

17. Rose Structural Genomics

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1 DNA Markers Available and Future Developments

The development of SSRs designed for rose has accelerated in the last several years and is now a focal point of the map development especially as we move towards developing a consensus map to combine the mapping data from the various maps that have been developed. In the past 5 years, there have been reports from Europe (Esselink et al., 2003; Debener, personal communication; Yan et al., 2005a; Hibrand-Saint Oyant et al., 2007), the USA (Zhang et al., 2006), and Japan (Kimura et al., 2006) describing the development of both genomic (256 primer pairs) and EST (44 primer pairs) based microsatellites. Of these, 168 of the genomic primer pair sequences are proprietary and are available via a MTA (material transfer agreement) with restrictions on their commercial use in breeding or in variety protection (Esselink et al., 2003; Yan et al., 2005a; Debener, personal communication, ConCipio) (Table 1).

Mapping work has shown that each of these major groups of microsatellites (Rh, Rw, and EST-SSRs) map to all 7 of the linkage groups of rose (Yan et al., 2005a; Zhang et al., 2006; Hibrand-Saint Oyant et al., 2007). The only set of SSRs mapped to several maps are those developed in the USA (Zhang et al., 2006). These 30 SSRs have been mapped to the 90–69 map (Zhang et al., 2006), the 97/7 map (Zhang, 2003), and the Hw map (Hibrand-Saint Oyant et al., 2007). Using this data, a preliminary partial consensus map was developed with 5 of the 7 linkage groups (LG) by Sriyani Rajapakse (Byrne et al., PAG talk, Jan 2007) (Fig. 1). Current work in the USA, Europe and Israel is working towards rose maps with sufficient overlapping microsatellites to enable the development of a consensus map for the rose genome.

With a primary interest in the use of molecular markers to aid in the development of highly disease resistant plant varieties (Byrne, 2007) several research groups have developed, characterized, and mapped *RGAs* (*resistance gene analogues*) and *PKs* (*protein kinase*) as an approach to find markers for the loci controlling resistance

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Table 1 Sources of SSRs developed for rose

DNA source	Nomenclature	Number	Availability	Reference
Genomic DNA from hybrid tea cv Sonia, robust sequence tagged microsatellite site	Rh/MiCD	27	MTA-PRI/BAFZ	Debener et al. (2001)
Genomic DNA from hybrid tea cv Sonia, robust sequence tagged microsatellite sites	Rh	24	MTA-PRI/BAFZ	Esselink et al. (2003)
Genomic DNA	Rh Rh MiCD	37 21 4	MTA-PRI/BAFZ Public-PRI/BAFZ	Yan et al. (2005a)
Genomic DNA	RMS	107	MTA-CC	Debener, personal communication
Genomic DNA	Rw	30	Public	Zhang et al. (2006)
<i>R. wichurana</i> cv Basye's Thornless	na	13	Public	Kimura et al. (2006)
Genomic DNA	na	4	Mapped but no sequence reported	Linde et al. (2006)
Hybrid tea cv Asamii Red 97/77 mapping	na	4	Mapped but no sequence reported	Linde et al. (2006)
Genomic DNA	Rw	20	Public	Hibrand-Saint Oyant et al. (2007)
<i>R. wichurana</i> cv Basye's Thornless EST - cDNA library from vegetative and floral buds of <i>R. wichurana</i> and 'Black Baccara'	C, CL, H	44	Public	Hibrand-Saint Oyant et al. (2007)

MTA = material transfer agreement, PRI = Plant Research International, BAFZ = Institute for Ornamental Plant Breeding, Ahrensburg, Germany, CC = Con/Cipio, Sangerhausen, Germany.

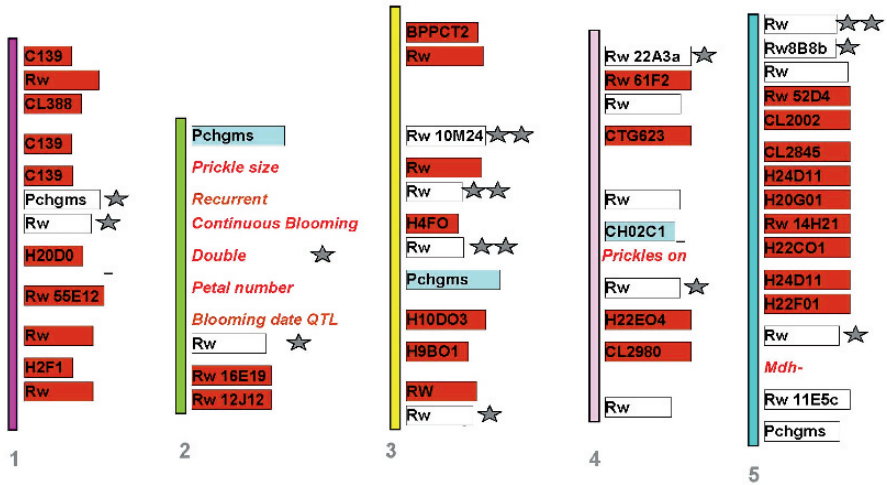


Fig. 1 Partial Consolidated rose map combining the tetraploid 90–69 F2 map and the diploid 97–7 and Hw maps. Consolidation done by Dr. Sriyani Rajapakse

to powdery mildew and black spot (Xu et al., 2005; Yan et al., 2005a; Linde et al., 2006; Hattendorf and Debener, 2007b). Thus far, RGAs have been mapped onto 3 mapping populations. This includes a few selected RGA derived RFLPs near the CRPM1 locus on the *Rosa roxburghii* map (Xu et al., 2005) and about 50 RGA loci mapped on both the 94/1 and 97/7 populations (Yan et al., 2005a; Linde et al., 2006). In both of the latter populations the RGAs clustered heavily on LGs 1 and 7 with few or none on the LGs 3 and 6. Interestingly there were no RGAs located close to the major powdery mildew QTL clusters or the *Rpp1* loci on LGs 3 and 4 although several co-localized with some minor QTLs on other LGs (Linde et al., 2006; Hattendorf and Debener, 2007b). The closest RGA locus to the *Rdr1* locus was about 20 cM away (Hattendorf and Debener, 2007a). The 24 PK loci mapped on the 94/1 population were not associated with disease resistance either (Yan et al., 2005a).

SNPs or single nucleotide polymorphisms represent the third generation of molecular markers. SNPs are the most abundant co-dominant marker class. In comparison to SSRs, due to their abundance, they can easily be detected by direct sequencing of genomic regions or ESTs. However as they are mainly bi-allelic, they are less polymorphic than SSRs. In plants, they can be used for diverse applications such as marker assisted selection, germplasm fingerprinting, gene mapping, population structure analysis (as LD analysis), and genome wide analysis. Furthermore different techniques have been developed in human to genotype with high throughput SNPs protocol (SNPlex, Illumina®), chip based technologies, Amplifluor®, Taq-Man®). As rose is a highly heterozygous plant, SNPs can be easily detected, and represent a large new source of markers. In rose, SNPs have been reported to exist

every 64–68 bp in the PR2 and PR5 genes in *Rosa roxburghii* which is comparable to the frequency seen in rice (170 bp), maize (48 bp) (Xu et al., 2007) and *Prunus mume* (55 bp) (Fang et al., 2005). In a study to discover new markers for resistance to powdery mildew, SNPs were searched for within the PR2 (pathogenesis-related gene family class 2: B-1,3-glucanase) and PR5 (pathogenesis-related gene family class 5: osmotin) genes as created in rose via degenerate primers. The 23 SNPs discovered were converted to SNAPs (single nucleotide amplified polymorphism) to create a simple efficient marker that is scored as absent or present. The SNAP primer pairs were tested and 19 gave good products and 17 were polymorphic and mapped in the *R. roxburghii* mapping population. Sixteen mapped to the same linkage group and one (Glu7) was linked to a minor QTL for powdery mildew (Xu et al., 2007). This approach has promise as an additional procedure for finding markers for targeted regions of the genome.

2 Use of Markers for Identification and Studies of Rose Population Structure, Taxonomy, Domestication, and Diversity Studies

Since the early 1990s, the papers published using various molecular markers in the study of rose varieties, germplasm, and species has increased dramatically from 0 to 1 per year to 5–6 per year. This increase corresponded to the development of the PCR based markers which were less expensive per unit of information than either isozymes or genomic probe technology such as RFLPs, mini satellites or microsatellites.

Varietal identification has been an important field of inquiry especially as it pertains to patent rights of roses and other plants. UPOV (International Union for the Protection of New Varieties) introduced the concept of essentially derived varieties (EDV) in 1991 to protect the rights of breeders (UPOV, 1991). In the case of roses, this would be the right of the original breeder to any commercially useful sports (somatic mutations) of the varieties that they develop. It has been shown repeatedly that either RAPDs (Torres et al., 1993; Gallego and Martinez, 1996; Matsumoto and Fukui, 1996; Debener et al., 1997, 2000; Benedetti et al., 2001; Mohapatra and Rout, 2005), AFLPs (Debener et al., 2000; Zhang et al., 2001; Vosman et al., 2004; Wen and Deng, 2005) or SSRs (Esselink et al., 2004; Rusanov et al., 2005; Scariot et al., 2006; Babaei et al., 2007) are very useful to distinguish among varieties and their seedlings but not necessarily between their sports. Consequently it is a straightforward process to determine whether a plant is a sport of a variety. Of these three markers, RAPDS is the least consistent among different laboratories (Jones et al., 1997) and consequently is the least desirable choice. The most consistent among laboratories and easiest to genetically interpret are SSRs and ISSRs which were recently improved (Laurent Crespel, personal communication). Nevertheless, AFLPs have been shown to be sufficiently consistent among laboratories to

easily distinguish among sports and seedlings of rose varieties (Vosman et al., 2004) and thus useful for EDV evaluations.

These three markers, beyond being used for varietal identification are versatile and have been used effectively in assessing the segregation patterns in dog roses (Werlemark et al., 1999; Nybom et al., 2004, 2006), quantifying the heterozygosity of roses (Crespel et al., 2001), in bulked segregant analysis in search of a marker for the *Rdr1* gene (Malek et al., 2000), the identification of outcrosses (Debener et al., 2003), and in a range of diversity and phenetic studies. The early studies used RAPDs and mostly examined a few varieties and/or species (Debener et al., 1996; Millan et al., 1996; Walker and Werner, 1997; Olsson et al., 2000). A few topics such as the relationships among rose species (Matsumoto et al., 1998; Jan et al., 1999; Wissemann and Ritz, 2005; Koopman et al., manuscript submitted) and the diversity of *Rosa damascena* (Iwata et al., 2000; Baydar et al., 2004; Rusanov et al., 2005; Tabaei-Aghdaei et al., 2006; Babaei et al., 2007; Kiani et al., 2008) have been studied with a variety of molecular markers all of which support the same conclusions confirming the usefulness of molecular markers.

3 Current Situation for Linkage Maps

Genetic mapping for rose has been done or is being developed in both diploid and tetraploid rose populations (Tables 2 and 3). The diploids consist of three groups of crosses. The German populations (94/1 and 97/7) that are based on an introgression population combining traits of *R. multiflora* with those of Garden roses (Debener and Mattiesch, 1999; Linde and Debener, 2003; Yan et al., 2005b; Linde et al., 2006). The second group involves various crosses with *R. wichurana*. This includes the population developed in France (Hw) (Crespel et al., 2002), in Spain (Dugo et al., 2005) and in the USA (WOB) (Shupert et al., 2007). It is also interesting to note that the *R. wichurana* genotype used in both the Spain and the USA rose mapping populations is the same genotype, 'Basye's Thornless'. The third mapping population is a population of *Rosa roxburghii*, developed to study the inheritance of powdery mildew resistance (Xu et al., 2005).

On the tetraploid level, a map has been developed with the 90-69 F₂ population which is a complex hybrid that involves parentage of cultivated roses and both tetraploid (*R. carolina* and *R. virginiana*) and diploid (*R. rugosa rubra* and *R. wichurana* Basye's Thornless') species in its recent breeding history (Rajapakse et al., 2001; Zhang et al., 2006). In the mapping efforts for the black spot resistance gene, *Rdr1*, three tetraploid populations, all crosses with the rose 91/100-5 which is heterozygous for the *Rdr1* gene, were used in a bulked segregant analysis study to locate markers that could be mapped onto the diploid map. The third tetraploid population, a cross between the cut flower varieties 'Golden Gate' and 'Fragrant Cloud' was made to study the complex traits of fragrance and post harvest quality (Zamir, personal communication).

Table 2 Maps developed for rose

Name of population	Population	Markers	Linkage groups	Map length (cM/marker)	Map length (cM/marker)	% loci with distorted segregation	Reference
94/IR	93/1-117 × 93/1-119 (60 F ₁) half sibs derived from R, multiflora × Garden rose progeny diploid	157 RAPD 119 AFLP Blfo – single/double corolla Bifa – white/pink flower color	7	326 cM (2.4 cM/marker)	370 cM (2.6 cM/marker)	16%	Debener and Mattiesch (1999)
94/IR	Same as above, 60 additional markers	321 markers 20 AFLP 27 microsatellites 8 RFLP 5 SCAR	7	na	na	17%	Debener et al. (2001)
94/I	93/1-119 × 93/1-117 (88 F ₁) Reciprocal cross of 94/IR Parental and integrated maps	360 AFLP 26 PK 88 SSR 29 RGA 41 others Rdr1, Bifa-3, Blfo-2,	7	487 cM (1.9 cM) Integrated map 545 cM	490 cM (2.0 cM)	22%	Yan et al. (2005a) and Hilbrand-Saint Oyant et al. (2007)

Table 2 (continued)

Name of population	Population	Markers	Linkage groups	Map length (cM/marker)	Map length (cM/marker)	% loci with distorted segregation	Reference
97/7	95/13–39 × Sp3 270 F ₁ Integrated map	172 AFLP 50 RGAs 4 SSRs 1 CAP (Rd1) 1 Bac end derived marker 4 morphological (black spot, stem prickles, double flowers, white stripes) QTL trait, powdery mildew resistance	7	370 cM (2.6) Integrated map 418 cM (1.8 cM/marker)	354 cM (2.4)	Na	Linde et al. (2006)
97/7	Same as above	95 (79 AFLP, 15 SSR, CAP), Dc, Rpm, Rbs	7	360 cM 3.7 cM	376 cM 3.8 cM	33%	Zhang (2003)
90–69 F ₂	(82–1134 × 86–7)F ₂ 52 plants tetraploid	171, 167 AFLP prickles/petiole MDH	15, 14	682 cM	902 cM	??	Rajapakse et al. (2001)

Table 2 (continued)

Name of population	Population	Markers	Linkage groups	Map length (cM/marker)	Map length (cM/marker)	% loci with distorted segregation	Reference
	Same as above	256, 286	20, 14	920 cM	770 cM	15%	Zhang et al. (2006)
	Partial map integration	19 rose SSRs					
		2 heterologous SSRs					
Hw	H190 × R. wichurana	68, 108 AFLP	8, 6	238 cM (3.7 cM)	287 cM (3.1 cM)	39% (29–50%)	Crespel et al. (2002)
	91 plants diploid	Recurrent/seasonal bloom					
		Double/single corolla					
		QTL prickle density					
	Same as above	105, 136 SSRs	7	432 cM (4.0)	438 cM (3.0)	26%, 10%	Hibrand-Saint Oyant et al. (2007)
		QTL traits (petal number, bloom date)					
Spain	Blush Noisette × R. <i>wichurana</i>	130 (85, 49) RAPD	7	388 cM (5.6 cM/marker)	260 cM (5.83 cM/marker)	15%	Dugo et al. (2005)
	'Basye's Thornless'	2 heterologous SSRs					
		1 morphological traits (Bifo)					
		4 QTL traits (flower size, leaf size, resistance to powdery mildew, days to flowering)					

Table 3 Details on rose mapping families

Name ploidy	Female	Comments	Male	Comments	Reference
94/IR 2x	93/1–117	Parents are selected from open pollinated population of 81/42–15 which derived from introgression program with <i>R. multiflora</i> and various garden roses	93/1–119	Same as female parent	Debener and Mattiesch (1999)
94/1 2x	93/1–119	Same as above	93/1–117	Same as female parent	Yan et al. (2005a)
97/7 2x	95/13–90	Parents are selected from open pollinated population derived from introgression program with <i>R. multiflora</i> and various garden roses	Sp3 (= 82/78–1)	Same as female parent	Linde et al. (2006)
97/7 2x	95/13–90 (R-pm)	(88/124–46 × 82/78–1)	82/78–1 (S-pm)	Backcross segregating for PM race 9 S/R	Linde and Debener (2003)
95/1 95/2 95/3 4x	91/100–5	Has Rdr1 gene conferring resistance to broad range of black spot races	Caramba Charme Heckenzauber	Susceptible to black spot	Malek et al. (2000) – BSA to find marker for Rdr1 Yan et al. (2006) – marker association analysis for PM resistance

Table 3 (continued)

Name	ploidy	Female	Comments	Male	Comments	Reference
90-69 F ₂ 4x	90-69 (= 86-7 × Basye's Blueberry)	86-7 = (R. wichurana 'Bayse's Thornless' × R. rugosa rubra) chromosomes doubled with colchicine Basye's Blueberry (82-1134) = [(Rosa carolina L. × 'Hugh Dickson') open pollinated] × 74-193. 74-193 = [(Rosa carolina L. × 'Hugh Dickson') open pollinated] × (Rosa virginiana alba Mill. × 'Betty Morse').	Dihaploid of 4x R. hybrida cv Zambra	Progeny produced by selfing the female	Same as female	Rajapakse et al. (2001) and Zhang et al. (2006)
Hw 2x	H190	Resistant to powdery mildew	Dihaploid of 4x R. hybrida cv Zambra	R. wichurana hybrid	Original paper states it is R. wichurana but since heterozygous for recurrent it is probably a hybrid with China rose	Crespel et al. (2002) and Hilbrand-Saint Oyant et al. (2007)
Spain 2x	Blush Noisette	Champney's Pink Cluster seedling = Pink China rose (= Parsons's Pink?) × Rosa moschata	Champney's Pink Cluster seedling = Pink China rose (= Parsons's Pink?) × Rosa moschata	R. wichurana	Same R. wichurana clone as used in the mapping work in Texas	Dugo et al. (2005)
Roxburghii 2x	Guinong No. 6	Resistant to powdery mildew	Resistant to powdery mildew	Guinong No. 5	Susceptible to powdery mildew	Xu et al. (2005, 2007)
WOB 2x	Old Blush	Rosa chinensis	Rosa chinensis	WOB-26	R. wichurana Basye's Thornless × Old Blush	Shupert et al. (2007)
GGFC 4x	Golden Gate	Excellent vase life but non fragrant cut flower variety.	Excellent vase life but non fragrant cut flower variety.	Fragrant Cloud	Very fragrant but poor vase life cut flower rose variety	Zamir (personal communication)

Given the highly heterozygous nature of the parents in most of these crosses, the general approach to their analysis has been using the pseudo test cross approach first described by Grattapaglia and Sederoff (1994) for use in forest trees. To further complicate mapping, from 10 to 39% of the markers have exhibited distorted segregation (Table 2). This segregation distortion could be caused by the interspecific nature of the crosses used, self incompatibility segregating in some of the populations, gametophytic selection by sub-lethal genes conferring low viability on the zygote, embryo, or seedling level or maybe competitive differences in the performance of genetically variable pollen. Whatever the reason, high levels of segregation distortion limit the quality of the map by limiting the number of markers that are used in making the initial framework map as the markers with distorted segregation ratios are only added in the last mapping step.

The tetraploid mapping requires larger populations as compared to the diploids for the same quality map and are more difficult to map because the mapping programs are designed for the diploid situation. Thus the mapping is generally restricted to loci that are behaving as diploids.

The lengths of the diploid maps reported vary from 238 to 545 cM on 6 to 8 linkage groups and the tetraploid maps vary from 674 to 920 cM on 14 to 23 linkage groups (Table 2). Thus the total length of the diploid is about 500 cM with an average chromosome length between 70 and 80 cM (Yan et al., 2005a). The density of the maps ranges from low of 5.83 cM/marker (Dugo et al., 2005) to a high of 1.9 cM/marker (Yan et al., 2005a) with the majority being at medium density of 2.5–4.0 cM/marker (Table 2).

The earliest maps used RAPDs and AFLPs (Debener and Mattiesch, 1999; Rajapakse et al., 2001) and consisted of male and female parent maps as these markers do not lend themselves for map integration. Later as other markers such as RFLPs, SSRs, RGAs, PKs, SCARs, CAPs (Table 2) and most recently SNP derived SNAPs (Xu et al., 2007) were developed they have been and are being incorporated into the maps. At the present time there are several hundred microsatellites available for rose (Esselink et al., 2003; Yan et al., 2005a; Kimura et al., 2006; Zhang et al., 2006) and mapping of these have allowed the integration of the male and female maps (Yan et al., 2005a; Linde et al., 2006; Zhang et al., 2006; Hibrand-Saint Oyant et al., 2007). With microsatellite mapping data a preliminary consensus map for 5 of the 7 chromosomes has been constructed for the maps of 97/7, 90-69 F₂, and the Hw (Rajapakse, personal communication; Byrne et al., 2007 – PAG meeting abstract) (Fig. 1). As the various research groups place other SSRs and codominant markers on the maps, a rose consensus map will be developed.

The objective of mapping is to better understand the organization of the genome in question and to find markers for specific traits that might facilitate the breeding process. Consequently, a range of qualitative and quantitative trait loci have been placed on the maps. These include qualitative traits such as loci that control pink/white flower color, single/double flower corolla, white petal stripes, black spot resistance, powdery mildew resistance, recurrent flowering, and stem and petiole prickles. Among the QTLs mapped include those controlling powdery mildew resistance, plant vigor, stem prickle density and size, leaf size, flower size, days to

flowering or to 50% bloom, and petal number (Table 4). Unfortunately, although these QTL studies are interesting, most used a small number of progeny which limits the accuracy of the mapping and thus the usefulness of the markers identified for the specific traits. In these mapping studies, a number of close linkages between a trait and a marker such as a RAPD or AFLP have been reported as well as a SCAR (SCM10) and two CAP (Rd1, RdY) markers for Rdr1 (Malek et al., 2000; Kaufmann et al., 2003; Zhang, 2003), two SCAR markers for Rpp1 (Linde et al., 2004) and two RGAs (RGA22C, Glu 7 RGA) for a major and minor QTL for powdery mildew resistance (Xu et al., 2005, 2007).

4 Inheritance of Known Characters

Roses have been cultivated for several thousand years but only since the late part of the 19th century have breeders been doing controlled crosses in the development of new varieties as opposed to planting out open pollinated seed and selecting among the seedlings (Krüssmann, 1981). At present, there are a few public breeding efforts, hundreds of small private breeders and scores of large breeding operations that name and release several hundred new varieties of roses every year throughout the world. In spite of all this breeding effort, the inheritance of the major traits is poorly understood due to the lack of public research into the breeding and genetics of the species. Nevertheless, in recent years in conjunction with the development of linkage maps of the rose this knowledge has increased several fold (Table 4).

The earliest reports on the inheritance of traits in the USA focussed on ornamental characteristics and were not necessarily well documented but revealed the breeder's conclusions from a few documented cases and his breeding experience (Hurst, 1941; Lammerts, 1945; Morey, 1954). This was followed with additional work in the 1960s on the inheritance of red color (Lammerts, 1960, 1964), 1970s on the inheritance of the recurrent bloom trait (Semeniuck, 1971a, b), in the 1980s in Holland, Canada and India, and finally in the last 20 years a flurry of activity connected with the development of genetic linkage maps for a variety of rose mapping populations in the USA, Asia (China), and Europe (Spain, Germany, Holland, and France).

5 Flower Traits

The most important trait in roses is the *recurrent blooming* trait, a probable vernalization mutation which reduces the juvenility period and allows the plant to continuously bloom without any need for a vernalization period. This trait was introduced from China during the period of exploration and was initially integrated into European roses by random crosses from gardens where both types grew. This transformed the rose into the most popular ornamental plant in the world. As early as 1941, Hurst indicated that the recurrent trait was recessive to the seasonal bloom

Table 4 Genetic control of phenotypic characters

Character	Genetic control	Studied population	Remarks	References
Adaptation traits				
Black spot resistance	Major genes <i>Rdt1</i> <i>Rbs</i> Additive	91/100-5, F ₂ , backcrossed to susceptible Caramba, F ₁ with susceptible cv Hechenzauber, Parisier Charme, and Elima 97/7 Old Blush × WOB13/21/26	Resistance dominant and race specific	Malek and Debener (1998), Malek et al. (2000), Debener et al. (2003), Yan et al. (2005a) Zhang (2003) Shupert et al. (2007)
Powdery mildew resistance	Major genes Dominant <i>Rpp1</i> CRPM1 <i>Rpm</i> QTLs <i>Pm1</i> , <i>Pm2</i> 28 QTLS, 2 main regions <i>Rpm1</i> , <i>Rpm2</i> Minor QTL Polygenic	Tetraploid (Crimson Glory × Captain Thomas and others) 97/9 Roxburghii 97/7 Spain 97/7 97/7 Roxburghii	Resistance dominant and in recent studies appear race specific	Lammerts (1945) Zhang (2003), Linde et al. (2004), Xu et al. (2005) Zhang (2003), Dugo et al. (2005), Linde et al. (2006), Xu et al. (2007)
Nematode resistance	Polygenic	Diallel using 3 <i>R. multiflora</i> and 2 <i>R. indica</i> rootstocks	Wang et al. (2004b)	
Cold hardiness	Additive	Diploid and tetraploid populations	Field evaluations, h ² ranged from 51% to 92%	Svejda (1979)

Table 4 (continued)

Character	Genetic control	Studied population	Remarks	References
Flower traits				
Recurrent blooming	Major gene R/r r4	<i>R. wichurana</i> , Goldlocks × <i>R. wichurana</i> Hybrid tea × <i>R. centifolia</i> , F ₁ and F ₂ Diploid <i>R. multiflora</i> populations HW Old Blush × WOB13/21/26 97/7	Non recurrent dominant over recurrent	Semeniuck (1971a, b) Vries and Dubois (1984) Debener (1999) Crespel et al. (2002) Hibrand-Saint Oyant et al. (2007) Shupert et al. (2007) Zhang (2003)
Repeat flowering ability	Major gene, Rb	97/7	Dominant, ability to flower in summer	Dugo et al. (2005) Hibrand-Saint Oyant et al. (2007)
Flowering time	QTLs	Blush Noisette × <i>R. wichurana</i> HW	■ 50% of flowering ■ First flower to stage 1	Lammerts (1945) Debener (1999) Debener and Mattiesch (1999) Dugo et al. (2005) Crespel et al. (2002) Hibrand-Saint Oyant et al. (2007) Zhang (2003) Shupert et al. (2007) Zhang (2003) Hibrand-Saint Oyant et al. (2007)
Number of petals	Major gene D/d Blfo d6 NP Dc QTLs	Tetraploid populations Diploid <i>R. multiflora</i> populations 94/1R Spain Hw 97/7 Old Blush × WOB13/21/26 97/7 Hw	Dominant (single/double) Lammerts (1945) indicates expression is also dose dependent	Lammerts (1945) Debener (1999) Debener and Mattiesch (1999) Dugo et al. (2005) Crespel et al. (2002) Hibrand-Saint Oyant et al. (2007) Zhang (2003) Shupert et al. (2007) Zhang (2003) Hibrand-Saint Oyant et al. (2007)

Table 4 (continued)

Character	Genetic control	Studied population	Remarks	References
Flower size	QTL Additive	Spain Old Blush × WOB13/21/26	Flower diameter	Dugo et al. (2005)
Pink vs. white	Major gene, B1/a	Diploid <i>R. multiflora</i> populations Old Blush × WOB13/21/26	Flower diameter, petal length Shupert et al. (2007) report codominance	Shupert et al. (2007) Debener (1999)
Presence of anthocyanins	Major gene, A/a	Tetraploid	Presence of anthocyanins is dominant	Shupert et al. (2007) Lammerts (1964)
Magenta red color Individual pigments	Major gene, M/m Additive	2 tetraploid populations Tetraploid populations	Expression of M is dose dependent	Lammerts (1960) Vries et al. (1980) and Marshall et al. (1983)
Pale, pink, dark pink and crimson	QTLs	97/7		Zhang (2003)
Yellow	Major gene	<i>Rosa foetida</i> × Hybrid teas, F1 and back crosses	Dominant	Vries and Dubois (1978) Lammerts (1960)
Light vs. dark yellow		Tetraploid populations	Light dominant over dark yellow	
Yellow and silver reverse	Major gene	Tetraploid populations	Recessive to normal	Lammerts (1945)
Male sterility	Major gene	F ₁ : <i>R. setigera</i> × <i>R. brunoni</i>	Dominant	Lewis and Basye (1961)
Moss character	Major gene	Hybrid tea × <i>R. centifolia mucosa</i> , F ₁ and F ₂	Dominant	Vries and Dubois (1984)
Fragrance	Major gene Quantitative	Bo × Anna, tetraploids Tetraploid roses	Dominant gene control presence/absence of monoterpene alcohol and aldehyde pathway	Cherri-Martin et al. (2007) and Lammerts (1945)

Table 4 (continued)

Character	Genetic control	Studied population	Remarks	References
Plant traits				
Spreading vs. sprawling growth	Major gene	90–69 F ₂	Codominant	Rajapakse et al. (2001)
Dwarf vs. non dwarf	Major gene, D	Polyantha × <i>R. chinensis minima</i>	Dominant	Dubois and Vries (1987)
Climbing vs dwarf or bush growth type	Major gene	Tetraploid populations	Dominant	Lammerts (1945) and Morey (1954)
Plant vigor (10 parameters)	QTLs	94/1		Yan et al. (2007)
Leaf size	QTLs	Old Blush × WOB13/21/26 94/1	Leaf width, length Leaf area, weight	Shupert et al. (2007) Yan et al. (2007)
		Tetraploid populations 97/7	Leaf width Leaf area	Lammerts (1945) Zhang (2003) Lammerts (1945)
Glossy vs dull foliage	Major gene	Tetraploid populations		
Stem prickles	Major gene QTLs Additive	Diploid <i>R. multiflora</i> populations Old Blush × WOB13/21/26 HW Tetraploid populations 97/7	Prickles dominant	Debener (1999) Shupert et al. (2007) Crespel et al. (2002) Lammerts (1945) Linde et al. (2006) Zhang (2003)
Prickle size	QTLs	97/7		
Petiole prickles	Major gene	90–69 F ₂ , tetraploid	Independent of stem prickles locus	Rajapakse et al. (2001)
Malate dehydrogenase	Major gene	90–69 F ₂	Codominant	Rajapakse et al. (2001)
Old Blush × WOB13/21/26 = Old Blush × WOB13, × WOB21, and WOB26, all WOB are siblings from the cross <i>R. wichurana</i> ‘Basye’s Thornless’ × Old Blush				

but it was not established until 1971 by Semeniuck (1971a, b) and then further confirmed by several others (Vries and Dubois, 1984; Debener, 1999; Crespel et al., 2002; Dugo et al., 2005). Recently it has been mapped on the Hw map (Crespel et al., 2002) (Tables 2 and 3).

The inheritance of the *flower form* (single vs. double flowers) was first reported in 1999 (Debener, 1999; Debener and Mattiesch, 1999) as a dominant allele in the locus conferring the double corolla/flower state and has since been confirmed in other rose progenies (Crespel et al., 2002; Yan et al., 2005b; Linde et al., 2006; Shupert et al., 2007). This locus has been mapped on several rose populations with different names: Blfo, d6, Dc, NP (Debener and Mattiesch, 1999; Crespel et al., 2002; Zhang, 2003; Linde et al., 2006; Hibrand-Saint Oyant et al., 2007). Preliminary data using SSR markers showed that *Blfo* and *NP/d6* are on the same homologous linkage group (Hibrand-Saint Oyant, personal communication). Within the double corolla/flower category there is a wide range of petals from 5 to several hundred. Genetic analysis in several populations indicates that the number of petals within the double flower is additive and controlled by several QTLs (Debener et al., 2001; Zhang, 2003; Hibrand-Saint Oyant et al., 2007).

Flower size (flower diameter, petal length) appears to be additively inherited with a high ($h^2 > 0.70$) heritability (Lal et al., 1982; Dugo et al., 2005; Shupert et al., 2007). Mapping of this trait indicated that there were 4 major QTL loci, 2 each on the first two linkage groups of each of the parents (Dugo et al., 2005).

Flower production has not been well studied. A small study in India indicated that floriferousness (number of flowers a plant produced) was highly heritable with a broad sense heritability of 0.96. More recent work focussed on flower production during the warm summer months and mapped a single gene (*Rb* = repeat bloom) on the D2 linkage group of the 97/7 progeny (Zhang, 2003).

Flower color in rose is extremely important and has been studied repeatedly beginning with early studies which indicated which colors were dominant over the others and suggestions on the breeding course to obtain specific colors (Lammerts, 1945; Morey, 1954). Subsequent studies by Lammerts (1960; 1964) with tetraploid roses concluded that there was a gene *A/a* which controlled the presence of cyanidin (red) and a gene *M/m* which controlled the magenta color. With the magenta color gene, the color was dependent on the gene dose with dark purple being homozygous dominant (*MMMM*), a solerino purple corresponding to a duplex condition (*MMmm*) and a homozygous recessive state (*mmmm*) giving a non fading currant red (assuming a red background with dominant A allele present). Since the pink to red color is controlled by a range of anthocyanins, the inheritance of specific anthocyanins (quercetin, kaempferol, cyanidin, peonin and pelargonidin) was examined in tetraploid roses. Both these studies came to the conclusion that these pigments were quantitatively inherited (Vries et al., 1980; Marshall et al., 1983). Recent work with diploid populations has identified a locus (*Bfla*) on the A2/B2 linkage group of the 94/1 map which controls pink and white color. In this case, pink is dominant over white although in one population (WOB), the heterozygous plants were a lighter pink as compared to the homozygous pink plants (Debener, 1999; Debener and Mattiesch, 1999; Yan et al., 2005b; Shupert et al., 2007). Finally in the 97/7

population, when the flower color was rated into 4 categories (Crimson, dark pink, pink, and pale) several QTLs were located on the 4th linkage group of this map (Zhang, 2003).

Beyond anthocyanins, the color in roses is determined by a range in carotenoids which give colors in the *yellow/orange* range. Lammerts (1945; 1960) hypothesized from his breeding experience that deep yellow was recessive to light yellow. The only other study describes a general breeding procedure to develop yellow everblooming roses utilizing *R. foetida* as the source of yellow flower color. Although the authors never hypothesize its mode of inheritance, the breeding procedure indicates that yellow is dominant as it is expressed in the F₁ and segregates in the back cross progenies (Vries and Dubois, 1978).

The presence or absence of *white stripes* on the petals, although it did not segregate as expected for a single dominant trait, was nevertheless mapped onto the 97/7 rose map on the 3rd linkage group along with the loci for double flowers and prickles (Linde et al., 2006).

QTLs for *flowering time* (50% bloom) were located on two chromosomes by Dugo et al. (2005) and another QTL (first bloom) was located on another chromosome by Hibrand-Saint Oyant et al., (2007). It has been suggested that the location of the QTLs were different because the flowering times were measured differently, and thus the two groups measured different aspects of this complex trait (Hibrand-Saint Oyant et al., 2007).

Flower fragrance is a very complex trait which is controlled by a multitude of chemical pathways as well as environmentally sensitive (Verhoeven et al., 2003) but has been bred for successfully over the years as evidenced by the presence of wonderfully fragrant varieties. The inheritance appears to be quantitative (Lammerts, 1945) but recent work looking at the monoterpene alcohol and aldehyde pathway that is responsible for the typical European rose fragrance indicates that there is also a major gene is responsible for turning the pathway on and off (Cherri-Martin et al., 2007) in addition to an array of genes that modify the quantity of the various scent components. Current work in the functional genomics of fragrance in rose is beginning to identify the key enzymes that create and regulate the various fragrance components and promises to lead to the development of better tools and understanding of this essential trait (Vainstein et al., 2003)

6 Plant Traits

In studies of *growth type*, the climbing growth types was found to be dominant over non-climbing growth types (Lammerts, 1945; Morey, 1954), and the dwarf type was found to be dominant to non dwarf types (Dubois and Vries, 1987). It is not known if these two traits are controlled at the same locus. In a recent mapping study, when a spreading bush growth type was crossed with a sprawling ground cover growth type the resultant F₁ plant was of an intermediate growth type. Upon selfing the F₁

plant, the F₂ segregated for all three types in a ratio to suggest that these forms were inherited co dominantly (Rajapakse et al., 2001).

Other growth type related traits such as the *length of the flowering stem* (Lammerts, 1945), *the branch number*, *plant height* and *plant spread* (Lal et al., 1982) all were inherited as polygenic characters with the last three with a high broad sense heritability ($h^2 = 0.88-0.95$) (Lal et al., 1982).

Plant vigor, an important trait in cut rose breeding, was measured using 10 parameters (number of nodes, stem thickness, shoot length, chlorophyll content, leaf area, specific leaf weight, leaf dry weight, stem dry weight, total dry weight and growth rate) in a replicated progeny at two sites. The additive h^2 for each individual trait ranged from moderate to moderately high (0.48–0.71). QTL analysis identified 42 QTLs which clustered mainly on three chromosomes (I-2, I-6, I-7 of 94/1 population). Very importantly it was shown that although a GxE interaction exists it was much smaller than the main genetic effect of the trait (Yan et al., 2007).

Leaf size whether measured as leaf width, leaf area, or leaflet number was found to be quantitative in nature (Lammerts, 1945; Zhang, 2003; Shupert et al., 2007)

There is a major locus controlling the presence or absence of *stem prickles* with the presence being the dominant allele (Debener, 1999; Linde et al., 2006; Shupert et al., 2007). Another independent locus controls the presence or absence of petiole prickles (Rajapakse et al., 2001). Among germplasm with the dominant gene for stem prickles, the density and size of the prickles is quantitatively inherited (Lammerts, 1945; Lal et al., 1982; Crespel et al., 2002; Zhang, 2003).

Additional traits that have been analyzed include the *male sterility*, *dwarfness*, the *moss* trait (dominant with modifiers), *MDH-2* (co-dominant), *foliage glossiness* (glossy dominant over dull), *flower neck strength* (quantitative), and the *ability of rose callus to form somatic embryos* (additive) (Lammerts, 1945; Lewis and Basye, 1961; Vries and Dubois, 1984; Rajapakse et al., 2001; Burrell et al., 2006).

7 Adaptation Traits

There have been numerous reports on the varietal differences in resistance to black spot (Wenefrida and Spencer, 1993; Carlson-Nilsson, 2000), powdery mildew (Mence and Hildebrandt, 1966; Atkiss, 1978; Ferrero et al., 2001), nematodes (Wang et al., 2004a), and cold hardiness (Lehmushovi, 1987; Karam and Sullivan, 1991). As might have been expected for black spot and powdery mildew both major gene and quantitative inheritance has been reported.

Two major genes (Rdr1, Rbs) have been mapped for black spot resistance within 10 cM on the same linkage group (Malek and Debener, 1998; Debener et al., 2003; Zhang, 2003; Yan et al., 2005b). The Rdr1 locus was found tightly linked to an AFLP marker (M10) which was converted into a SCAR (SCM10), several RFLPs (BMA1-4) (Malek et al., 2000) and several BAC end markers (Kaufmann et al., 2003). Subsequently one of the RFLP fragments (BMA3) was converted into

CAP marker (RdrY) (Zhang, 2003). These markers may be useful in MAS (marker assisted selection).

Powdery mildew resistance was first reported as a dominant gene in 1945 by Lammerts and more recently the dominant resistance genes *Rpp1* (Linde and Debener, 2003; Linde et al., 2004) and *Rpm* (Zhang, 2003) as well as a major resistance QTL, *CRPM1* (Xu et al., 2005) have been mapped. A SCAR marker has been developed for the *Rpp1* loci and a RGA (Resistance Gene Analogue) derived RFLP marker (RGA22C) has been located close to the *CRPM1* locus (Xu et al., 2005) which should facilitate MAS (Linde et al., 2004). Other QTLs for powdery mildew have also been located on maps of 3 rose mapping populations (Zhang, 2003; Dugo et al., 2005; Xu et al., 2005, 2007; Linde et al., 2006). Unfortunately, at this point it is not known how these powdery mildew resistance major genes or QTLs are related.

Resistance to both nematodes (*Meloidogyne hapla*) and winter cold have been reported to be polygenic (Svejda, 1977b, a, 1979; Wang et al., 2004b).

8 Physical Maps, BAC Libraries and Current Situation for Positional Cloning

The construction of BAC libraries is the first step towards the construction of a physical map and the positional cloning of genes of interest in rose. Thus far two BAC libraries have been constructed and one is under construction (Kaufmann et al., 2003; Hess et al., 2007). Thus far there is a BAC library constructed from a colchicine-induced tetraploid of *Rosa rugosa* var *alba* cv C5-23 which has been used for chromosome walking and contig assembly for the Rdr1 black spot resistance gene (Kaufmann et al., 2003). The other BAC library was constructed from the *Rosa chinensis* cv 'Old Blush' with the objective of using it for positional cloning of the recurrent blooming gene (Hess et al., 2007). The two libraries are complementary as they are constructed from genetically diverse genotypes and used different restriction enzymes (*HindIII* versus *BamHI*) for the partial digestion step. A third library from the multiflora derived black spot resistant 88/124-46 rose comprises 60,000 clones with an average insert size of 46 kb. This is being done with pCLC04541 cosmid that allows the transmission of small inserts via *Agrobacterium*. The objective of this library is to achieve complementation of the black spot resistance gene Rdr1 (Kaufmann et al., 2003; Debener, personal communication).

In the construction of both BAC libraries, the basic procedure describes by Zhang (2003) was modified to minimize the interference of the high levels of polysaccharides and phenols in rose tissue which tend to lower the resultant DNA quality. Although both the German (Kaufmann et al., 2003) and the American (Hess et al., 2007) laboratories grew the plants in the greenhouse and put the leaves through a dark treatment for 3–8 days before extraction, they differed in the subsequent steps. With the *R. rugosa* library, high levels of PVP 40 (4%), 0.13% DIECA, 0.1% ascorbic acid, and 0.5% 2-mercaptoethanol was used in the extraction buffer to counter-

act the high phenolic concentration of the initial extraction (Kaufmann et al., 2003). The approach with the 'Old Blush' library was to heavily fertilize and prune the rose bushes to induce rapid growth in the dark followed by an increased number of wash/filter steps (from 1–2 to 6) of the nuclei before they were embedded into the LMP agarose plugs (Hess et al., 2007).

Although a contig of the Rdr1 locus was constructed and the several markers (AFLP, CAP and BAC end markers) were mapped within a cM of the Rdr1 locus, the high heterozygosity of the rose genome created the situation of having allelic forms of the same locus. As compared to creating a BAC library of the homozygous plant, this situation in a heterozygous plant essentially doubles the work involved in the development of a contig and positional cloning of a gene (Kaufmann et al., 2003).

9 Synteny to Other Rosaceous Crops

The comparative genome studies will allow the transfer of genetic and genomic information between species (e.g. orthologous gene controlling disease resistance or flowering) and may help to elucidate the genome relationships and evolution within the Rosoideae tribe (*Rosa*, *Fragaria* and *Rubus*, mainly) and more distant genera within the Rosaceae family (such *Malus*, *Pyrus* or *Prunus*).

The alignment of the genetic maps reveals a high synteny between species of a same genus, for instance, it was proposed that the *Prunus* genome can be treated as a single genetic entity (Arus et al., 2006), with a single exception of a reciprocal translocation. In rose, the first step was to develop consensus markers with other Rosaceae species. The first attempt was done using heterologous microsatellite primer pairs from *Malus*, *Prunus*, and *Fragaria*. Of the 31 apple, 22 peach and 8 sour cherry SSRs screened on rose DNA only a two apple, 6 peach, and none of the sour cherry SSRs were mapped to a rose map (Rajapakse et al., 2001; Dugo et al., 2005; Zhang et al., 2006; Hibrand-Saint Oyant et al., 2007). Recently, the screening of strawberry primers on rose DNA revealed a much higher rate of good amplification and polymorphism and seven new consensus polymorphic SSR markers were developed (Hibrand-Saint Oyant et al., 2007). Anonymous SSRs are not convenient markers for genome comparison in Rosaceae. Their transferability is too low (problem of amplification and present of the SSR) between the tribes. However, within the tribe, in the case of SSR, in the coding sequence (as EST-SSR) the transferability is higher, and those markers can be used in synteny studies (Rousseau et al., 2006). SSRs from *Fragaria* were transferred to *Rosa* (and vice versa) not by looking for SSR polymorphism in the homologue sequences but by detecting SNPs using the SSCP technique. By such a method, the transferability was increased to 10%. Furthermore, strawberry homologues of candidate genes for floral initiation in rose were isolated in strawberry (Rousseau et al., 2006). Twenty four candidate genes were tested and 25% can be amplified and were polymorphic in strawberry.

From these new consensus markers, Rousseau et al. (2006) started a macrosynteny study between *Rosa* and *Fragaria*. The 24 markers provided anchor points to link the 7 homologous linkage groups. Preliminary results indicate numerous rearrangements between *Rosa* and *Fragaria* (Hibrand Saint Oyant L. and Denoyes, unpublished). New consensus markers need to be developed, and those markers have also to be tested in other species from the Rosoideae tribe (*Rubus*) and Rosaceae family. Possible good consensus markers are marker based on coding sequences that are single or low copy. This is the case for COS (Conserved Orthologue Set) previously developed in tomato (Fulton et al., 2002) or the Gene Pair Haplotype developed in strawberry (Davis et al., 2008).

Interestingly, macrosynteny between the strawberry and rose diploids reveal that the locus controlling recurrent blooming and perpetual flowering in rose and strawberry respectively are homologous (Hibrand Saint Oyant L. and Denoyes B., unpublished). This raised the question whether the *RB* locus has the same function as genes for seasonal/recurrent flowering in strawberry (Albani et al., 2004) and primocane bearing in blackberry and raspberry (Lopez-Medina and Moore, 1999; Lim and Knight, 2000).

To date, QTL mapping has been the method of choice for localizing the genetic basis of ornamental traits in rose. However QTL mapping presents limitations as the need for large progenies (especially in perennial species as rose), the time and space necessary for their phenotyping, and the fact that traits depend on the environment. Now genetics are moving towards LD (Linkage Disequilibrium) mapping to identify genomic regions contributing to specific phenotypes. LD mapping identifies correlations between a trait and a marker (reviewed by Mackay and Powell, 2007). According to LD decay, LD mapping may help to validate candidate genes or detect new QTLs in genome wide associations. The major advantage of LD mapping is that you do not need crosses as it relies on population samples. Development of LD mapping will need an international effort for the development of adequate populations (determination of the number of individual, population structure) and high density marker map to identify genome wide associations. The development of high density, based on SSR or SNP map will be feasible with the complete genome sequencing of rose.

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