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Reticulate evolution and genomic innovation shape rose diversity and breeding potential

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Abstract

Ornamental roses constitute one of the most economically and culturally important horticultural groups within the genus *Rosa* and exhibit extensive morphological diversity and substantial commercial value. Characterized by long generation cycles, complex genetic backgrounds, and a protracted and ambiguous domestication process, ornamental roses are further distinguished by their complex taxonomic history and diverse germplasm resources. In recent years, advances in genomics and molecular biology have rapidly expanded genomic resources for roses, which have gradually clarified their domestication history, key morphological traits, and underlying genetic foundations. Concurrently, updated phylogenetic and genomic evidence has highlighted the reticulate evolutionary history of the genus *Rosa* and provided new insights into species relationships, trait diversification, and breeding potential. Based on these advances, this review outlines the phylogeny and evolutionary context of the genus *Rosa* and the historical trajectory of rose classification and domestication, and further summarizes recent progress in the genetic regulation and breeding of major ornamental and agronomic traits, such as flower color, flower form, fragrance, recurrent flowering, and disease resistance. Ornamental roses represent an important research system for genetic improvement in ornamental plants and provide a valuable framework for understanding the domestication, trait evolution, and molecular breeding of perennial ornamental crops.

Keywords: *Rosa*, Ornamental rose, Taxonomy, Genome, Genetic regulation, Molecular breeding

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Introduction

Plants of the genus *Rosa* (roses) represent one of the most economically and culturally significant groups within the Rosaceae family. They hold a central position in the global ornamental plant industry and serve as important raw materials for perfumes, cosmetics, and pharmaceuticals. Millennia of horticultural cultivation and extensive interspecific hybridization have given rise to over 35,000 cultivars[1], exhibiting remarkable phenotypic diversity in flower color, fragrance, morphology, blooming period, and stress resistance[2]. This variation not only supports a vast and continuously expanding rose industry but also makes the genus *Rosa* a valuable system for studying ornamental trait evolution, secondary metabolic pathways, flowering regulation, and floral morphogenesis[3].

However, the complex genetic systems of roses continue to pose persistent challenges for taxonomy, germplasm utilization, and breeding. Widespread gene flow, hybrid origins, and polyploidization events within the genus have resulted in blurred species boundaries and overlapping characteristics among traditional morphological classification systems. These factors have long hindered accurate identification of germplasm resources and the establishment of a rigorous phylogenetic framework[4,5]. Although progress has been made through molecular markers and nuclear and plastid phylogenetics[6], reticulate evolution, introgression, and historical hybridization continue to obscure many fundamental evolutionary relationships within the genus.

In recent years, the rapid development of high-throughput sequencing, long-read assembly, and chromosome-scale scaffolding has led to the successive publication of high-quality chromosome-level genomes for multiple rose species[7–10]. These genomic resources have substantially advanced the resolution of domestication history, hybridization events, and evolutionary lineages. They also provide important opportunities for identifying functional genes and loci underlying key ornamental and agronomic traits, such as flower color, fragrance, floral architecture, recurrent flowering, and disease resistance[11]. While previous reviews have provided valuable insights into rose genetics, many have focused primarily on specific aspects, such as classical morphological taxonomy, individual ornamental traits, or phytochemical properties. In contrast, this review aims to provide an integrated summary of recent advances in the classification and phylogenetic system of ornamental roses, the domestication and breeding history of modern roses, genomic innovation and genomic resources, and the genetic regulation and breeding potential of major traits. By linking taxonomic revision, evolutionary history, genome resources, trait-associated genes and loci, and breeding strategies, this review provides a theoretical reference for functional gene research and genome-informed improvement of ornamental roses.

Classification of ornamental roses

Ornamental roses belong to the genus *Rosa* within the family Rosaceae. The genus *Rosa* comprises approximately 150–200 species, widely distributed across temperate and subtropical habitats in the Northern Hemisphere[12,13]. Over its long taxonomic history, the study of roses has

undergone a gradual shift from descriptive morphology to molecular-marker-based and genome-informed phylogenetic interpretation. However, owing to frequent hybridization, polyploidization, introgression, and morphological plasticity within the genus, many taxonomic challenges remain unresolved.

As early as the 19th century, the taxonomy of the genus *Rosa* faced significant challenges, although a classification framework based on morphological characteristics had already been proposed[14,15]. Later, Rehder reorganized the genus based on morphological traits such as flower color, prickles, fruits, and leaf shape, dividing it into four subgenera: *Hesperhodos*, *Hulthemia*, *Platyrhodon*, and subg. *Rosa*. The first three subgenera contain only one or two species each, while subg. *Rosa* includes most rose species and was further divided into several sections, including *Banksiae*, *Bracteatae*, *Caninae*, *Carolinae*, *Cinnamomeae*, *Gallicanae*, *Indicae*, *Laevigatae*, *Pimpinellifoliae*, and *Synstylae*. Wissemann further refined sect. *Caninae* by recognizing several subsections within this morphologically complex group[16]. In addition to morphology, classifications based on chemical traits have also been proposed. For example, 57 rose species and 16 subspecies from Asia, America, and Europe were grouped into three types according to their monoterpene dynamics during floral development and senescence[17]. However, due to frequent hybridization, polyploidization, and morphological plasticity within the genus, classifications based solely on morphological or chemical traits often show considerable overlap among groups and may encounter nomenclatural issues. For instance, the type species of the genus *Rosa*, *R. cinnamomea* L., belongs to the traditional sect. *Cinnamomeae*[18,19]. According to nomenclatural rules, the section name *Cinnamomeae* is invalid and should be replaced by the autonym sect. *Rosa*. Similarly, sect. *Chinenses* has often been used in place of the traditional sect. Indicae[20,21]. These revisions indicate that the classification of *Rosa* involves not only species delimitation but also the reinterpretation of historical taxonomic concepts under modern nomenclatural and systematic frameworks.

In horticultural classification, the American Rose Society categorizes roses into three groups: species roses, old garden roses, and modern garden roses. These categories are useful for describing cultivation history, garden use, and breeding background, but they do not necessarily correspond to natural phylogenetic lineages. The horticultural concept of 'China roses' is closely associated with *R. chinensis*, *R. gigantea*, and related germplasm from sect. *Chinenses*, as well as their hybrids with other rose lineages[7]. Therefore, botanical taxonomy and horticultural classification should be distinguished when discussing ornamental roses.

Subsequent studies have attempted to reconstruct the phylogeny of the genus *Rosa* using various molecular markers, including random amplified polymorphic DNA (RAPD)[22,23], DNA sequence analysis[24–30], microsatellite (SSR) markers[31–39], single nucleotide polymorphisms (SNPs)[40–42], and amplified fragment length polymorphism (AFLP) data[43–45]. Most of these studies concluded that earlier phenotype-based classifications[16] were partly subjective and often conflicted with molecular results, with only limited support for the monophyly of several traditionally recognized sections. Additional phylogenetic efforts have employed chloroplast DNA markers, such as matK, rbcL, and psbA-trnH, and nuclear markers, such as ITS and GAPDH, either separately or in combination[46–50]. However, many phylogenetic reconstructions have yielded weakly supported or inconsistent clades, suggesting that the evolutionary history of *Rosa* cannot be fully explained by a simple bifurcating tree. Frequent interspecific hybridization, incomplete lineage sorting, and introgression have likely further complicated phylogenetic resolution within the genus[51–53].

Similarly, Zhu et al. constructed phylogenies of sect. *Synstylae* and sect. *Chinenses* based on chloroplast DNA, nuclear DNA, and single-copy nuclear genes from 126 individuals. Their results indicated that neither section is strictly monophyletic; instead, they are closely related to sections such as *Caninae* and *Gallicanae*, forming a broader '*Synstylae* and allies' clade. Together with sect. *Rosa*, this group constitutes one of two major lineages within the genus[54]. More recent phylogeny-based analyses of sect. *Synstylae* and sect. *Chinenses* have further emphasized the complex species boundaries, morphological homoplasy, and incongruence between nuclear and plastid signals within these groups[55]. Other studies have suggested that *R.* subg. *Hesperhodos*, *R.* subg. *Hulthemia*, and *R.* subg. *Platyrhodon* should be downgraded to the sectional level, and that *R.* subg. *Rosa* is polyphyletic and can be divided into seven clades, with sections such as *Caninae*, *Gallicanae*, *Synstylae*, and *Chinenses* being poly- or paraphyletic[56]. However, the most recent reports indicate that *R.* subg. *Hesperhodos* and *R.* subg. *Hulthemia* are genetically the most distant from other rose groups and thus should be retained as distinct subgenera[1].

This taxonomic controversy is also reflected in the incongruence among phylogenetic datasets. As shown in Fig. 1, nuclear and plastid phylogenies exhibit different placements of several major rose lineages, particularly sect. *Chinenses*, sect. *Synstylae*, sect. *Gallicanae*, and sect. *Caninae*. These topological discrepancies are highlighted in Fig. 1 using consistent colors and annotations across the two phylogenies. Because nuclear markers reflect predominantly biparental genomic histories, whereas plastid markers generally trace maternal inheritance, their conflicting topologies indicate cytonuclear discordance within the genus *Rosa*. Such discordance may result from historical hybridization, introgression, chloroplast capture, incomplete lineage sorting, or a combination of these processes[1,51–56]. However, the two phylogenies alone do not determine the direction or extent of historical gene flow. Therefore, the classification of ornamental roses should be regarded as an evolving framework rather than a fixed system. Morphology-based taxonomy provides the historical basis for species recognition, horticultural classification reflects cultivation and breeding practices, and molecular and genomic evidence reveals a complex evolutionary history that cannot always be represented by a single bifurcating tree. Integrating nuclear genomic data, plastid genomes, population resequencing, and phylogenetic-network analyses will be necessary to further resolve relationships among major rose lineages and support germplasm conservation and molecular breeding.

Historical evolution of ornamental roses

Known as the 'Queen of Flowers', the rose has been a symbol of love and beauty throughout history and represents one of the most successfully domesticated ancient ornamental plants[57]. Today, it is one of the most widely cultivated ornamental plants, with over 35,000 cultivars, a number that continues to rise, although most modern varieties have been developed through relatively recent hybridization and breeding efforts[1].

The evolutionary history of roses extends far beyond their cultivation history. Fossil evidence indicates that rose species have existed for at least 30 million years, and several studies suggest that the divergence of species within the genus *Rosa* occurred approximately six million years ago[58–60]. In contrast, human cultivation and domestication of roses are much more recent and were shaped by regional cultivation practices, germplasm exchange, and repeated artificial selection. Roses were known in ancient Rome[61], and murals from the peak of the Minoan civilization on Crete depicted them. The Greeks associated roses with Aphrodite, the Muses, and grace[62]. In China, records of roses date back as far as 5,000 years[63].

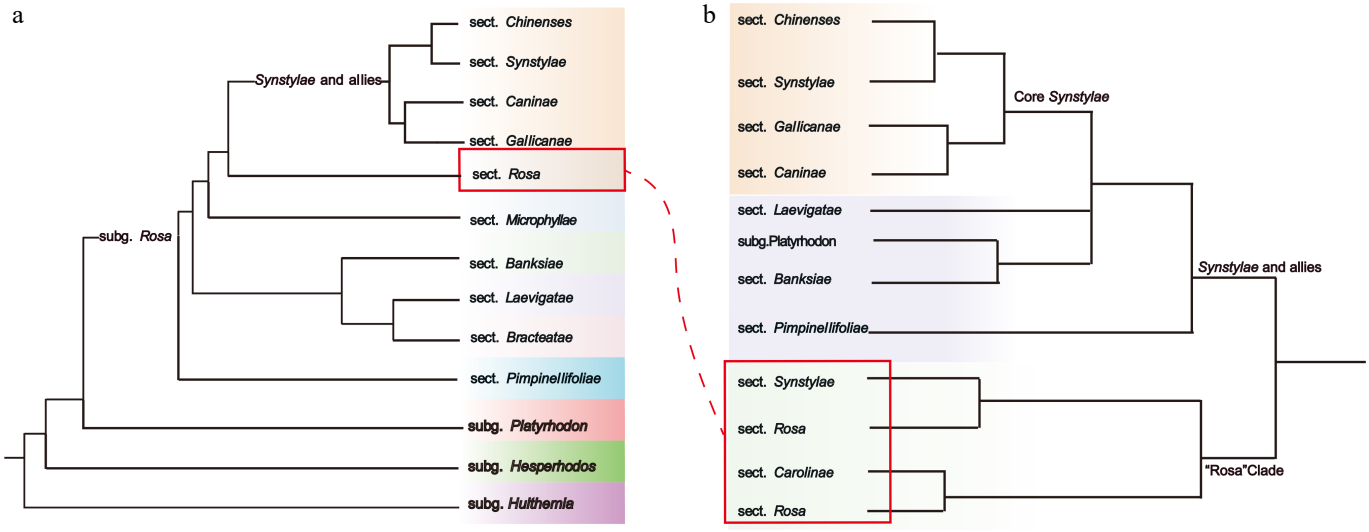

Fig. 1 Simplified nuclear and plastid phylogenies of major lineages in the genus *Rosa*.
(**a**) Nuclear phylogeny based on single-copy nuclear genes, simplified from Cheng et al.[1]. (**b**) Plastid phylogeny, simplified from Zhu et al.[54]. Corresponding groups are shown in the same colors, and highlighted labels indicate major cytonuclear topological discrepancies.

The domestication and improvement of ornamental roses followed a multi-regional pattern, with key germplasm resources distributed across Asia, Europe, West Asia, and the Mediterranean region[6,7]. Asian roses, particularly Chinese and tea rose germplasm represented by *R. chinensis*, *R. gigantea*, and related forms, contributed important traits such as recurrent flowering, diverse flower colors, and tea-like fragrance. Other Asian species, such as *R. multiflora*, also provided important genetic resources for modern rose breeding. In contrast, European old garden roses and related species, including *R. gallica*, *R. centifolia*, and *R. alba*, contributed traits such as cold hardiness, complex floral forms, and adaptation to temperate cultivation. West Asian and Mediterranean germplasm, including *R. damascena* and *R. moschata*, also played important roles in the development of cultivated roses, particularly in relation to fragrance and garden use[64,65].

By the 18th century, ornamental rose breeding had developed distinct characteristics in Europe and Asia. European roses were generally cold-hardy, often once-flowering, and had relatively limited flower colors. In contrast, Chinese rose germplasm was especially valuable because of its recurrent flowering habit and broader ornamental variation[66,67]. The introduction of Chinese and tea roses into Europe during the late 18th and early 19th centuries marked a turning point in modern rose breeding. Hybridization between Asian germplasm and European old garden roses generated new combinations of recurrent flowering, improved floral form, novel colors, fragrance, and adaptability, eventually giving rise to the ancestors of most modern roses, especially Hybrid Tea roses[3,64,68–70]. Although present-day rose cultivars are extremely diverse, the genetic background of modern roses traces back to a limited number of ancestral species and cultivar groups[67,71,72].

Previous studies indicated that species such as *R. chinensis*, *R. gigantea*, *R. multiflora*, *R. moschata*, *R. wichuraiana*, *R. gallica*, *R. foetida*, *R. rugosa*, and related germplasm contributed to the formation of modern cultivars. Among these contributions, recurrent flowering can be clearly traced to Chinese rose germplasm, particularly *R. chinensis* and its related cultivated forms[73–79]. Genomic studies have further refined this historical view. The genome of *R. chinensis* 'Old Blush' and resequencing of representative ancestral genotypes revealed mosaic genomic contributions from major rose lineages to modern cultivars[7]. More recently, the haplotype-resolved chromosome-scale genome of the tetraploid modern cultivar *Rosa hybrida* 'Samantha' and resequencing of 233 *Rosa* accessions provided direct genomic evidence for the complex origin and breeding history of modern roses[11]. Large-scale genomic and phenotypic analyses of wild *Rosa* species have further shown that wild germplasm remains an important reservoir for broadening the genetic basis of modern rose breeding[1].

Key ancestral cultivars evolved from early groups, such as Gallica, Damask, China, and Tea roses, to more recent groups, including Hybrid Perpetuals and Hybrid Tea roses[71]. During this process, the genetic background of European rose cultivars gradually shifted toward an increased contribution from Asian germplasm[65]. Hybrid descendants combined cold hardiness, disease resistance, and complex floral forms from European ancestors with recurrent flowering, novel colors, and fragrance-related traits from Asian roses. Based on historical and genomic evidence, Fig. 2 summarizes the domestication and breeding history of modern roses, highlighting the progressive integration of Asian, European, and West Asian germplasm and the contributions of wild species to the modern rose gene pool[1,11,71,80].

Overall, the historical evolution of ornamental roses is not merely a process of natural species divergence, but also a human-driven history of germplasm exchange, hybridization, and artificial selection. Centuries of selection for ornamental traits, including flower color, floral architecture, fragrance, recurrent flowering, and commercial traits such as vase life, disease resistance, and cultivation adaptability, have shaped the tens of thousands of cultivars observed today. With the development of genomic resources and molecular breeding technologies, the historical understanding of rose domestication is now being integrated with functional gene discovery and breeding innovation, providing new opportunities for the improvement of modern ornamental roses.

Genomic insights into ornamental roses

Reference genomes and haplotype-resolved genomic resources

Alongside the rapid advancement of omics technologies, genetic resources have been established for several species within the genus *Rosa*, laying a critical foundation for molecular breeding and trait evolution studies of ornamental roses. In early research, genome assemblies based on Illumina short-read sequencing played an important role. For example, the draft

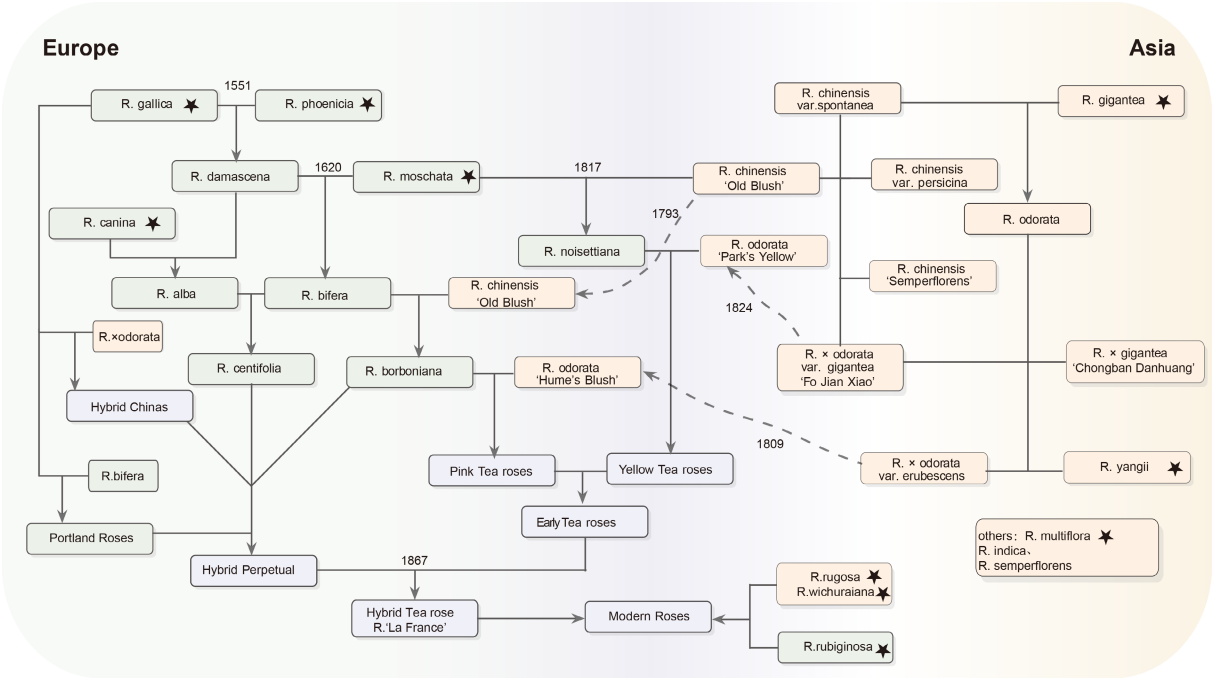

Fig. 2 Domestication and breeding history of modern roses.

The diagram illustrates the integration of Asian, European, and West Asian germplasm, with wild *Rosa* species and relatives indicated as important sources of ornamental, resistance, and adaptation-related traits.

genome of *Rosa multiflora*[81], though limited in contiguity, served as an early publicly available reference and provided a key starting point for subsequent comparative genomic and trait-related studies. To overcome assembly challenges posed by the generally high heterozygosity of *Rosa*, researchers began employing doubled-haploid materials combined with long-read sequencing. During this phase, *R. chinensis* 'Old Blush' emerged as a representative reference; Hibrand Saint-Oyant et al. produced a high-quality genome assembly using PacBio sequencing[8], and Raymond et al. further improved the assembly to chromosome-level quality through SMRT sequencing and chromosome-scale scaffolding[7]. These reference genomes greatly promoted studies on rose domestication, genome evolution, and the genetic basis of ornamental traits.

Subsequently, genomic resources for *Rosa* entered a period of accelerated and diversified development. After 2021, high-quality genomes of multiple wild species were successively published, such as the high-quality genome *R. rugosa*[60] and later *R. roxburghii*[9], significantly enriching phylogenetic studies of the genus and evolutionary analyses of important traits, including flower color, stress resistance, and secondary metabolism. Concurrently, genome assembly technology progressed toward haplotype-resolved and telomere-to-telomere levels. The haplotype-resolved genome of *R. chinensis* published in 2024 systematically resolved its highly heterozygous genome at the haplotype level for the first time[82]. A landmark breakthrough in recent years has been the genomic characterization of modern tetraploid garden roses. Zhang et al. assembled a haplotype-resolved, chromosome-scale tetraploid genome of the modern cultivar *Rosa hybrida* 'Samantha' and generated a genome variation map of 233 *Rosa* accessions, marking a shift in *Rosa* genomics from diploid model references to authentic and more complex breeding materials[11]. Thereafter, high-quality chromosome-level, haplotype-resolved, or telomere-to-telomere genomes of species such as *R. persica*, *R. hugonis*, *R. laevigata*, and *R. sterilis* were successively released, further expanding genomic coverage across key evolutionary branches of the genus[1,10,83,84] (Table 1).

Pangenomic resources and structural variation

Although these high-quality reference genomes have greatly advanced rose genomics, a single linear reference genome cannot fully represent the extensive genetic diversity of *Rosa*, particularly given its high heterozygosity, frequent hybridization, polyploidy, and abundant structural variation. This limitation is consistent with the broader transition in plant and horticultural genomics from single-reference assemblies to pangenomic and graph-based frameworks[85,86]. Recent *Rosa* pangenome studies have provided direct evidence for the value of this approach in roses. One pangenomic analysis constructed a pangenome of subg. *Rosa* using 26 accessions, including 23 newly assembled genomes and previously published high-quality genomes, and identified more than 1.8 million structural variations associated with key breeding traits such as continuous flowering, petal number, and petal discoloration[87]. Another study constructed a Rosaceae panproteome and a *Rosa* pangenome spanning wild roses, traditional garden roses, and modern rose lineages using a De Bruijn graph-based approach, revealing lineage-specific gene content variation, transposable element landscapes, and locus-level variation in key genes such as *MYB114*[88]. Together, these studies indicate that pangenomic resources can capture presence–absence variations, copy number variations, inversions, translocations, and regulatory structural variants that may be overlooked by a single reference genome, thereby providing a more comprehensive basis for studying rose genome evolution and genomics-directed breeding.

From genomic resources to genome-assisted breeding

The accumulation of rose genomic resources provides a practical basis for improving breeding efficiency. Traditional rose breeding relies heavily on repeated crossing, long-term phenotypic selection, clonal evaluation, and field or greenhouse testing. However, many target traits, including flower quality, recurrent flowering, vase life, disease resistance, plant architecture, and stress tolerance, are quantitative or environment-dependent, making direct selection time-consuming and inefficient[80,89].

Table 1. Representative genomic resources available for the genus *Rosa*.

Species/accession	Ploidy	Genome assembly	BUSCO completeness	Ref.
Rosa multiflora	Diploid (2x)	Draft scaffold-level genome	88.40%	[81]
R. chinensis 'Old Blush'	Diploid (2x)	Chromosome-level high-quality genome	93.50%	[7]
R. chinensis 'Old Blush' (HapOB)	Doubled haploid (2x)	Chromosome-level reference genome	95.00%	[8]
R. rugosa	Diploid (2x)	Chromosome-level high-quality genome	93.20%	[59]
R. chinensis 'Chilong Hanzhu'	Diploid (2x)	Haplotype-resolved chromosome-level genome	98.40%	[82]
R. sterilis	Diploid (2x)	Haplotype-resolved chromosome-level genome	98.60%	[84]
R. roxburghii	Diploid (2x)	Chromosome-level genome assemblies	98.3%; 91.7%	[9,84]
R. hybrida 'Samantha'	Tetraploid (4x)	Haplotype-resolved chromosome-level genome	98.70%	[11]
R. laevigata	Diploid (2x)	Chromosome-level high-quality genome	98.90%	[83]
R. hugonis	Diploid (2x)	Chromosome-level high-quality genome	98.60%	[10]
R. persica	Diploid (2x)	Telomere-to-telomere, phased and gap-free genome	98.90%	[1]

Rather than repeating the genomic resources described above, the key challenge is how to translate these resources into reliable breeding tools. High-quality reference genomes, transcriptomic datasets, high-density SNP arrays, polyploid genetic mapping tools, and multi-environment QTL analyses have provided a foundation for genome-assisted rose breeding[89,90]. Marker-assisted selection is most useful for traits controlled by major-effect genes or stable QTLs. In roses, molecular markers linked to recurrent flowering, prickle density, petal number, flower size, fragrance, and disease resistance have been reported in different genetic backgrounds[90–94]. SNP markers identified by GWAS may also help breeders select parental combinations or enrich favorable alleles, but marker effects still require validation across breeding populations, environments, and market classes before routine application[94,95].

For complex quantitative traits, genome-wide prediction and multi-omics-assisted selection may provide additional advantages by integrating genome-wide markers, transcriptomic profiles, metabolomic data, and high-throughput phenotyping[89]. However, genomic selection in roses remains less mature than in major crops because of limited large-scale training populations, complex ploidy, inconsistent phenotyping standards, and the high cost of multi-year evaluation. Recent pangenomic resources further expand the potential of genome-assisted breeding by capturing structural variants and gene-content variation that may be missed by a single linear reference genome[87,88]. Therefore, future rose breeding should combine haplotype-resolved genomes, population resequencing, pangenomes, trait mapping, standardized phenotyping, and multi-environment trials to identify functional alleles and structural variants associated with ornamental traits, disease resistance, stress resilience, and cultivation performance.

Genetic and epigenetic regulation of rose ornamental traits

With the accumulation of genomic resources and the rapid advancement of multi-omics technologies, research on the molecular basis of major ornamental traits in the genus *Rosa*, such as flower color, floral architecture, and floral scent, has made significant progress. In contrast to earlier studies that mainly described phenotypic variation and metabolic composition, recent research has increasingly focused on identifying rose-specific genes, regulatory modules, structural variations, and epigenetic or environmental factors that shape these traits. Therefore, this section focuses mainly on the genetic and regulatory mechanisms of ornamental traits that have been reported in roses, while evidence from other plants is discussed only as background where appropriate.

Pigmentation

The exceptional diversity of flower colors in ornamental roses is mainly determined by the accumulation, degradation, transport, and spatio-temporal regulation of pigments in petals. Anthocyanins are the principal pigments responsible for red, pink, and purple coloration in rose petals[96–98]. Their biosynthesis proceeds through the conserved phenylpropanoid and flavonoid pathways, in which structural genes such as *CHS*, *CHI*, *F3H*, *F3'H*, *DFR*, *ANS*, and *UFGT* function as key metabolic checkpoints[99]. In natural roses, the absence of flavonoid 3',5'-hydroxylase activity restricts delphinidin accumulation, which represents a major biochemical constraint on the production of blue flowers. Therefore, although transgenic strategies have attempted to redirect the anthocyanin pathway toward delphinidin-derived pigments, achieving stable blue coloration in roses remains difficult and has not fully overcome the intrinsic limitations of petal pigmentation, vacuolar pH, and co-pigmentation.

At the regulatory level, rose anthocyanin biosynthesis is controlled by transcriptional networks centered on R2R3-MYB transcription factors and their interaction with bHLH and WD40 proteins. In *Rosa chinensis* and modern rose cultivars, *RcMYB114* and *RhMYB114a* act as important positive regulators of anthocyanin accumulation by activating downstream structural genes. A transposable element-like insertion upstream of *RcMYB114* has been shown to alter its transcription and produce red petal coloration in rose, indicating that regulatory variation rather than coding variation alone can contribute to flower color diversification[100]. In addition, *RhMYB3b* functions as a negative regulator of anthocyanin biosynthesis, whereas *RhHY5* mediates light-responsive pigmentation by repressing *RhMYB3b* and activating *RhMYB114a*. Under high-light conditions, *RhHY5* promotes the formation of a *RhMYB114a*–bHLH–WD40 regulatory module and enhances the expression of anthocyanin structural genes; under low-light conditions, reduced *RhHY5* activity and increased *RhMYB3b* expression suppress anthocyanin accumulation[101].

Following biosynthesis, anthocyanin modification and transport are also critical for stable petal coloration. *RrGT1* promotes anthocyanin glycosylation and accumulation, whereas the *RcMYB75–RcGSTFL11* module coordinates anthocyanin biosynthesis and transport in rose[102–105]. These findings indicate that anthocyanin accumulation in roses is determined not only by biosynthetic flux but also by pigment modification and intracellular transport.

Carotenoids represent another important pigment class in roses and contribute to yellow and orange coloration[106–108]. In contrast to anthocyanin-rich red and pink petals, carotenoid-based colors are strongly affected by both carotenoid biosynthesis and degradation. Recent pangenomic analyses of roses identified a *CCD4* homolog as a major regulator associated with petal discoloration, suggesting that carotenoid cleavage and structural variation around pigment-related

loci are important contributors to rose color diversity[87]. However, because *CCD4*-mediated carotenoid degradation has also been studied extensively in other ornamental species, conclusions about specific *CCD4* functions in roses should be based primarily on rose-derived genetic, biochemical, or pangenomic evidence.

Taken together, rose petal pigmentation is shaped by the coordinated regulation of anthocyanin and carotenoid pathways, transcriptional regulators such as *MYB114*, *MYB3b*, and *HY5*, pigment modification and transport genes, and structural variations affecting key regulatory loci. Figure 3 integrates the conserved anthocyanin and carotenoid metabolic frameworks with rose-supported regulatory, modification, transport, and degradation mechanisms. Components supported by direct genetic, biochemical, or functional evidence in roses are highlighted, whereas conserved steps lacking direct validation in roses are shown in gray.

Floral architecture

Floral architecture is a major determinant of ornamental value in roses and includes petal number, flower form, floral organ identity, petal size, and the degree of stamen-to-petal transformation. Compared with many model plants, roses are particularly valuable for studying floral architecture because double flowers and multi-layered petals have been intensively selected during domestication and modern breeding. Therefore, this section focuses on rose-specific evidence related to floral organ identity and petal development rather than general developmental mechanisms from other species.

The ABCDE model provides a useful conceptual framework for understanding floral organ identity, but in roses the formation of double flowers is closely associated with altered expression of floral homeotic genes. In single-flowered wild-type roses, C-class AGAMOUS-like genes restrict petal identity and maintain reproductive organ development in the inner whorls. In double-flowered roses, reduced or spatially altered expression of *RhAG* weakens C-class function and allows stamens to undergo petaloid transformation, thereby increasing petal number[109]. This mechanism links the classical floral organ identity model with one of the most commercially important traits in rose breeding.

Several rose-specific regulators have been reported to modulate this process. The APETALA2 homolog *RcAP2* is associated with the number of petals derived from stamens and participates in the response of petaloid stamen formation to temperature fluctuations[110]. Its increased expression is related to enhanced stamen-to-petal conversion, suggesting that the antagonistic relationship between A-class and C-class regulatory activities contributes to petal number variation in

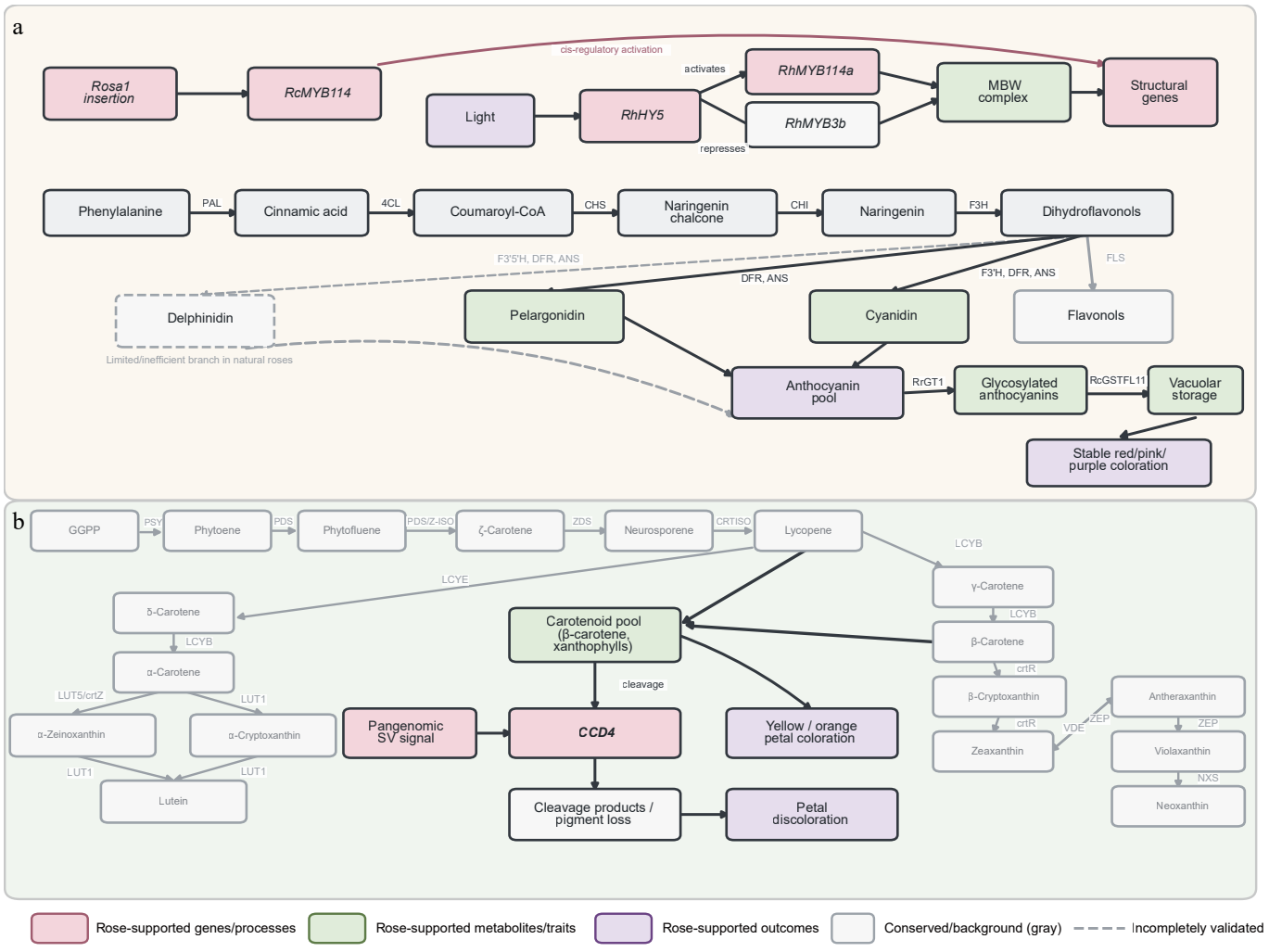

Fig. 3 Major pathways and regulatory mechanisms of rose petal pigmentation.

(**a**) Anthocyanin biosynthesis, regulation, modification, and transport. (**b**) Carotenoid biosynthesis and *CCD4*-associated degradation. Colored elements indicate rose-supported evidence, whereas gray elements indicate conserved components lacking direct functional validation in roses.

roses. In addition, the NAC transcription factor *RhCUC3* has recently been reported to regulate petal number by modulating *RhAG* and related floral identity genes[111]. These results suggest that rose petal number is controlled not by a single pathway but by a regulatory network involving homeotic genes, boundary-related transcription factors, and environmental responsiveness.

Temperature-dependent variation in petal number is also an important feature of roses. Low temperature can promote petaloid stamen formation in some cultivars, partly through changes in the expression of floral identity genes and upstream regulators. For example, *RhMYB17* has been reported to activate *RhAP2* and *RhAP2L*, thereby influencing the balance between A-class and C-class gene activity and promoting stamen petaloidy under low-temperature conditions[112]. Such findings provide a mechanistic explanation for the common horticultural observation that some rose cultivars produce flowers with higher petal numbers under cooler conditions.

Spontaneous floral mutants provide additional evidence for the genetic regulation of rose floral architecture. *Rosa* chinensis '*Viridiflora*', an ancient green-flower mutant, exhibits homeotic transformation of floral organs into sepal-like or leaf-like structures and is therefore useful for understanding floral organ identity in roses. Studies of this mutant have implicated MADS-box genes, including *RcAG2*, *RcFUL*, and other ABCDE-related genes, in the regulation of floral organ specification and flower shape[113,114]. These findings support the view that floral architecture in roses is shaped by coordinated changes in organ identity genes rather than by petal number regulators alone.

Beyond organ identity and petal number, petal size is another important ornamental trait. Recent work has shown that the cytokinin-responsive *RhRR1–RhSCL28* transcription factor module positively regulates petal size by promoting cell division and activating cell cycle-related genes[115]. This indicates that final flower form depends not only on the conversion of stamens into petals, but also on the control of petal cell proliferation and organ expansion. Together, rose floral architecture is controlled through the coordinated regulation of floral organ identity, stamen-to-petal conversion, and petal cell proliferation.

Floral scent

Floral scent is a key aesthetic and commercial trait of roses. Rose fragrance is composed of diverse volatile organic compounds, including terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, and other aromatic compounds[116]. Different species and cultivars show marked variation in scent intensity and composition[117–119]. In general, classic rose-like scent is strongly associated with 2-phenylethanol and monoterpene alcohols such as geraniol, whereas tea-like scent in Tea and Hybrid Tea roses is closely related to phenolic methyl ethers such as 3,5-dimethoxytoluene[120]. Figure 4 summarizes the major rose-specific biosynthetic routes underlying floral scent, with emphasis on pathways and enzymes supported by genetic, biochemical, or functional evidence in roses.

Benzenoid and phenylpropanoid scent compounds in roses are derived mainly from L-phenylalanine and related aromatic metabolic pathways. 2-Phenylethanol, one of the dominant rose scent compounds, can be produced from L-phenylalanine through phenylacetaldehyde. Enzymatic studies in rose petals identified aromatic amino acid decarboxylase (AADC) and phenylacetaldehyde reductase (PAR) as key enzymes catalyzing the conversion of L-phenylalanine to phenylacetaldehyde and then to 2-phenylethanol[121]. These findings establish the AADC/PAR-mediated route as a major rose-supported pathway for 2-phenylethanol biosynthesis.

Phenolic methyl ethers are important contributors to rose scent, particularly in tea-scented roses. Rose O-methyltransferases participate directly in the biosynthesis of 3,5-dimethoxytoluene and related compounds. Orcinol O-methyltransferases, including OOMT1 and OOMT2, catalyze the sequential methylation reactions leading to 3,5-dimethoxytoluene, whereas phloroglucinol O-methyltransferase (POMT) contributes to the production of 1,3,5-trimethoxybenzene in *R. chinensis*[122,123]. These enzymes therefore represent key determinants of phenolic methyl ether composition and tea-like scent variation in roses.

Terpenoid scent biosynthesis in roses differs from the canonical monoterpene synthase pathway commonly described in many plants. In roses, geraniol formation is mediated by a non-canonical cytosolic pathway. The Nudix hydrolase *RhNUDX1* converts geranyl diphosphate (GPP) into geranyl phosphate, which is then dephosphorylated by an as-yet-uncharacterized phosphatase to produce geraniol[3]. Subsequent studies showed that the cytosolic bifunctional geranyl/farnesyl diphosphate synthase *RcG/FPPS1* provides MVA-derived GPP for NUDX1-dependent geraniol biosynthesis in rose flowers[124]. Current evidence therefore supports the cytosolic *RcG/FPPS1–RhNUDX1* route as the principal characterized pathway for geraniol production in rose petals, whereas the contribution of canonical plastidial terpene synthases requires further evaluation.

Rose scent also includes sesquiterpenoid components. Functional diversification of the NUDX gene family has been shown to contribute to sesquiterpene biosynthesis in rose. In *Rosa* × *wichurana*, *RwNUDX1-2* uses farnesyl diphosphate (FPP) to produce farnesyl phosphate, which is further converted to (E,E)-farnesol and related sesquiterpenoids[125]. This functional diversification of NUDX proteins expands their role from monoterpene production to sesquiterpenoid scent formation in roses.

In addition to terpenoids and phenolic methyl ethers, eugenol and related phenylpropene compounds contribute to floral scent variation. Recent work identified a *de novo*-originated gene, *SCREP*, as a regulator of eugenol biosynthesis and rose scent diversification, highlighting the role of lineage-specific genetic innovation and transposable element-associated regulatory changes in the evolution of rose fragrance[126]. This finding illustrates how lineage-specific gene innovation and transposable element-associated regulatory changes have contributed to the diversification of rose fragrance.

Rose floral scent is therefore generated through several experimentally supported metabolic routes, including AADC/PAR-mediated 2-phenylethanol biosynthesis, OOMT/POMT-mediated phenolic methyl ether formation, *RcG/FPPS1–RhNUDX1*-dependent geraniol biosynthesis, *RwNUDX1-2*-associated farnesol production, and *SCREP*-related eugenol biosynthesis. Pathway steps lacking direct evidence in roses, such as NPP formation and inter-compartmental IPP transport, remain hypothetical and require experimental validation. Accordingly, experimentally supported rose pathways are shown in color in Fig. 4, whereas conserved or proposed reactions lacking direct functional validation in roses are shown in gray.

Cultivation and breeding of ornamental roses

Global industry landscape and market-driven breeding objectives

Roses are among the most important ornamental crops and are widely used for cut-flower production, garden landscaping, potted cultivation, and fragrance-related applications[127]. Among these categories, fresh cut roses are the most clearly represented in international trade and constitute a highly globalized ornamental commodity. Studies of the global

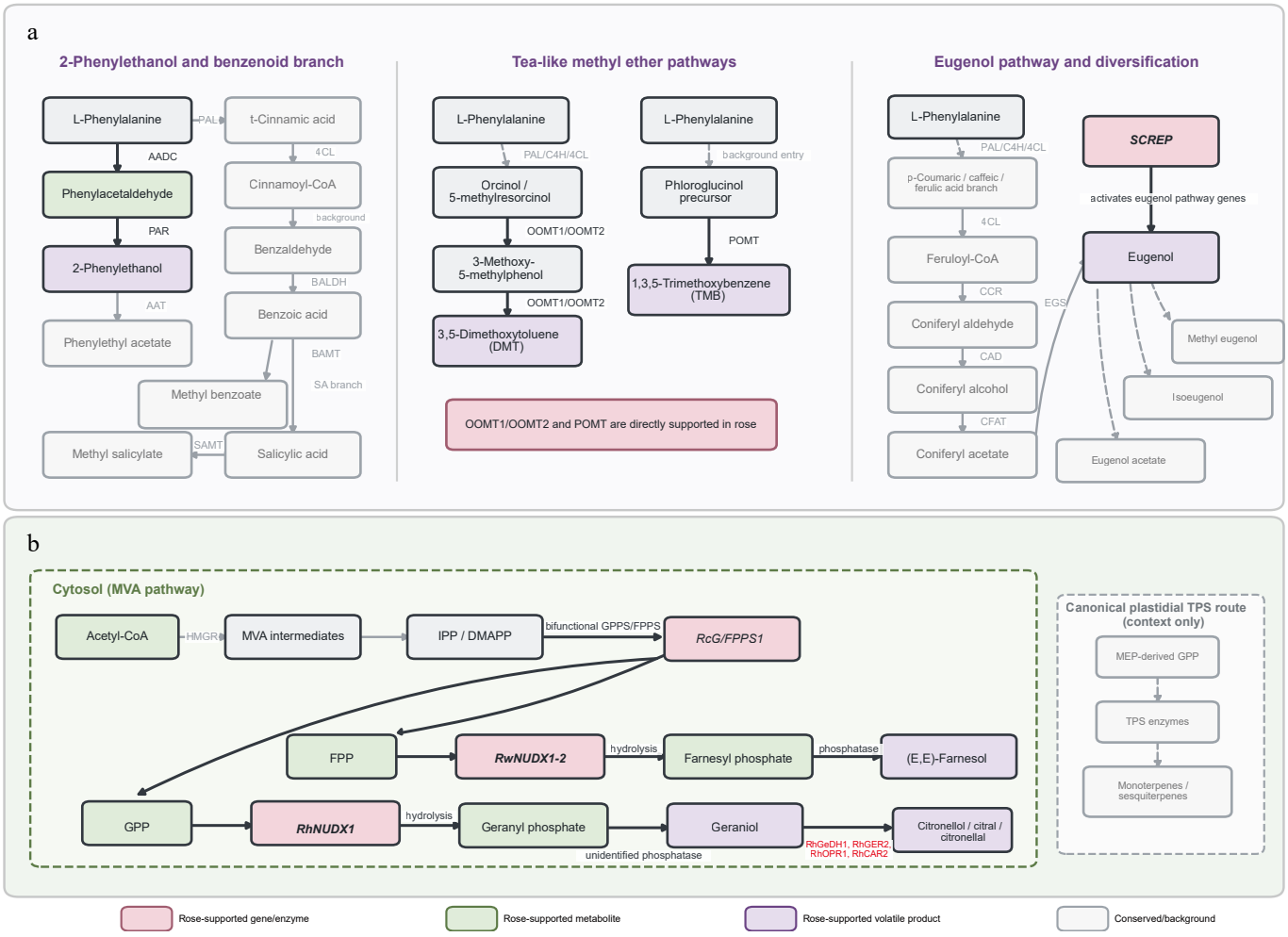

Fig. 4 **Major biosynthetic pathways of rose floral scent.**

(**a**) Phenylalanine-derived and phenylpropanoid/benzenoid pathways. (**b**) Cytosolic NUDX-dependent terpenoid pathways. Colored elements indicate rose-supported evidence, whereas gray elements indicate conserved or proposed steps lacking direct validation in roses.

ornamental plant and cut-flower trade indicate that the Netherlands, Colombia, Ecuador, Kenya, and other flower-producing regions in Europe, Latin America, and East Africa occupy important positions in international floriculture and cut-flower supply chains[128–130]. In contrast, garden roses and potted roses are more strongly linked to domestic nursery production, urban landscaping, home gardening, and retail markets, whereas essential-oil roses are concentrated in specific aromatic rose production regions and are often recorded within fragrance, essential-oil, or processed agricultural product categories. Therefore, exact global proportions among cut roses, garden roses, potted roses, and essential-oil roses are difficult to standardize across countries, but these market categories clearly represent distinct industrial demands.

China provides a representative example of this diversified industry structure. In Yunnan, flower-growing clusters around Dounan mainly produce fresh-cut flowers that are traded through the Dounan market, whereas other flower-growing regions may be more closely associated with petal processing and fragrance-related products[131]. In addition, Chinese industrial-type or fragrance-related roses include Kushui rose, Pingyin rose, Jinbian rose, and related Rosa germplasm used for essential oil, aroma, or processed rose products[132,133]. These regional and product-type differences illustrate that rose breeding objectives are strongly shaped by market type and end use rather than by ornamental appearance alone.

Accordingly, cut rose breeding emphasizes long and straight stems, uniform flower quality, stable color, long vase life, postharvest tolerance, and suitability for protected cultivation and long-distance transport[89,134]. Garden and landscape roses require recurrent flowering, attractive plant architecture, environmental adaptability, heat and cold tolerance, disease resistance, and low maintenance requirements. Potted roses require compact growth, synchronized flowering, abundant blooms, and stable performance under container cultivation and retail conditions. Essential-oil roses require high floral biomass, stable volatile composition, and efficient essential-oil yield. Thus, modern rose breeding increasingly integrates aesthetic value, cultivation adaptability, stress resilience, postharvest performance, and market-specific commercial traits.

Breeding for ornamental traits

Ornamental value remains the primary target of rose breeding. Major ornamental traits include flower color, floral architecture, fragrance, recurrent flowering, petal size, flower longevity, plant architecture, and prickle density. Many of these traits are difficult to evaluate accurately in early breeding generations because they are influenced by developmental stage, environmental conditions, and genetic background[80]. Therefore, the identification of stable genetic markers and causal genes is essential for improving breeding efficiency.

Flower color has long been one of the most important breeding targets in roses. Classical breeding has generated extensive color variation, including red, pink, yellow, orange, white, and multicolored petals. Rose petal coloration is mainly determined by anthocyanin and carotenoid metabolism, together with regulatory genes and structural variations affecting pigment biosynthesis, degradation, transport, and storage. Genes and loci related to anthocyanin accumulation, such as *MYB114* homologs, *RhMYB3b*, *RhHY5*, glycosyltransferases, and glutathione S-transferase-like transporters, provide potential targets for marker-assisted selection and molecular breeding. However, the development of true blue roses remains challenging because natural roses lack efficient delphinidin-based pigmentation, and previous transgenic attempts have not fully overcome constraints related to pigment composition, vacuolar pH, and co-pigmentation.

Floral architecture, especially petal number and flower form, is another key determinant of market value. Double flowers and high petal numbers are associated with stamen-to-petal transformation and altered expression of floral organ identity genes, such as *RhAG*, *RcAP2*, *RhCUC3*, and related MADS-box regulatory genes[109,112–114]. Several QTLs and major-effect loci for flower form, petal number, and flower size have been reported[91,92]. These findings indicate that combining traditional phenotypic selection with molecular markers linked to floral architecture may accelerate the development of cultivars with stable and attractive flower forms.

Fragrance is highly valued in garden roses and essential-oil roses but has often been weakened during selection for cut-flower traits such as vase life, uniformity, and transport tolerance. Rose scent is controlled by multiple biosynthetic routes, including 2-phenylethanol, monoterpenes such as geraniol, phenolic methyl ethers such as 3,5-dimethoxytoluene, and phenylpropene derivatives such as eugenol[3,116,120]. Because scent is a complex quantitative trait affected by both volatile biosynthesis and emission dynamics, breeding for fragrance requires the integration of metabolic profiling, transcriptomics, and sensory evaluation. Rose-specific genes such as *RhNUDX1*, *RcG/FPPS1*, OOMT genes, AADC/PAR-related genes, and *SCREP* provide important candidate targets for restoring or enhancing fragrance in modern cultivars.

Recurrent flowering is one of the most important traits introduced from Chinese rose germplasm into modern roses. Functional variation in *KSN*, a homolog of TERMINAL FLOWER 1 (*TFL1*), has been shown to play a central role in the recurrent flowering habit[135]. The identification of flowering-related loci and markers has facilitated early prediction of flowering behavior and improved the efficiency of breeding programs[136]. In addition to recurrent flowering, traits such as reduced prickle density, miniature plant habit, long vase life, and delayed petal senescence are increasingly important for specific market types. These traits should be considered together with flower color, form, and fragrance in multi-trait breeding strategies. Representative genes, loci, and regulatory modules associated with major ornamental traits and their potential applications in rose breeding are summarized in Table 2.

Breeding for disease resistance and stress resilience

Although ornamental value remains the primary determinant of cultivar acceptance, disease resistance has become an increasingly important breeding objective because modern rose production requires environmentally friendly cultivation systems with reduced pesticide input. Major diseases such as black spot, powdery mildew, downy mildew, rust, and rose rosette disease can severely affect plant growth, ornamental quality, marketability, and landscape performance. Therefore, resistance breeding is essential not only for reducing production costs but also for supporting sustainable rose cultivation.

Black spot, caused by the hemibiotrophic fungus *Diplocarpon rosae*, is one of the most destructive rose diseases. Multiple major resistance loci and QTLs have been reported in roses. The best-characterized locus, *Rdr1*, was identified from *Rosa multiflora* and is located on chromosome 1. Comparative genomic analyses revealed that the *Rdr1* region contains a complex cluster of Toll/interleukin-1 receptor–nucleotide-binding site–leucine-rich repeat (TNL) genes[137]. Other major resistance loci, including *Rdr2*, *Rdr3*, and *Rdr4*, have also been identified in different genetic backgrounds[93,138]. Recent QTL mapping studies using multi-parental diploid rose populations further detected resistance-associated regions on multiple linkage groups and

Table 2. **Representative genes, loci, and regulatory modules associated with major ornamental traits in roses.**

Trait	Gene/locus or module	Main function or evidence	Ref.
Flower color	*Rosa1–RcMYB114*	A transposable element-like insertion upstream of *RcMYB114* alters its transcription and promotes red petal coloration.	[100]
Flower color	*RhHY5–RhMYB114a–RhMYB3b*	A light-responsive module that balances positive and negative regulation of anthocyanin biosynthesis.	[101]
Flower color	*RrGT1*; *RcMYB75–RcGSTFL11*	*RrGT1* promotes anthocyanin glycosylation and accumulation, whereas the *RcMYB75–RcGSTFL11* module coordinates anthocyanin biosynthesis and transport in rose.	[103,105]
Flower color	*CCD4* homolog and associated structural variation	Pangenomic structural variation links carotenoid cleavage to petal discoloration.	[87]
Floral architecture	*RhAG*	Reduced expression and low-temperature-associated DNA hypermethylation weaken C-class function and increase petal number.	[109]
Floral architecture	*RcAP2*; *RhCUC3*	Regulate stamen-derived petal number and floral organ identity, including temperature-responsive petaloidy.	[110,111]
Floral architecture	*RhMYB17–RhAP2/RhAP2L*	Promotes stamen-to-petal transformation under low-temperature conditions.	[112]
Floral architecture	*RcAG2*; *RcFUL*	Associated with homeotic floral organ conversion and flower-shape change in '*Viridiflora*'.	[113,114]
Petal size	*RhRR1–RhSCL28*	A cytokinin-responsive module that promotes cell division and petal enlargement.	[115]
Recurrent flowering	*KSN*/*TFL1*-related flowering control	A central flowering-repressor pathway and associated flowering-time loci that support early selection for recurrent flowering.	[7,136]
Floral scent	AADC/PAR	Sequential conversion of L-phenylalanine to phenylacetaldehyde and then to 2-phenylethanol.	[121]
Floral scent	OOMT1/OOMT2; POMT	Biosynthesis of 3,5-dimethoxytoluene and 1,3,5-trimethoxybenzene associated with tea-like scent.	[122,123]
Floral scent	*RcG/FPPS1–RhNUDX1*	Cytosolic MVA-derived GPP supply and non-canonical geraniol biosynthesis.	[3,124]
Floral scent	*RwNUDX1-2*	Conversion of FPP to farnesyl phosphate supports (E,E)-farnesol biosynthesis.	[125]
Floral scent	*SCREP*	A *de novo*-originated gene that regulates eugenol biosynthesis and rose scent diversification.	[126]

showed that some QTLs overlap with known Rdr loci[139]. These results provide useful markers for DNA-informed breeding and for pyramiding resistance loci from different germplasm sources.

Powdery mildew is another important disease affecting roses. A dominant resistance gene, *Rpp1*, has been reported to confer resistance to specific powdery mildew races[140,141], and several QTLs related to powdery mildew resistance have been identified in different mapping populations[142–148]. In addition to race-specific resistance genes, susceptibility genes also provide potential targets for durable resistance. The *MLO* gene family is well known for its role in powdery mildew susceptibility in many plant species. In roses, several *MLO* homologs have been identified, and functional studies indicate that *RhMLO1* and *RhMLO2* are required for powdery mildew infection. Silencing *RhMLO1* enhances resistance to powdery mildew, suggesting that *RhMLO* genes may serve as promising susceptibility targets for resistance breeding[149–151].

Beyond fungal disease resistance, wild *Rosa* species and old garden roses provide valuable alleles for abiotic-stress adaptation and should be incorporated into breeding programs through introgression and genome-assisted selection. Representative genes, major loci, and QTLs associated with black spot and powdery mildew resistance are summarized in Table 3.

Conclusions and future prospects

Roses represent one of the most important ornamental crops, with complex taxonomic relationships, a long history of domestication, and extensive phenotypic diversity. In this review, we summarized the transition of rose classification from traditional morphology-based taxonomy to molecular and genome-informed phylogenetic interpretation, emphasizing the roles of hybridization, introgression, polyploidization, and cytonuclear discordance in shaping the complex evolutionary history of the genus *Rosa*. We further reviewed the domestication and breeding history of ornamental roses, particularly the fusion of Asian and European germplasm that contributed to recurrent flowering, diverse flower colors, fragrance, floral architecture, and the formation of modern rose cultivars. Recent chromosome-level, haplotype-resolved, and tetraploid genome assemblies have provided new resources for understanding the origin, evolution, and genetic improvement of roses.

Future rose research should place greater emphasis on connecting genomic variation with trait formation and breeding value. High-quality reference genomes, population resequencing, haplotype-resolved assemblies, and pangenomic resources now make it possible to identify not only single nucleotide polymorphisms but also presence–absence variations, copy number variations, inversions, translocations, and transposable element-associated regulatory changes. These forms of variation are particularly important in roses because of their high heterozygosity, frequent interspecific hybridization, and polyploid backgrounds. Therefore, pangenome and graph-based approaches are expected to provide a more comprehensive framework for resolving lineage-specific genomic diversity, improving the use of wild *Rosa* germplasm, and identifying functional alleles associated with ornamental traits and stress resilience. However, these genomic resources should be integrated with accurate phenotyping, transcriptomic and metabolomic analyses, and functional validation to avoid overinterpreting candidate loci without experimental support.

From a breeding perspective, future improvement of ornamental roses should integrate aesthetic quality, cultivation performance, and environmental sustainability. Flower color, floral architecture, fragrance, recurrent flowering, vase life, prickle density, disease resistance, and abiotic stress tolerance should be considered as coordinated breeding targets rather than independent traits. Marker-assisted selection may be particularly useful for major-effect genes and stable loci, such as those associated with recurrent flowering or disease resistance, whereas genomic selection and multi-omics-assisted prediction may help improve complex quantitative traits after sufficient training populations and standardized phenotyping systems are established. Precision breeding technologies, including genome editing, may provide additional opportunities for manipulating validated susceptibility genes or regulatory loci, but their application in roses still requires efficient transformation systems, careful assessment of multi-allelic effects in polyploid backgrounds, and consideration of commercial and regulatory constraints. Overall, integrating germplasm resources, genomic tools, functional biology, and practical breeding objectives will be essential for developing rose cultivars with improved ornamental value, resilience, and sustainable cultivation potential. Together, these advances indicate that reticulate evolution and genomic innovation jointly shape rose diversity and provide a foundation for future breeding.

Author contributions

The authors confirm contributions to the paper as follows: study conception and design, manuscript framework, and overall supervision: Cai Y, Yang Y, Wang C; draft manuscript preparation, literature collection, manuscript organization, and revision: Dai Z, Xu F, Cui Y; literature review and reference checking, manuscript editing: Chen Y, Zhang G, Li X; revising and improving the manuscript critically for important intellectual content: Cai Y, Yang Y, Wang C, Dai Z, Xu F. All authors reviewed the results and approved the final version of the manuscript.

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Table 3. Representative genes, loci, and QTLs associated with black spot and powdery mildew resistance in roses.

Disease	Gene/locus or QTL	Main function or evidence	Ref.
Black spot	*Rdr1*	A major chromosome 1 resistance locus containing a complex cluster of TIR–NBS–LRR genes.	[137]
Black spot	*Rdr2–Rdr4*	Additional major resistance loci identified in diverse diploid and tetraploid genetic backgrounds.	[93,138]
Black spot	Resistance QTLs	Multi-parental mapping detected resistance regions on several linkage groups, including QTLs overlapping known *Rdr* loci.	[139]
Powdery mildew	*Rpp1*	A dominant race-specific resistance gene; molecular mapping and SCAR markers support marker-assisted selection.	[140,141]
Powdery mildew	Resistance QTLs	Pathotype- and environment-dependent QTLs have been identified in diploid and tetraploid rose populations.	[142–148]
Powdery mildew	*RhMLO1*/*RhMLO2*	Susceptibility genes required for infection; silencing *RhMLO1* enhances resistance to powdery mildew.	[149–151]

Conflict of interest

The authors declare that they have no conflict of interest.

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