of genes needed for VOC emission. The active transposable elements of *Antirrhinum* may explain the rapid evolution and genetic instability of different traits in *Antirrhinum*, which, in turn, may facilitate the adaptation of *Antirrhinum* to local pollinators (Ruiz-Hernández et al. 2017).

Floral VOCs emission

The regulation and emission of floral VOCs are influenced by VOC metabolism and by several additional factors, including hormones, flower age, pollination status, photoperiod, temperature, light quality, and other plant and environmental factors (Cna'ani et al. 2015; Alcantud et al. 2023). A quantitative analysis of methyl benzoate emissions from the flower petals of *A. majus* cv. Maryland True Pink within a 48-h period indicated a rhythmic fluctuation of VOC emissions (Dudareva et al. 2000; Zeng et al. 2017). The snapdragon LATE ELONGATED HYPOCOTYL (*AmLHY*) encodes for a transcription factor that regulates the rhythm of these emissions, which was shown to have a dual function by both activating floral growth and the rhythmic emission of both FVTs and FVBPs (Terry et al. 2019).

Global climate change has a dramatic impact on all living organisms on our planet. Determining whether and how air temperature affects plant physiology and phenotype is crucial. A two-year snapdragon study revealed that cold and heat strongly influenced flowering time and the quantity and quality of floral VOCs emitted. While flowers grown under optimal conditions exhibited increased scent emissions after opening, plants grown at low or high temperatures did not exhibit an increase in scent emissions after flower opening (Alcantud et al. 2023). Moreover, the total amounts of VOCs released were reduced in the high and low temperatures relative to plants grown at the optimal temperature (Alcantud et al. 2023). Thus, climate change may reduce scent emissions from snapdragon, which might influence pollination rates.

Light quality influences the expression of TFs involved in the biosynthesis of floral fragrances. In snapdragon plants treated with different light qualities, blue light augmented the release of myrcene, ocimene, and methyl benzoate more than other light wavelengths. The expression levels of pertinent genes encoding TPSs, *AmBAMT*, and CALMODULIN (*CAM*) were similarly induced, as well as Ca^{2+} flux. Additionally, blue light enhanced the expression of genes encoding enzymes associated with JA metabolism, such as 12-oxo-phytodienoic acid reductase (*OPR*), allene oxide cyclase (*AOC*), lipoxygenase (*LOX*) and coronatine-insensitive 1 (*COI1*, JA receptor). Different light qualities were proposed to induce calcium signaling and activate JA signaling, which subsequently induced gene expression and VOC biosynthesis in snapdragon (Yang et al. 2022). However, the details of the underlying regulatory mechanisms require further study. The blue light-induced increase in ocimene and myrcene provides evidence that blue light signaling activates TFs that promote the expression of genes associated with VOC biosynthesis and emission. An RNA-seq analysis of

snapdragon treated with different light qualities revealed that two TFs, *AmMYB24* and *AmMYB63*, were induced and reached high levels of expression in plants exposed to blue light. *AmMYB24* was shown to interact with *AmCRY1*, a key receptor for blue light signaling. Moreover, the transactivation activity of *AmMYB24* decreased when *AmCRY1* expression was silenced in flowers. Finally, *AmMYB24* was shown to upregulate the transcription of *AmOCS* by binding the MYBCOREAT-CYCB1 motif in its promoter region, ultimately resulting in the increased biosynthesis and production of large amounts of ocimene (Han et al. 2022).

Accumulation of pigments and the emergence of color in snapdragon flowers

Accumulation of pigments in snapdragon flowers

Different floral pigments accumulate at various levels in the different *Antirrhinum* species. The three key groups of pigments responsible for the natural attractiveness of floral colors are betalains, carotenoids, and flavonoids. Floral color is most often provided by colored flavonoid pigments. For example, flavonoids contribute to the bright yellow color of the flowers in snapdragon (Ono et al. 2006). The *A. majus* aureusidin synthase (*AmAS1*) is a key enzyme for accelerating aurone biosynthesis from chalcones. Anthocyanins are widely distributed in flowering plants and are derived from the flavonoid pathway (Kong et al. 2003; Grotewold 2006). Anthocyanins are natural water-soluble pigments ranging from red to purple and blue (Kong et al. 2003). In snapdragon, yellow-pigmented flowers are associated with anthocyanin biosynthesis disruption (e.g. mutants that lack flavanone 3-hydroxylase (F3H) activity) (Ono et al. 2006). Phytoene desaturase (PDS) commits geranylgeranyl diphosphate to carotenoid biosynthesis. Although the *AmPDS* gene is expressed throughout the entire snapdragon plant, its highest expression levels were found in the upper lobes when flowers were fully opened and in leaves (Han et al. 2022).

As mentioned before in this review, the products of the flavonoid and lignin biosynthetic pathways are derived from L-Phe and the core phenylpropanoid pathway, which utilizes PAL to deaminate L-Phe to yield *t*-CA. Pigment biosynthesis occurs at the phenylpropene branch of the pathway, which is also involved in lignin biosynthesis. TFs were shown to be involved in the regulation of the corresponding structural genes.

Several TFs are associated with the phenylpropene pathway in *Antirrhinum*. The abundance and molecular structure of magenta-colored anthocyanins are regulated by the *Rosea1* (*Ros1*), *Rosea2* (*Ros2*), and *Venosa* genes, which encode MYB-related TFs. Pigmentation differences between at least six species native to Spain

and Portugal could be attributed to changes in the activity of the *Rosea* and *Venosa* loci affecting anthocyanin biosynthesis. Differences in the expression of genes that encode MYB-related TFs could largely explain the natural variation in anthocyanin pigments in snapdragon (Schwinn et al. 2006). A flower-specific gene cloned from snapdragon, *AmMYB305*, induces phenylpropene and flavonoid biosynthesis in the flowers (Sablowski et al. 1994). *AmMYB308* is the first suppressor of anthocyanin accumulation identified in snapdragon. *AmMYB308* overexpression suppresses the accumulation of soluble phenylpropanoids and their derivatives, including two flavonoids (Tamagnone et al. 1998).

Several genes control the rate and structure of anthocyanins biosynthesized in snapdragon flowers. The *Delila* (*Del*) and *perilla* genes regulate red anthocyanin pigmentation patterns in snapdragon plants (Goodrich et al. 1992). A series of *pallida* alleles, which encode an enzyme required for pigment biosynthesis, can produce different spatial color patterns in *Antirrhinum* flowers (Goodrich et al. 1992). The overexpression of *Del* elevates the transcription of genes associated with antioxidant and anthocyanin biosynthesis, increasing antioxidant activity and anthocyanin production, which in turn, enhances biotic stress tolerance (Naing et al. 2017).

Influence of cell shape and light reflectance on floral color

While conventional wisdom says that pigment concentration is the main influencer of color intensity, the reality is that color perception is the result of reflected light. Most petals have conical cells on the surface. Early work in *Antirrhinum* demonstrated that weak alleles of *DEF* displayed petals with combinations of flat and conical cells (Schwarz-Sommer et al. 1992). Mutants in the *MIXTA* gene revealed that conical cells reflect light in such a way that despite having normal levels of anthocyanins, flowers appear pale (Noda et al. 1994). Conical cell formation results from activation of the organ identity B-function genes that, in turn, activate a set of *V-myb avian myeloblastosis viral oncogene homolog* (MYB) genes of the *MIXTA* family (Glover et al. 1998; Brockington et al. 2013). Indeed, flower iridescence plays a key role in pollinator attraction but also constitutes an essential component of our perception of flower color (Glover et al. 1998; Ruiz-Hernández et al. 2021).

Genes that influence the snapdragon plant architecture

Wild *Antirrhinum* plants range from tall and upright, short and upright to vines. Commercially popular cultivars include tall cultivars sold as cut flowers and short cultivars generally used as potted and ground cover plants. Traits that

influence plant architecture and vary among major snapdragon ornamental varieties include height, phyllotaxy, and bending of inflorescences and stems. Increased plant height facilitates plants to outcompete neighboring plants for light and primarily constitutes an ecological adaptation strategy (Moles et al. 2009). Plant height was not comprehensively evaluated in the major studies of plant architecture in snapdragon. These studies focused on other characteristics, such as phyllotaxy and inflorescence architecture. Correlations between variations in shape and size (allometry), flower and leaf arrangements on stems, inflorescences, and phyllotaxy are major components of natural diversity in snapdragon (Carpenter et al. 1995; Feng et al. 2009).

The key floral meristem genes *floricaula* (*flo*) and *squamosa* (*squa*) facilitate a change in leaf phyllotaxy from spiral to whorled and similarly influence the inflorescence phyllotaxis in *Antirrhinum* (Carpenter et al. 1995; Bradley et al. 1996) (Table 2). The flower arrangement on a modified stem, the inflorescence, and all inflorescence aspects and properties are controlled by three pathways. The first pathway depends on the expression of the *flo* gene and is induced rapidly under long-day conditions. The second pathway affects internode length, leaf size, and stem trichomes but does not affect floral meristems. The third pathway controls the transition from a whorled to a spiral phyllotaxy in plants during the vegetative stage and is not influenced by day length (Carpenter et al. 1995; Bradley et al. 1996).

Phyllotaxy shifts occur in snapdragon throughout its entire life cycle (Wang et al. 2017). During the vegetative growth stage, the shoot apical meristem (SAM) produces leaf primordia with regular phyllotaxy. Then, it becomes an inflorescence meristem when the plant enters the reproductive growth stage (Kwon et al. 2005). The MADS-box transcription factor family contributes to the vegetative to reproductive growth transition and to floral organ identity determination (Honma and Goto 2001). In *A. majus*, the homeobox gene *ROSULATA* (*ROA*) is involved in stem cell maintenance at the inflorescence meristem (Kieffer et al. 2006).

Plant appearance and shape multiformity depend considerably on the number and extent of lateral branches, phyllotaxy, and internode elongation. If internode elongation is insufficient, the crowding of leaves and flowers will lead to decreases in leaf size, increases in leaf number, significant increases in floral size, and reductions in floral number (Weiss et al. 2016a). Additionally, axillary buds influence the appearance of plants. In snapdragons, the axillary meristem (AM) formation requires *ERAMOSA* (*ERA*) which encodes a GRAS transcription factor. The fundamental role of *ERA* in AM formation matches the role of *LAS/MONOCULM 1/ERA* in preventing cell differentiation in boundary regions and in promoting AM formation (Mizzotti et al. 2017).

Snapdragon cut flower production is an important economic activity around the world. One of the biggest problems for snapdragon cut flower production and their preservation is stem bending, which greatly affects the viewing quality and bottle length. A recent study revealed that ethylene effectively retards stem curving in snapdragon. The mechanism underpinning stem bending is associated with stem curvature, ethylene production, relative shoot elongation (RSE), and lignin content (Soe et al. 2022). The involvement of ethylene and lignin in the mechanism underlying stem bending is supported by vase life experiments in ethylene-treated cut flowers from different cultivars of snapdragon and the expression of genes involved in lignin and ethylene production (*i.e.* *PAL*, *4CL*, *ACS1*, *ACO1*, and *ACO2*). Although it is known that ethylene inhibits stem bend in snapdragon cultivars, the ethylene-responsive mechanism remains to be studied in the future (Naing et al. 2021).

Whole-genome sequencing and research methods

The recently published reference genome of the highly inbred laboratory line (*A. majus* cv. J17) will significantly enhance fundamental research in snapdragon,

Table 2 Genes that influence the snapdragon plant architecture

Genes	Gene fuctions	References
<i>floricaula</i> (<i>flo</i>), <i>squamosa</i> (<i>squa</i>)	Facilitate a change in leaf phyllotaxy from spiral to whorled and similarly influence the inflorescence phyllotaxis	Carpenter et al. 1995; Bradley et al. 1996
<i>ROSULATA</i> (<i>ROA</i>)	Homeobox gene that maintains the stem cells of the inflorescence meristem	Kieffer et al. 2006
<i>ERAMOSA</i> (<i>ERA</i>), <i>LAS</i> , <i>MONOCULM 1</i>	The formation of the axillary meristem (AM) requires <i>ERAMOSA</i> (<i>ERA</i>), encoding a GRAS transcription factor. The fundamental role of <i>ERA</i> in AM formation is similar to the role of <i>LAS/MONOCULM 1/ERA</i> in preventing the cell differentiation in boundary regions and in promoting AM formation	Mizzotti et al. 2017
<i>PAL</i> , <i>4CL</i> , <i>ACS1</i> , <i>ACO1</i> , <i>ACO2</i>	Related to lignin and ethylene production	Naing et al. 2021
<i>LAS</i> LATERAL SUPPRESSOR, <i>PAL</i> phenylalanine ammonia lyase, <i>4CL</i> 4-coumarate, CoA ligase, <i>ACS</i> 1-aminocyclopropane-1-carboxylic acid synthetase, <i>ACO</i> 1-aminocyclopropane-1-carboxylic acid oxidase		

promoting its utilization as a model organism, particularly for addressing intricate questions that are challenging to resolve using other model plants (Li et al. 2019). The genome contains 37,714 annotated loci, of which 20,824 had a GO term classification related to biological and molecular functions. Further annotation increased the number of genes with GO terms to 26,109 (Alcantud et al. 2023). Recently, a new WGD of a self-incompatible *A. hispanicum* line was published, revealing the evolutionary dynamics of the S-locus supergene underlying the genetic control of self-incompatibility (Zhu et al. 2023). These two complete genomes could serve as an excellent foundation for studying the genetics and evolutionary mechanism of flower formation and morphology in snapdragons.

Furthermore, the utilization of CRISPR/Cas 9 genome editing technology will accelerate the generation of genetic variants (Li et al. 2019). Other recent advancements in snapdragon research include a simplified method for rapid regeneration and an efficient *Agrobacterium*-mediated transformation applying AgNO₃ that is superior to previous methods (Hoshino and Mii 1998; Cui et al. 2004; Lian et al. 2020). Snapdragon is a valuable model plant for genetic and evolutionary research, but its decreased genetic transformation efficiency limits the application of transgenic methods in functional genomics (Tan et al. 2020). Despite snapdragon transformation efficiency improvements, it remains inferior to *A. thaliana* and *Solanum lycopersicum*. Moreover, the regeneration process for snapdragon is relatively lengthy. Therefore, we eagerly anticipate more efficient and expedited transformation systems to accelerate snapdragon genetic research. The utilization of viral vectors and virus-induced gene silencing (VIGS) as transient gene expression methods for snapdragon genes, employing tobacco rattle virus (TRV), has been embraced as an alternative approach to generate transiently transformed lines (Kim et al. 2011; Tan et al. 2020).

Conclusions

Garden snapdragon is an economically important and popular ornamental flowering plant, and a good model system for plant flower morphology research as well. Antirrhinums also have exceptional qualities that are valuable for further commercial applications. In addition to serving as an important ornamental herb flower, snapdragon is edible, has medicinal value, and serves as a raw material for the cosmetic and perfume industries. As summarized in this review, snapdragon is far from sufficiently researched and marketed. To improve snapdragon ornamental value, the mechanisms that influence floral pattern formation, color enrichment, synthesis, and regulation of important pigments should be studied in more detail. A better understanding of the genes that

contribute to floral VOC biosynthesis among the different native species and cultivars is needed to improve the olfactory qualities of snapdragon. At the same time, to increase snapdragon popularity as an edible plant, the balance between nutrient accumulation in its flowers and its unpleasant flavor should be established. By improving utility and economic value while simultaneously enhancing ornamental properties, we can maximize the usefulness and value of ornamental crops. At the same time, resilient flowers contribute to environmental sustainability. Thus, studies on snapdragon flower shape, fragrance, pigmentation, and their resilience against stress and climate change can potentially influence and accelerate similar research efforts in many crops. Extensive research has been undertaken covering all aspects of the ornamental properties of snapdragons, and more than thirty inbred lines have been generated and assessed in various laboratories, providing valuable resources for future studies (Weiss et al. 2016b; Alcantud et al. 2023). With these recent genetic advancements and current knowledge, snapdragon research is positioned to advance substantially, further expanding its commercial applications.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s44281-023-00019-y>.

Additional file 1: Supplementary Fig. 1. Sequence comparison between *Antirrhinum majus* L. *DICHOTOMA* (*AmDICH*) and gene from the snapdragon whole genome data (WGD).

Additional file 2: Supplementary Fig. 2. Sequence comparison between *Antirrhinum majus* L. *CYCLOIDEA* (*AmCYC*) and gene from the snapdragon whole genome data (WGD).

Acknowledgements

Not applicable.

Authors' contributions

ZQ gave the general idea of the full review and was responsible for writing the main content. XS & YK collected and organized snapdragon research contents. XS & SS drew the figures. MEC gave additional idea of research information. BY & LC revised the context. All authors read and approved the final manuscript.

Funding

This research was funded by the Natural Science Foundation of China (NO. 32360419), the Fundamental Research Program of Yunnan Province (NO. 202001AS070039), the Education and Scientific Research Foundation of Yunnan Province (NO. 2021Y252).

Availability of data and materials

The datasets during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

Authors declare that they have no competing interests.

Author details

¹Yunnan Province Engineering Research Center for Functional Flower Resources and Industrialization, Kunming, People's Republic of China. ²College of Landscape Architecture and Horticulture Sciences, Southwest Forestry University, Kunming, People's Republic of China. ³Instituto de Biotecnología Vegetal, Universidad Politécnica de Cartagena, Cartagena, Spain.

Received: 27 May 2023 Revised: 2 November 2023 Accepted: 3 November 2023

Published online: 21 December 2023

References

- Alcantud R, Weiss J, Terry MI, Bernabé N, Fuensanta VN, Jesualdo TFB, et al. Flower transcriptional response to long term hot and cold environments in *Antirrhinum majus*. *Front Plant Sci.* 2023;14:1120183. <https://doi.org/10.3389/fpls.2023.1120183>.
- Alejandra MM, Cindy GB, Savidge B, Yanofsky MF. Molecular characterization of the *Arabidopsis* floral homeotic gene *APETALA1*. *Nature.* 1992;360:273–7. <https://doi.org/10.1038/360273a0>.
- Almeida J, Galego L. Flower symmetry and shape in *Antirrhinum*. *Int J Dev Biol.* 2005;49:527–37. <https://doi.org/10.1387/ijdb.041967ja>.
- Asrar A, Abdel-Fattah G, Elhindi K. Improving growth, flower yield, and water relations of snapdragon (*Antirrhinum majus* L.) plants grown under well-watered and water-stress conditions using arbuscular mycorrhizal fungi. *Photosynthetica.* 2012;50:305–16. <https://doi.org/10.1007/s11099-012-0024-8>.
- Baur E. Vererbungs- und bastardierungsversuche mit *Antirrhinum*. *Z Vererbungslehre.* 1911;6:201–16. <https://doi.org/10.1007/BF01778369>.
- Baxter CE, Costa MM, Coen ES. Diversification and co-option of RAD-like genes in the evolution of floral asymmetry. *Plant J.* 2007;52:105–13. <https://doi.org/10.1111/j.1365-3113.2007.03222.x>.
- Boncan DAT, Tsang SS, Li C, Lee IH, Lam HM, Chan TF, et al. Terpenes and terpenoids in plants: interactions with environment and insects. *Int J Mol Sci.* 2020;21:7382. <https://doi.org/10.3390/ijms21197382>.
- Bradley D, Carpenter R, Sommer H, Hartley N, Coen E. Complementary floral homeotic phenotypes result from opposite orientations of a transposon at the plena locus of *Antirrhinum*. *Cell.* 1993;72:85–95. [https://doi.org/10.1016/0092-8674\(93\)90052-r](https://doi.org/10.1016/0092-8674(93)90052-r).
- Bradley D, Vincent C, Carpenter R, Coen E. Pathways for inflorescence and floral induction in *Antirrhinum*. *Development.* 1996;122:1535–44. <https://doi.org/10.1242/dev.122.5.1535>.
- Brockington SF, Ruben AF, Landis JB, Alcorn K, Walker RH, Thomas MM, et al. Evolutionary analysis of the mixta gene family highlights potential targets for the study of cellular differentiation. *Mol Biol Evol.* 2013;30:526–40. <https://doi.org/10.1093/molbev/mss260>.
- Carpenter R, Copsey L, Vincent C, Doyle S, Magrath R, Coen E. Control of flower development and phyllotaxy by meristem identity genes in *Antirrhinum*. *Plant Cell.* 1995;7:2001–11. <https://doi.org/10.1105/tpc.7.12.2001>.
- Cna'ani A, Muhlemann JK, Ravid J, Masci T, Klempien A, Nguyen TT, et al. *Petunia* × *hybrida* floral scent production is negatively affected by high-temperature growth conditions. *Plant Cell Environ.* 2015;38:1333–46. <https://doi.org/10.1111/pce.12486>.
- Coen ES, Meyerowitz EM. The war of the whorls: genetic interactions controlling flower development. *Nature.* 1991;353:31–7. <https://doi.org/10.1038/353031a0>.
- Corley SB, Carpenter R, Copsey L, Coen E. Floral asymmetry involves an interplay between TCP and MYB transcription factors in *Antirrhinum*. *Proc Natl Acad Sci USA.* 2005;102:5068–73. <https://doi.org/10.1073/pnas.0501340102>.
- Costa MM, Fox S, Hanna AI, Baxter C, Coen E. Evolution of regulatory interactions controlling floral asymmetry. *Development.* 2005;132:5093–101. <https://doi.org/10.1242/dev.02085>.
- Crawford BCW, Nath U, Carpenter R, Coen ES. CINCINNATA controls both cell differentiation and growth in petal lobes and leaves of *Antirrhinum*. *Plant Physiol.* 2004;135:244–53. <https://doi.org/10.1104/pp.103.036368>.
- Cubas P, Lauter N, Doebley J, Coen E. The tcp domain: a motif found in proteins regulating plant growth and development. *Plant J.* 1999a;18:215–22. <https://doi.org/10.1046/j.1365-3113.1999.00444.x>.
- Cubas P, Vincent C, Coen E. An epigenetic mutation responsible for natural variation in floral symmetry. *Nature.* 1999b;401:157–61. <https://doi.org/10.1038/43657>.
- Cui ML, Ezura H, Nishimura S, Kamada H, Handa T. A rapid agrobacterium-mediated transformation of *Antirrhinum majus* L. by using direct shoot regeneration from hypocotyl explants. *Plant Sci.* 2004;166:873–9. <https://doi.org/10.1016/j.plantsci.2003.11.021>.
- Davies B, Marcos EC, De Andrade SE, Saedler H, Sommer H. Multiple interactions amongst floral homeotic mads box proteins. *EMBO J.* 1996;15:4330–43. <https://doi.org/10.1002/j.1460-2075.1996.tb00807.x>.
- Delgado-Benarroch L, Causier B, Weiss J, Egea-Cortines M. Formosa controls cell division and expansion during floral development in *Antirrhinum majus*. *Planta.* 2009a;229:1219–29. <https://doi.org/10.1007/s00425-009-0910-x>.
- Delgado-Benarroch L, Weiss J, Egea-Cortines M. The mutants compacta ähnlich, Nitida and Grandiflora define developmental compartments and a compensation mechanism in floral development in *Antirrhinum majus*. *J Plant Res.* 2009b;122:559–69. <https://doi.org/10.1007/s10265-009-0236-6>.
- Dudareva N, Andersson S, Orlova I, Gatto N, Reichelt M, Rhodes D, et al. The nonmevalonate pathway supports both monoterpene and sesquiterpene formation in snapdragon flowers. *Proc Natl Acad Sci USA.* 2005;102:933–8. <https://doi.org/10.1073/pnas.0407360102>.
- Dudareva N, Klempien A, Muhlemann JK, Kaplan I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. *New Phytol.* 2013;198:16–32. <https://doi.org/10.1111/nph.12145>.
- Dudareva N, Martin D, Kish CM, Kolosova N, Gorenstein N, Fäldt J, et al. (E)-beta-ocimene and myrcene synthase genes of floral scent biosynthesis in snapdragon: function and expression of three terpene synthase genes of a new terpene synthase subfamily. *Plant Cell.* 2003;15:1227–41. <https://doi.org/10.1105/tpc.011015>.
- Dudareva N, Murfitt LM, Mann CJ, Gorenstein N, Kolosova N, Kish CM, et al. Developmental regulation of methyl benzoate biosynthesis and emission in snapdragon flowers. *Plant Cell.* 2000;12:949–61. <https://doi.org/10.1105/tpc.12.6.949>.
- Durfee T, Roe JL, Sessions RA, Inouye C, Serikawa K, Feldmann KA, et al. The F-box-containing protein UFO and agamous participate in antagonistic pathways governing early petal development in arabidopsis. *Proc Natl Acad Sci U S A.* 2003;100:8571–6. <https://doi.org/10.1073/pnas.1033043100>.
- Egea-Cortines M, Saedler H, Sommer H. Ternary complex formation between the MADS-box proteins squamosa, deficiens and globosa is involved in the control of floral architecture in *Antirrhinum majus*. *EMBO J.* 1999;18:5370–9. <https://doi.org/10.1093/emboj/18.19.5370>.
- El-Nashar Y. Response of snapdragon (*Antirrhinum majus* L.) to blended water irrigation and arbuscular mycorrhizal fungi inoculation: uptake of minerals and leaf water relations. *Photosynthetica.* 2017;55:201–9. <https://doi.org/10.1007/s11099-016-0650-7>.
- Farré-Armengol G, Fernández-Martínez M, Filella I, Junker RR, Peñuelas J. Deciphering the biotic and climatic factors that influence floral scents: a systematic review of floral volatile emissions. *Front Plant Sci.* 2020;11:1154. <https://doi.org/10.3389/fpls.2020.01154>.
- Feng X, Wilson Y, Bowers J, Kennaway R, Bangham A, Hannah A, et al. Evolution of allometry in *Antirrhinum*. *Plant Cell.* 2009;21:2999–07. <https://doi.org/10.1105/tpc.109.069054>.
- Fernandes L, Casal S, Pereira JA, Saraiva JA, Ramalhosa E. Edible flowers: a review of the nutritional, antioxidant, antimicrobial properties and effects on human health. *J Food Compos.* 2017;60:38–50. <https://doi.org/10.1016/j.jfca.2017.03.017>.
- Galego L, Almeida J. Role of divaricata in the control of dorsoventral asymmetry in *Antirrhinum* flowers. *Genes Dev.* 2002;16:880–91. <https://doi.org/10.1101/gad.221002>.
- Glover BJ, Maria PR, Martin C. Development of several epidermal cell types can be specified by the same MYB-related plant transcription factor. *Development.* 1998;125:3497–08. <https://doi.org/10.1242/dev.125.17.3497>.
- González-Barrio R, Periago MJ, Luna-Recio C, García-Alonso FJ, Navarro-González I. Chemical composition of the edible flowers, pansy (*Viola wittrockiana*) and snapdragon (*Antirrhinum majus*) as new sources of bioactive compounds. *Food Chem.* 2018;252:373–80. <https://doi.org/10.1016/j.foodchem.2018.01.102>.
- Goodrich J, Carpenter R, Coen ES. A common gene regulates pigmentation pattern in diverse plant species. *Cell.* 1992;68:955–64. [https://doi.org/10.1016/0092-8674\(92\)90038-e](https://doi.org/10.1016/0092-8674(92)90038-e).

- Gorospe JM, Monjas D, Fernández-Mazuecos M. Out of the mediterranean region: worldwide biogeography of snapdragons and relatives (tribe Antirrhineae, Plantaginaceae). *J Biogeogr.* 2020;47:2442–56. <https://doi.org/10.1111/jbi.13939>.
- Grotewold E. The genetics and biochemistry of floral pigments. *Annu Rev Plant Biol.* 2006;57:761–80. <https://doi.org/10.1146/annurev.arplant.57.032905.105248>.
- Gutierrez-Cortines ME, Davies B. Beyond the ABCs: ternary complex formation in the control of floral organ identity. *Trends Plant Sci.* 2000;5:471–6. [https://doi.org/10.1016/s1360-1385\(00\)01761-1](https://doi.org/10.1016/s1360-1385(00)01761-1).
- Guzmán B, Gómez JM, Vargas P. Bees and evolution of occluded corollas in snapdragons and relatives (*Antirrhineae*). *Perspect Plant Ecol.* 2015;17:467–75. <https://doi.org/10.1016/j.ppees.2015.07.003>.
- Guzmán B, Gómez JM, Vargas P. Is floral morphology a good predictor of floral visitors to *Antirrhineae* (snapdragons and relatives)? *Plant Biol (Stuttg).* 2017;19:515–24. <https://doi.org/10.1111/plb.12567>.
- Han J, Li T, Wang X, Zhang X, Bai X, Shao H, et al. *AmMYB24* regulates floral terpenoid biosynthesis induced by blue light in snapdragon flowers. *Front Plant Sci.* 2022;13:885168. <https://doi.org/10.3389/fpls.2022.885168>.
- Hileman LC, Kramer EM, Baum DA. Differential regulation of symmetry genes and the evolution of floral morphologies. *Proc Natl Acad Sci USA.* 2003;100:12814–9. <https://doi.org/10.1073/pnas.1835725100>.
- Honma T, Goto K. Complexes of mads-box proteins are sufficient to convert leaves into floral organs. *Nature.* 2001;409:525–9. <https://doi.org/10.1038/35054083>.
- Horiuchi J, Badri DV, Kimball BA, Negre F, Dudareva N, Paschke MW, et al. The floral volatile, methyl benzoate, from snapdragon (*Antirrhinum majus*) triggers phytotoxic effects in *Arabidopsis thaliana*. *Planta.* 2007;226:1–10. <https://doi.org/10.1007/s00425-006-0464-0>.
- Hoshino Y, Mii M. Bialaphos stimulates shoot regeneration from hairy roots of snapdragon (*Antirrhinum majus* L.) transformed by agrobacterium rhizogenes. *Plant Cell Rep.* 1998;17:256–61. <https://doi.org/10.1007/s002990050388>.
- Hu J, Chang X, Zhang Y, Yu X, Qin Y, Sun Y, et al. The pineapple mads-box gene family and the evolution of early monocot flower. *Sci Rep.* 2021;11:849. <https://doi.org/10.1038/s41598-020-79163-8>.
- Hudson A, Critchley J, Erasmus Y. The genus *Antirrhinum* (snapdragon): a flowering plant model for evolution and development. *CSH Protoc.* 2008;2008:pdemo100. <https://doi.org/10.1101/pdb.emo100>.
- Jingyun Z, Meenu M, Xu B. A systematic investigation on free phenolic acids and flavonoids profiles of commonly consumed edible flowers in China. *J Pharm Biomed Anal.* 2019;172:268–77. <https://doi.org/10.1016/j.jpba.2019.05.007>.
- Jofuku KD, Den Boer BG, Van Montagu M, Okamoto JK. Control of *Arabidopsis* flower and seed development by the homeotic gene *APETALA2*. *Plant Cell.* 1994;6:1211–25. <https://doi.org/10.1105/tpc.6.9.1211>.
- Keck E, McSteen P, Carpenter R, Coen E. Separation of genetic functions controlling organ identity in flowers. *EMBO J.* 2003;22:1058–66. <https://doi.org/10.1093/emboj/cdg097>.
- Kieffer M, Stern Y, Cook H, Clerici E, Maulbetsch C, Laux T, et al. Analysis of the transcription factor wuschel and its functional homologue in *Antirrhinum* reveals a potential mechanism for their roles in meristem maintenance. *Plant Cell.* 2006;18:560–73. <https://doi.org/10.1105/tpc.105.039107>.
- Kim B, Inaba J, Masuta C. Virus induced gene silencing in *Antirrhinum majus* using the cucumber mosaic virus vector: functional analysis of the AINTEGUMENTA (AM-ANT) gene of *A. majus*. *Hortic Environ Biotechnol.* 2011;52:176–82. <https://doi.org/10.1007/s13580-011-0172-y>.
- Knudsen JT, Eriksson R, Gershenzon J, Ståhl B. Diversity and distribution of floral scent. *Bot Rev.* 2006;72:1–120. [https://doi.org/10.1663/0006-8101\(2006\)72\[1:DADOFS\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2006)72[1:DADOFS]2.0.CO;2).
- Kong JM, Chia LS, Goh NK, Chia TF, Brouillard R. Analysis and biological activities of anthocyanins. *Phytochemistry.* 2003;64:923–33. [https://doi.org/10.1016/s0031-9422\(03\)00438-2](https://doi.org/10.1016/s0031-9422(03)00438-2).
- Kries H, Kellner F, Kamilein MO, O'Connor SE. Inverted stereocontrol of iridoid synthase in snapdragon. *J Biol Chem.* 2017;292:14659–67. <https://doi.org/10.1074/jbc.M117.800979>.
- Kumari P, Bhargava B. Phytochemicals from edible flowers: opening a new arena for healthy lifestyle. *J Funct Foods.* 2021;78:104375. <https://doi.org/10.1016/j.jff.2021.104375>.
- Kwon CS, Chen C, Wagner D. Wuschel is a primary target for transcriptional regulation by splayed in dynamic control of stem cell fate in *Arabidopsis*. *Genes Dev.* 2005;19:992–1003. <https://doi.org/10.1101/gad.1276305>.
- Li M, Zhang D, Gao Q, Luo Y, Zhang H, Ma B, et al. Genome structure and evolution of *Antirrhinum majus* L. *Nat Plants.* 2019;5:174–83. <https://doi.org/10.1038/s41477-018-0349-9>.
- Lian Z, Nguyen CD, Wilson S, Chen J, Gong H, Huo H. An efficient protocol for agrobacterium-mediated genetic transformation of *Antirrhinum majus*. *Plant Cell Tiss Org.* 2020;142:527–36. <https://doi.org/10.1007/s11240-020-01877-4>.
- Long MC, Nagegowda DA, Kaminaga Y, Ho KK, Kish CM, Schnepf J, et al. Involvement of snapdragon benzaldehyde dehydrogenase in benzoic acid biosynthesis. *Plant J.* 2009;59:256–65. <https://doi.org/10.1111/j.1365-3113X.2009.03864.x>.
- Lu B, Li M, Yin R. Phytochemical content, health benefits, and toxicology of common edible flowers: a review (2000–15). *Crit Rev Food Sci.* 2016;56:S130–48. <https://doi.org/10.1080/10408398.2015.1078276>.
- Luo D, Carpenter R, Copsey L, Vincent C, Clark J, Coen E. Control of organ asymmetry in flowers of *Antirrhinum*. *Cell.* 1999;99:367–76. [https://doi.org/10.1016/s0092-8674\(00\)81523-8](https://doi.org/10.1016/s0092-8674(00)81523-8).
- Luo D, Carpenter R, Vincent C, Copsey L, Coen E. Origin of floral asymmetry in *Antirrhinum*. *Nature.* 1996;383:794–9. <https://doi.org/10.1038/383794a0>.
- Manassero NGU, Viola IL, Welchen E, Gonzalez DH. Tcp transcription factors: architectures of plant form. *Biomol Concepts.* 2013;4:111–27. <https://doi.org/10.1515/bmc-2012-0051>.
- Manchado-Rojo M, Delgado-Benarroch L, Roca MJ, Weiss J, Egea-Cortines M. Quantitative levels of deficiencies and globosa during late petal development show a complex transcriptional network topology of b function. *Plant J.* 2012;72:294–07. <https://doi.org/10.1111/j.1365-3113X.2012.05080.x>.
- Manchado-Rojo M, Weiss J, Egea-Cortines M. Validation of aintegumenta as a gene to modify floral size in ornamental plants. *Plant Biotechnol J.* 2014;12:1053–65. <https://doi.org/10.1111/pbi.12212>.
- Mizzotti C, Galliani BM, Dreni L, Sommer H, Bombarely A, Masiero S. *ERAMOSA* controls lateral branching in snapdragon. *Sci Rep.* 2017;7:41319. <https://doi.org/10.1038/srep41319>.
- Mizzotti C, Galliani B, Masiero S. The backstage of the abc model: the *Antirrhinum majus* contribution. *Plant Biosyst.* 2014;148:176–86. <https://doi.org/10.1080/11263504.2013.877531>.
- Moles AT, Warton DI, Warman L, Swenson NG, Laffan SW, Zanne AE, et al. Global patterns in plant height. *J Ecol.* 2009;97:923–32. <https://doi.org/10.1111/j.1365-2745.2009.01526.x>.
- Murfitt LM, Kolosova N, Mann CJ, Dudareva N. Purification and characterization of s-adenosyl-L-methionine: benzoic acid carboxyl methyltransferase, the enzyme responsible for biosynthesis of the volatile ester methyl benzoate in flowers of *Antirrhinum majus*. *Arch Biochem Biophys.* 2000;382:145–51. <https://doi.org/10.1006/abbi.2000.2008>.
- Naing AH, Park KI, Ai TN, Chung MY, Han JS, Kang YW, et al. Overexpression of snapdragon *Delila (Del)* gene in tobacco enhances anthocyanin accumulation and abiotic stress tolerance. *BMC Plant Biol.* 2017;17:65. <https://doi.org/10.1186/s12870-017-1015-5>.
- Naing AH, Soe MT, Yeum JH, Kim CK. Ethylene acts as a negative regulator of the stem-bending mechanism of different cut snapdragon cultivars. *Front Plant Sci.* 2021;12:745038. <https://doi.org/10.3389/fpls.2021.745038>.
- Nakagawa A, Kitazawa MS, Fujimoto K. A design principle for floral organ number and arrangement in flowers with bilateral symmetry. *Development.* 2020;147:dev182907. <https://doi.org/10.1242/dev.182907>.
- Navard O, Dabos P, Carnus E, Tremoussaygue D, Hervé C. TCP transcription factors predate the emergence of land plants. *J Mol Evol.* 2007;65:23–33. <https://doi.org/10.1007/s00239-006-0174-z>.
- Negre F, Kish CM, Boatright J, Underwood B, Shibuya K, Wagner C, et al. Regulation of methylbenzoate emission after pollination in snapdragon and petunia flowers. *Plant Cell.* 2003;15:2992–3006. <https://doi.org/10.1105/tpc.016766>.
- Negre F, Kolosova N, Knoll J, Kish CM, Dudareva N. Novel s-adenosyl-L-methionine: salicylic acid carboxyl methyltransferase, an enzyme responsible for biosynthesis of methyl salicylate and methyl benzoate, is not involved in floral scent production in snapdragon flowers. *Arch Biochem Biophys.* 2002;406:261–70. [https://doi.org/10.1016/S0003-9861\(02\)00458-7](https://doi.org/10.1016/S0003-9861(02)00458-7).

- Noda K, Glover BJ, Linstead P, Martin C. Flower colour intensity depends on specialized cell shape controlled by a myb-related transcription factor. *Nature*. 1994;369:661–4. <https://doi.org/10.1038/369661a0>.
- Ono E, Masako FM, Nakamura N, Fukui Y, Keiko YS, Yamaguchi M, et al. Yellow flowers generated by expression of the aureone biosynthetic pathway. *Proc Natl Acad Sci USA*. 2006;103:11075–80. <https://doi.org/10.1073/pnas.0604246103>.
- Orlova I, Nagegowda DA, Kish CM, Gutensohn M, Maeda H, Varbanova M, et al. The small subunit of snapdragon geranyl diphosphate synthase modifies the chain length specificity of tobacco geranylgeranyl diphosphate synthase in planta. *Plant Cell*. 2009;21:4002–17. <https://doi.org/10.1105/tpc.109.071282>.
- Perez-Rodriguez M, Jaffe FW, Butelli E, Glover BJ, Martin C. Development of three different cell types is associated with the activity of a specific myb transcription factor in the ventral petal of *Antirrhinum majus* flowers. *Development*. 2005;132:359–70. <https://doi.org/10.1242/dev.01584>.
- Pires TC, Barros L, Celestino SB, Ferreira IC. Edible flowers: emerging components in the diet. *Trends Food Sci Tech*. 2019;93:244–58. <https://doi.org/10.1016/j.tifs.2019.09.020>.
- Pires EO Jr, Di Gioia F, Roupheal Y, Ferreira I, Caleja C, Barros L, et al. The compositional aspects of edible flowers as an emerging horticultural product. *Molecules*. 2021;26:6940. <https://doi.org/10.3390/molecules26226940>.
- Qiao Z, Hu H, Shi S, Yuan X, Yan B, Chen LQ. An update on the function, biosynthesis and regulation of floral volatile terpenoids. *Horticulturae*. 2021;7:451. <https://doi.org/10.3390/horticulturae7110451>.
- Qualley AV, Widhalm JR, Adebisi F, Kish CM, Dudareva N. Completion of the core β -oxidative pathway of benzoic acid biosynthesis in plants. *Proc Natl Acad Sci USA*. 2012;109:16383–8. <https://doi.org/10.1073/pnas.1211001109>.
- Raimundo J, Sobral R, Bailey P, Azevedo H, Galego L, Almeida J, et al. A subcellular tug of war involving three myb-like proteins underlies a molecular antagonism in *Antirrhinum* flower asymmetry. *Plant J*. 2013;75:527–38. <https://doi.org/10.1111/tpj.12225>.
- Rebocho AB, Kennaway JR, Bangham JA, Coen E. Formation and shaping of the *Antirrhinum* flower through modulation of the cup boundary gene. *Curr Biol*. 2017;27:2610–22. <https://doi.org/10.1016/j.cub.2017.07.064>.
- Rop O, Mlecek J, Jurikova T, Neugebauerova J, Vabkova J. Edible flowers—a new promising source of mineral elements in human nutrition. *Molecules*. 2012;17:6672–83. <https://doi.org/10.3390/molecules17066672>.
- Ruiz-Hernández V, Hermans B, Weiss J, Egea-Cortines M. Genetic analysis of natural variation in *Antirrhinum* scent profiles identifies benzoic acid carboxymethyl transferase as the major locus controlling methyl benzoate synthesis. *Front Plant Sci*. 2017;8:27. <https://doi.org/10.3389/fpls.2017.00027>.
- Ruiz-Hernández V, Joubert L, Rodríguez-Gómez A, Artuso S, Patrick JG, Gómez PA, et al. Humans share more preferences for floral phenotypes with pollinators than with pests. *Front Plant Sci*. 2021;12:647347. <https://doi.org/10.3389/fpls.2021.647347>.
- Sablowski RW, Moyano E, Culianez-Macia FA, Schuch W, Martin C, Bevan M. A flower-specific myb protein activates transcription of phenylpropanoid biosynthetic genes. *EMBO J*. 1994;13:128–37. <https://doi.org/10.1002/j.1460-2075.1994.tb06242.x>.
- Schwarz-Sommer Z, Hue I, Huijser P, Flor PJ, Hansen R, Tetens F, et al. Characterization of the *Antirrhinum* floral homeotic mads-box gene deficiencies: evidence for DNA binding and autoregulation of its persistent expression throughout flower development. *EMBO J*. 1992;11:251–63. <https://doi.org/10.1002/j.1460-2075.1992.tb05048.x>.
- Schwarz-Sommer Z, Huijser P, Nacken W, Saedler H, Sommer H. Genetic control of flower development by homeotic genes in *Antirrhinum majus*. *Science*. 1990;250:931–6. <https://doi.org/10.1126/science.250.4983.931>.
- Schwinn K, Venail J, Shang Y, Mackay S, Alm V, Butelli E, et al. A small family of myb-regulatory genes controls floral pigmentation intensity and patterning in the genus *Antirrhinum*. *Plant Cell*. 2006;18:831–51. <https://doi.org/10.1105/tpc.105.039255>.
- Soe MT, Naing AH, Kim SR, Kim CK. Characterizing the effects of different chemicals on stem bending of cut snapdragon flower. *Plant Methods*. 2022;18:4. <https://doi.org/10.1186/s13007-021-00835-1>.
- Sokornova SV, Matveeva TV. Iridoid glycosides of the tribe *Antirrhineae*. *Phytochem Rev*. 2022;21:1185–07. <https://doi.org/10.1007/s11101-021-09774-0>.
- Stracke R, Werber M, Weisshaar B. The *R2R3-MYB* gene family in *Arabidopsis thaliana*. *Curr Opin Plant Biol*. 2001;4:447–56. [https://doi.org/10.1016/s1369-5266\(00\)00199-0](https://doi.org/10.1016/s1369-5266(00)00199-0).
- Stubbe H. Genetics and cytology of *Antirrhinum* L. sect. *Antirrhinum*. Jena: Veb Gustav Fischer Verlag; 1966.
- Tabeta H, Gunji S, Kawade K, Ferjani A. Leaf-size control beyond transcription factors: compensatory mechanisms. *Front Plant Sci*. 2022;13:1024945. <https://doi.org/10.3389/fpls.2022.1024945>.
- Tamagnone L, Merida A, Parr A, Mackay S, Culianez-Macia FA, Roberts K, et al. The *ammyb308* and *ammyb330* transcription factors from *Antirrhinum* regulate phenylpropanoid and lignin biosynthesis in transgenic tobacco. *Plant Cell*. 1998;10:135–54. <https://doi.org/10.1105/tpc.10.2.135>.
- Tan Y, Bukys A, Molnár A, Hudson A. Rapid, high efficiency virus-mediated mutant complementation and gene silencing in *Antirrhinum*. *Plant Methods*. 2020;16:145. <https://doi.org/10.1186/s13007-020-00683-5>.
- Terry MI, Pérez-Sanz F, Navarro PJ, Weiss J, Egea-Cortines M. The snapdragon late elongated hypocotyl plays a dual role in activating floral growth and scent emission. *Cells*. 2019;8:920. <https://doi.org/10.3390/cells8080920>.
- Theissen G. Evolutionary developmental genetics of floral symmetry: the revealing power of Linnaeus' monstrous flower. *BioEssays*. 2000;22:209–13. [https://doi.org/10.1002/\(sici\)1521-1878\(200003\)22:3%3c209::Aid-bies1%3e3.0.Co;2-j](https://doi.org/10.1002/(sici)1521-1878(200003)22:3%3c209::Aid-bies1%3e3.0.Co;2-j).
- Theissen G, Saedler H. Plant biology: floral quartets. *Nature*. 2001;409:469–71. <https://doi.org/10.1038/35054172>.
- Tholl D, Kish CM, Orlova I, Sherman D, Gershenzon J, Pichersky E, et al. Formation of monoterpenes in *Antirrhinum majus* and *Clarkia breweri* flowers involves heterodimeric geranyl diphosphate synthases. *Plant Cell*. 2004;16:977–92. <https://doi.org/10.1105/tpc.020156>.
- Van Moerkercke A, Schauvinhold I, Pichersky E, Haring MA, Schuurink RC. A plant thiolase involved in benzoic acid biosynthesis and volatile benzenoid production. *Plant J*. 2009;60:292–302. <https://doi.org/10.1111/j.1365-3113.2009.03953.x>.
- Vanholme R, De Meester B, Ralph J, Boerjan W. Lignin biosynthesis and its integration into metabolism. *Curr Opin Biotech*. 2019;56:230–9. <https://doi.org/10.1016/j.copbio.2019.02.018>.
- Vargas P, Liberal I, Ornos C, Gómez JM. Flower specialisation: the occluded corolla of snapdragons (*Antirrhinum*) exhibits two pollinator niches of large long-tongued bees. *Plant Biol J*. 2017;19:787–97. <https://doi.org/10.1111/plb.12588>.
- Wang D, Cao G, Fang P, Xia L, Cheng B. Comparative transcription analysis of different *Antirrhinum* phyllotaxy nodes identifies major signal networks involved in vegetative-reproductive transition. *PLoS One*. 2017;12:e0178424. <https://doi.org/10.1371/journal.pone.0178424>.
- Wei L, Yan-Lin Z, Hong-Shuang X, Li-Jun X, Shao-Xia G. Arbuscular mycorrhizal fungi promote photosynthesis in *Antirrhinum majus* L. Under low-temperature and weak-light conditions. *Not Bot Horti Agrob*. 2023;51:13012–12. <https://doi.org/10.1007/s11099-016-0650-7>.
- Weiss J, Alcantud-Rodríguez R, Toksöz T, Egea-Cortines M. Meristem maintenance, auxin, jasmonic and abscisic acid pathways as a mechanism for phenotypic plasticity in *Antirrhinum majus*. *Sci Rep*. 2016a;6:19807. <https://doi.org/10.1038/srep19807>.
- Weiss J, Mühlemann JK, Ruiz-Hernández V, Dudareva N, Egea-Cortines M. Phenotypic space and variation of floral scent profiles during late flower development in *Antirrhinum*. *Front Plant Sci*. 2016b;7:1903. <https://doi.org/10.3389/fpls.2016.01903>.
- Wheldale M, Bateson W. The inheritance of flower colour in *Antirrhinum majus*. *Proc R Soc Lond B*. 1907;79:288–305. <https://doi.org/10.1098/rspb.1907.0020>.
- Wheldale M, Bateson W. The colours and pigments of flowers with special reference to genetics. *Proc R Soc Lond B*. 1909;81:44–60. <https://doi.org/10.1098/rspb.1909.0006>.
- Wright GA, Lutmerding A, Dudareva N, Smith BH. Intensity and the ratios of compounds in the scent of snapdragon flowers affect scent discrimination by honeybees (*Apis mellifera*). *J Comp Physiol A*. 2005;191:105–14. <https://doi.org/10.1007/s00359-004-0576-6>.
- Xiong L, Yang J, Jiang Y, Lu B, Hu Y, Zhou F, et al. Phenolic compounds and antioxidant capacities of 10 common edible flowers from China. *J Food Sci*. 2014;79:C517–525. <https://doi.org/10.1111/1750-3841.12404>.

- Yamaguchi N. Leafy, a pioneer transcription factor in plants: a mini-review. *Front Plant Sci.* 2021;12:701406. <https://doi.org/10.3389/fpls.2021.701406>.
- Yang Y, Wang S, Leng P, Wu J, Hu Z. Calcium and jasmonate signals mediate biosynthesis of the floral fragrance regulated by light quality in snapdragon. *Plant Growth Regul.* 2022;97:91–100. <https://doi.org/10.1007/s10725-022-00807-y>.
- Yazaki K, Arimura GI, Ohnishi T. 'Hidden' terpenoids in plants: their biosynthesis, localization and ecological roles. *Plant Cell Physiol.* 2017;58:1615–21. <https://doi.org/10.1093/pcp/pcx123>.
- Zeng L, Wang X, Kang M, Dong F, Yang Z. Regulation of the rhythmic emission of plant volatiles by the circadian clock. *Int J Mol Sci.* 2017;18:2408. <https://doi.org/10.3390/ijms18112408>.
- Zhi Y, Zhou Q, Leng X, Zhao C. Mechanism of remediation of cadmium-contaminated soil with low-energy plant snapdragon. *Front Chem.* 2020;8:222. <https://doi.org/10.3389/fchem.2020.00222>.
- Zhu S, Zhang Y, Copsy L, Han Q, Zheng D, Coen E, et al. The snapdragon genomes reveal the evolutionary dynamics of the S-locus supergene. *Mol Biol Evol.* 2023;40:msad080. <https://doi.org/10.1093/molbev/msad080>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.