

ORIGIN OF CULTIVATED ROSES AND APPROACHES USED TO STUDY IMPORTANT ROSE TRAITS

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ABSTRACT: Different societies throughout human history have highlighted roses as a symbolic value and great cultural importance. Roses secondary purpose is the production of essential oils for the perfume and cosmetic industries, but they are widely used as garden ornamental plants and as cut flowers. Domestication of roses has a long and complex history, and the rose species have been hybridized across wide geographic areas such as Europe, Asia, and the Middle East. The domestication processes selected very important flower characters such as recurrent flowering, double flowers, petal colours, and fragrance. The molecular and genetic events that determine some of these flower characters cannot be studied using model species such as *Arabidopsis thaliana*, or at least only in a limited manner. Aim of this review was to approach and highlight development of genetic and genomic tools for roses, and then focus on recent advances that have helped understanding the molecular mechanisms of some rose floral traits.

Key words: *flower, rose, botany, genetic, selection*

INTRODUCTION

The genus *Rosa* belongs to the large family of the Rosaceae. Roses have been cultivated since antiquity in China, western Asia, and northern Africa. The main purpose in the days for wild roses was to be multiplied and used as a proof fence against animals, why in meanwhile other civilisations such as Romans, Greeks, and Persians used domesticated roses as floral ornaments and as medicinal plants. Spontaneous interspecific hybrids, such as *Rosa*×*damascena*, have been stabilized by vegetative propagation. In ancient times missionaries introduced Chinese roses to Europe. The subsequent extensive hybridization amongst the Chinese, European, and Middle-Eastern roses formed the genetic basis of the modern rose cultivars nowadays (Pécricx, 2011). Today, roses are one of the most commonly cultivated ornamental plants in the world. They are highly popular as garden ornamental plants and cut flowers. They are also in enormous demand in the perfume and cosmetic industries (Gudin, 2003). Today's contemporary roses are recognizable through large variety of characteristics such as flower shape, colour, and fragrance (Bendahmane et al., 2013). Understanding the genetic and molecular mechanisms that regulate described traits is not just a fascinating question of basic rose biology, but will also be tool for understand nature of selected traits during rose domestication over the years (Mazzolari et al., 2017). The aim of this

paper is to review current knowledge about molecular and genetic approaches in understanding the genetic and molecular mechanisms controlling important rose traits.

CULTIVATED ROSES ORIGIN

The genus *Rosa* comprises nearly 200 species, between which only 8–20 species have contributed to the genetic developing of present cultivars, namely variety *Rosa*×*hybrida* (Gudin, 2001; Cabello-Hurtado et al., 2016). Each of these species has shared their own part for a specific trait. For example, *Rosa gallica* and other robust polyploid species has gave the trait of cold hardiness, *Rosa chinensis* has gave trait of recurrent blooming, and *Rosa foetida* has gave the yellow flower color as her trait (Chen et al., 2015). However, despite such apparent spread of crystal plane orientations, the genome of modern rose varieties seems to bear the remains of a massive introgression of *Rosa chinensis* alleles (Martin et al., 2001). Nevertheless the genome of *Rosa*×*hybrida* is a mix of several parental genomes, the origin of its genetic variation is relatively homogeneous because of the intensive backcrossing to *Rosa chinensis* cultivars during the processes of varietal creation (Qi et al., 2018). One of the major hindrances to the creation of novel rose varieties stems from such lack of allelic variation compounded by the difficulty in introgressing alleles of interest from wild diploid species due to the polyploidy barrier. More than half of the wild rose species are polyploid, ranging from $2n=2x=14$ to $2n=8x=56$, with permanent sexual pentaploids such as *Rosa canina* exhibiting unusual asymmetric meiosis (Kovarik et al., 2008). Decade ago, karyotyping of *Rosa prealucens* from the Sino-Himalayan region revealed decaploidy, the highest naturally occurring ploidy of the genus (Jian et al., 2010). A study of Pécrix et al. (2011) suggests a possible evolutionary mechanism involving ploidy changes in response to adverse environmental conditions, such as exposure to high temperature. Therefore, manipulating temperature may be a strategy to overcome the ploidy barrier to introgress wild alleles of interest to contemporary rose cultivars.

APPROACHES TO STUDY IMPORTANT ROSE TRAITS

There are several very important rose traits if take a look from a commercial point of view. Nowadays commercial traits includes plant architecture, flower development, architecture, and senescence, scent biosynthesis and emission, ease of reproduction, and resistance to biotic and abiotic stresses. During the past two decade, molecular and genetic approaches were used to identify and functionally characterize genes and gene networks associated with important rose traits and their inheritance among cultivated roses. Initial cloning relied on candidate gene approaches. However, until early 2000, very little information was available on gene expression in rose (Bendahmane et al., 2013). At the same time, a number of laboratories created high-density linkage maps with the hope of locating or tag genes associated with important flowering traits. Till know, linkage analysis in rose has been complicated by the quasi-impossibility of obtaining inbred lines, due to self-incompatibility and high heterozygosity. Many mapping populations exist and were used to unravel the genetic basis of monogenic or oligogenic characters such as the simple corolla, pink flower, recurrent blooming, and three volatile components of scent (Spiller et al., 2011; Moghaddam et al., 2012). When it comes to identifying the genes controlling such traits in roses the mapping populations

are usually of insufficient size, typically less than one hundred individuals for the diploid maps, so that the observation of co-localization between one candidate gene and the locus of interest can be misleading. Not only is it difficult to carry out genetic analysis on quantitative and multigenic flower characteristics on a small mapping population, but also phenotyping roses can be demanding because many of the complex flowering traits are affected by environmental factors. Phenotyping has to be done on a pluri-annual basis, and such a task can be extremely labour intensive for complex traits such as inflorescence architecture (Linde et al., 2006). There is clearly a trade-off between the accuracy of phenotyping and size of the mapping population. Because each of the above approaches has limitations, combinations of genetic mapping, quantitative trait locus (QTL) analyses, and candidate gene approaches are being undertaken by a number of research groups in order to identify genes and genetic pathways associated with important rose traits.

DETERMINATION OF ROSE MORPHOGENESIS, FLOWERING TIME, COLOUR AND SENESCENCE

Like most core eudicots, the flower of wild-type roses consists of four organ types: five sepals, five petals, and a large number of stamens and carpels are arranged in concentric whorls, with the sepals occupying the outermost whorl. The number of stamens and carpels varies among rose species. Through mutant analysis, molecular cloning, and functional characterization of the corresponding genes in model species such as *Antirrhinum thaliana* and *Antirrhinum majus*, several groups have helped establish a model which shows that the combinatory actions of four classes of homeotic genes (A, B, C, and E) determine flower organ identity and trigger the developmental programmes required for flower organogenesis (Irish, 2010). In *Rosa* sp., the number of flower organs, especially that of petals, greatly influences flower architecture. While the wild roses have a simple flower with typically five petals per flower, the modern roses have double flowers consisting of more than then petals. In a number of species, researchers have uncovered some morphological, developmental, and genetic aspects of the double flower phenotype and it was not until 2010 that the underlying molecular mechanisms were first unravelled in *Rosa*. Dubois et al. (2010) demonstrated that in *Rosa* sp. the orthologue of *AGAMOUS* (*RhAG*) was differentially expressed in double flowers as compared with simple flowers. Using *in situ* hybridization, they showed that in double flower roses, *RhAG* expression is down-regulated and its domain of expression is restricted towards the centre of the floral meristem, hence allowing more petals and fewer stamens to form. The same research has also demonstrated that the restriction of the *RhAG* (C-function) expression domain towards the centre of the floral meristem was selected independently in two major regions of rose domestication.

Roses are perennial shrubs with axillary buds that undergo floral transition in late autumn, remain dormant in winter, and bloom in spring when temperatures are permissive. Short-day cultivars of roses flower once a year in spring; most of the ever-blooming long-day cultivars flower recurrently until autumn or even until the first frost. The flowers occurring in spring originate from buds that have undergone floral transition in autumn. The flower burst of rose buds needs light. White, far-red, or blue light can trigger bud burst. Bud blooming also requires sucrose, but experiments on bud explants showed that sucrose alone in the dark fails to trigger bud burst. Both light and sucrose function as signals that are necessary for bud burst and vacuolar invertase

activity that permits sucrose catabolism (Rabot et al., 2012). In non-recurrent cultivars, floral transition occurs within the main and axillary buds during short photoperiods in autumn and early spring. In recurrent flowering cultivars, floral transition also occurs during long photoperiods such as in late spring and summer. Petals in roses exhibit such a wide variety of colours that the only colour absent from this genus is blue. The absence of the blue colour is a result of roses lacking the flavonol 3',5'-hydroxylase (F3'5'H) activity to generate dihydromyrcetin, a precursor of delphinidin. Delphinidin is at the origin of the blue colour. However, roses can be forced to harbour the blue colour. Katsumoto et al. (2007) first knocked down endogenous rose dihydroflavonol 4-reductase (DFR) to reduce the production of red anthocyanin precursors, and overexpressed the *viola* DFR that uses dihydromyrcetin to make delphinidin from Iris. The petals of these roses exclusively accumulated delphinidin and showed blue hues (Katsumoto et al., 2007). However, because of the numerous parameters controlling the final petal colour, such as vacuolar pH or genetic background, these delphinidin-enriched flowers exhibited blue–purple-like petal colours. Yellow and orange rose petals mostly contain carotenoid pigments. The pink and red colours are due to anthocyanins and in particular to 3,5-diglycosyl anthocyanidins in association with 3-glycosylated flavonols. Three enzymes encoding flavonoid 3-glycosyltransferases (*RhGT1–RhGT3*) have been characterized. *RhGT1* was shown to be expressed in petals of cultivars that synthesize cyanidine 3-glucoside from cyanidins. *RhGT2* and *RhGT3* are co-expressed in rose petals with the flavonol synthase gene and catalyse 3-glycosylation of flavonols (Fukuchi-Mizutani et al., 2011). The pathways leading to petal colour in angiosperms are well characterized (Koes et al., 2005).

The molecular bases of petal senescence and abscission are of great research interest as senescence and abscission processes influence the vase life of cut flowers (Rogers, 2012). Abscisic acid is usually involved in petal senescence in both ethylene sensitive and ethylene insensitive senescence processes. Abscisic acid levels were reported to be higher in senescent rose petals concomitant with reduced flower water potential and reduced water uptake. However, the action of abscisic acid in rose senescing petals remains uncharacterized. Similar to other senescent organs, senescent rose petals have increased endogenous H₂O₂ levels and they exhibit decreased activities of antioxidant enzymes (Kumar et al., 2008). So far, there is no report on autophagy, nucleic acid degradation, protein turnover, or nutrient remobilization processes in senescing rose flowers. In roses, ethylene was shown to promote petal abscission through cell wall modifications. Ethylene levels dramatically increase during rose petal senescence, probably through the activity of the rose 1-aminocyclopropane-1-carboxylate synthase in petals (Wang et al., 2004).

CONCLUSIONS

Around past twenty years has witnessed the development of a number of molecular and genetic tools for the study of rose. These tools were instrumental for the discovery of the molecular and genetic basis of flower initiation and development in *Rosa* sp. First, many rose mapping populations were used to unravel the genetic basis of the monogenic or oligogenic characters such as simple corolla, pink flower, recurrent blooming, and scent based on three volatile components. However, because these mapping populations are usually small, co-localization between a given candidate gene and the locus of interest was unsuccessful. The rose genome sequence could also be useful to help understand

the molecular bases for important ornamental traits, which can in turn facilitate and accelerate rose breeding by marker-assisted selection or genomic selection, and to study genetic diversity and genome evolution. Altogether, these arguments prove that the rose can be an excellent model for ornamental species and especially woody ornamentals.

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