Towards the Rose Genome Sequence and Its Use in Research and Breeding

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Abstract

Rose is one of the most economically important ornamental crops worldwide. *Rosa* sp. can become a model for woody ornamentals. Its genome size is relatively

small (560 Mb), its genetic history with ploïdy events is well documented, and rose has a short life for a woody plant. Furthermore, different tools are available, including transcriptomic tools, genetic maps and genetic transformation protocols. Rose represents an original model for studying some ornamental traits that cannot be addressed in other model plant species such as *Arabidopsis*. Some of these traits, such recurrent blooming, flower morphogenesis or scent production and emission, are of economic interest. Different groups involved in rose genetics and genomics gathered to form the 'Rose Genome Sequence Initiative'. Our objective is to obtain a high quality rose genome sequence of the diploid *R. chinensis* 'Old Blush'. One important issue is the high level of heterozygosity of roses. To tackle this issue, different strategies are proposed: production of a haploid and development a high density genetic map to anchor the genome. This genetic map will be developed from a cross between 'Old Blush' and *R. wichurana.* The genotype *R. chinensis* 'Old Blush' will be sequenced using NGS technologies. The data will be assembled and arranged using the high-density map. In order to increase ESTs and to facilitate genome annotation, we have recently produced ESTs from various tissues of 'Old Blush' under different conditions. Digital expression (RNA Seq) was obtained from the different tissues and data are available on the following web site (https:// iant.toulouse.inra.fr/plants/rosa/FATAL/). The rose genome sequence will be a great step to help identifying the molecular basis of ornamental traits and also to study genetic diversity and genome evolution in the genus *Rosa* and in the *Rosaceae* family.

INTRODUCTION

Rose is the most economically important ornamental crop worldwide (accounting for approximately 30% of the market) with the top rank for cut flower production and sales as well as being a major garden ornamental and potted flowering plant. Rose is also an important source for perfume and natural oils are extracted from roses (especially *R. damascena* and *R. centifolia*). In different societies, rose is a symbolic plant with a cultural and hedonic importance. Rose, the genus *Rosa*, is a member of the *Rosaceae* family, with important crops for fruit (as apple, peach, strawberry) and flower production (as rose). Within the *Rosaceae* family, rose can become a model for woody ornamental plants. Rose presents different advantages. It has a relatively small genome size (approximately 560 Mbp). It can be genetically transformed (Debener and Hibrand-Saint Oyant, 2009), even if transformation is still laborious, time-consuming and with low efficiency. For a polycarpic woody plants, rose has a short life cycle: about one year, as seedlings from continuous-flowering roses can flower the same spring. Furthermore, some important processes that can hardly be addressed using model species such as *Arabidopsis thaliana*, can be studied in the rose. For example, the rose is an ideal model to address recurrent blooming (Iwata et al., 2012; Randoux et al., 2012), flower morphogenesis (i.e., double flower formation (Dubois et al., 2010)), scent biosynthesis and emission, etc. (Scalliet et al., 2008). The rose exhibits a high scent complexity (Kovats, 1987; Shalit et al., 2004). Moreover, some scent biosynthesis pathways are unique or not yet identified in other model species (Kaminaga et al., 2006; Scalliet et al., 2006, 2008).

However, rose is a difficult material for genetic studies. The ploïdy level varied within the genus from diploid to decaploid roses. The majority of cultivated roses are di- or-tetraploid. Furthermore rose is highly heterozygous. In a survey of heterozygocity using 32 microsatellites markers, heterozygocity varies from 36 to 87% (Soules, 2009), with the lowest value for *R. chinensis* var. *spontanea* and the highest for the old Chinese cultivated genotype 'Single Cerise China'.

To become a model plant for woody perennials, genetics and genomics tools have to be developed. Rose is still in the infancy of genomics when compared to other model plants or crops (as *Arabidopsis*, rice, maize or strawberry). In the first part of this article, we will present the different genomic resources that have been recently developed and published in rose. In a second part, we will briefly present the rose genome sequencing

initiative and the perspectives opened by the rose genome sequence.

ROSE GENOMICS TOOLS

EST and Micro-Arrays Studies

In the last few years, the main genomic studies in rose were mainly transcriptomic approach. Transcriptomics is the study of the transcriptome, the complete set of RNA transcripts produced by the genome at any on time. Ten years ago, first generation of sequencing was used to produce EST (Expressed Sequence Tags) and discovered new genes. In 2008, around 5,000 unigenes were known in rose, less than 20% of known genes if we consider that the rose genome contains around 30,000 genes. These EST have been obtained from floral tissues during the floral transition (Foucher et al., 2008) and development (Channelière et al., 2002) and scent production (Guterman et al., 2002). This first series of EST was used to develop microarrays and study the transcriptome during different developmental processes. Using a dedicated micro-array (350 selected genes printed on a slide), Guterman et al. (2002) compared the gene expression during petal development (stages 1 and 4) and between perfume and non-perfume rose cultivars ('Fragrant Cloud', FC, and 'Golden Gate', GG, respectively). They identified genes up-regulated during FC petal maturation and showed higher expression in FC flowers than in GG. Among those genes, a few were related to secondary metabolism and might code for enzymes involved in scent production such as 2 OMT (O-methyltransferase), a monoterpene synthase, decarboxylase, hydrolases, aminotranferases and aldehyde dehydrogenase (Guterman et al., 2002). This first transcriptomic experiment successfully isolated candidate genes involved in scent production or emission.

Recently, using a Rosa Affymetrix array, with 4,765 unique genes, Dubois et al. (2011) studied the transcriptome during the floral process: from floral induction to early and late floral stage development. This analysis allowed the identification of genes associated with floral induction and development. For floral induction, we have compared the transcriptome at three different stages of two once-flowering roses, *R.* × *wichurana* and *R. hybrid*a 'Félicité et Perpétue'. We analyzed genes presenting same expression pattern between both genotypes. We identified already known floral activators (as *APETALA1* and *SUPPRESSOR OF CONSTANS1* homologues) in agreement with previous reported data (Remay et al., 2009). Furthermore, genes involved in hormone signaling are also regulated, suggested that ethylene and auxin may be involved in floral induction as proposed in other species. During early flower stage development, floral identity genes are up-regulated as *AGAMOUS* or *PISTILLATA* homologues, whereas floral identity gene are down-regulated as *SOC1*.

RNA Seq

Recently Next Generation Sequencing (NGS) technologies were used to discover new genes and study in silico their expression. Table 1 summarized the results from the two main studies (Dubois et al., 2012; Kim et al., 2012). These two studies contributed largely to increase the number of known unigenes in rose. A French consortium combined 454 and Illumina sequencing technologies to identify new genes from *R. chinensis* 'Old Blush' (Dubois et al., 2012). First, a 454 deep sequencing of 'Old Blush' was done on normalized cDNA libraries from various tissues, allowing after clustering the identification of more than 80,000 unigenes. Using OrthoMCL, we identified peptides that can be clustered into 14,000 protein families. Among them, 50% were common between rose, woodland strawberry, *Prunus* and *Arabidopsis*. Interestingly, 3,500 protein families were specific from rose and may represented rose specific proteins involved in specific processes. Furthermore, we developed a gene expression atlas for *R. chinensis* 'Old Blush'. We performed deep sequencing (Illumina sequencing) of non-normalized cDNA libraries from different tissues (buds, vegetative and floral shoots, flowers, petals, rose hips, roots) in response to biotic and abiotic stresses. From theses sequences, a database for digital expression was developed (http://iant.toulouse.inra.fr/R.chinensis).

Each sequence obtained was mapped against the 80,000 contigs. By counting the number of positive maps, transcript accumulation for one contig can be estimated (digital expression). For a selection of 23 genes with high or low expression, we validated the digital expression by qPCR (Dubois et al., 2012). In another study, a Korean team analyzed the transcriptome of flower tissues of 4 different rose genotypes: *R. hybrida* 'Vital', 'Maroussia', 'Sympathy' and *R. rugosa* 'Heading' (Kim et al., 2012). For each genotype, they identified around 14,000 contigs (http:// 210.218.199.249/rose/). The contigs were compared with already known *Rosaceae* genome sequence as apple, strawberry and peach.

Discovery of Micro RNA

miRNA are short (20-24 nt) non protein coding RNA, which were demonstrated to play important roles in regulating plant growth and development. miRNA regulate the expression of target mRNA post-transcriptionnaly through either cleavage of the targeted mRNA or translational repression. New sequencing technologies allow the identification of miRNA in non-sequencing organisms. Two recent studies have identified miRNA in rose (Kim et al., 2012; Pei et al., 2013). Using Illumina technology, miRNA libraries from flower tissues (Kim et al., 2012) or from petals treated with ethylene (Pei et al., 2013). To identify the miRNA, two different strategies were used: comparison with known miRNA or use of the *F. vesca* genome to identify miRNA precursors. Results obtained are summarized in Table 2. Kim et al. (2012) identified 267 unique miRNA tags. Among them, 25 were novel. Pei et al. (2013) identified 33 conserved miRNA and 47 putative new miRNA. Using RNA Seq, miRNA accumulation was demonstrated to vary during petal development and in response to ethylene treatment (Pei et al., 2013). Furthermore negative correlation for transcript accumulation was shown between miRNA and their target mRNA, suggesting that miRNA/mRNA target module were conserved in rose.

THE ROSE GENOME SEQUENCING INITIATIVE

The next step in the rose genomic adventure is to obtain a rose genome sequence. It was decided the creation of a rose genome sequencing initiative in order to obtain a high quality sequence of the rose genome. This initiative gathers all teams that are interesting in the rose genome sequence. All teams are welcome to contribute to this goal by participating in developing resources or supporting financially the project.

No homozygous material was available when starting the project. Therefore one of the main issues concerning rose genome sequencing will be to tackle the heterozygocity. The first choice was the selection of a genotype to sequence. We have chosen an old Chinese cultivated rose, *R. chinensis* 'Old Blush'. Different academic teams all over the world use 'Old Blush'. It is an historical genotype, introduced in Europe around 1760, and which has contributed to the introduction of important ornamental traits such as continuous flowering or tea-scent. 'Old Blush' is though to be an inter-specific cross between *R. chinensis* var. *spontanea* and *R. odorata* var. *gigantea* (Meng et al., 2011). Furthermore 'Old Blush' has different characteristics that make it a model plant for rose genetic and genomic studies. It is a rapid cycle genotype (as a continuous flowering rose) and highly fertile. Different genetic and genomics resources are available on this genotype as BAC library (Hess et al., 2007), EST (Dubois et al., 2012), F_1 progeny ((Byrne et al., 2007) and see below). A genetic transformation protocol has been developed and functional validation of interest genes is feasible (Vergne et al., 2010). However as all cultivated roses, the level of heterozygocity is high. Using 32 SSR, heterozygocity was estimated to 74% (Soules, 2009). In order to solve heterozygocity, we proposed different strategy based on development of a high genetic density map and production of haploids.

The first strategy was to develop a high genetic map from a F_1 progeny developed by INRA (Angers, France). This progeny was obtained from a cross between 'Old Blush' and *R.* × *wichurana* and contains more than 300 F_1 individuals. Important ornamental

traits segregate in this progeny as the mode of flowering (continuous flowering vs. once-flowering), type of flower (double vs. simple flower), flower color (pink vs. white), plant architecture (bushy vs. ground cover) and disease susceptibility to powdery mildew or black spot. To develop the genetic map, two types of markers are used. A first genetic draft was developed using microsatellite markers. The current genetic map contained 40 microsatellite markers for a size of 300 cM (Laurence Hibrand-Saint Oyant, pers. commun.). These SSR markers will help to anchor this new genetic map to previous published maps as the integrated consensus map (Spiller et al., 2011). This new genetic map will be enriched with SNP markers using the WagRhSNP Axiom array, which contains 68,893 SNPs. The SNP genotyping is under progress and this new genetic map will be used to anchor the rose genome sequence. In parallel, a haploid material from 'Old Blush' is under development by French groups (Angers and Lyon).

The next step will be the sequencing and the assembly of the genome. Presently, 'Old Blush' is under sequencing at the Genoscope (Evry, France). The sequencing is supported financially by INRA (France) and 'Pays de la Loire' (Region of France). For the rose annotation, synteny between rose and woodland strawberry, for which genome sequence is available (http://www.rosaceae.org), can be used. The genera *Rosa* and *Fragaria* belong to the *Rosoideae* tribe in the *Rosaceae* family; and good micro and macro-synteny were demonstrated. At the whole genome, a good correspondence is found between rose linkage groups and strawberry chromosomes. The Table 3 summarizes the results obtained by our group in collaboration with B. Desnoyé (INRA, Bordeaux, unpublished data) and by Israeli team (Gar et al., 2011) . For instance, almost all rose genetic markers of linkage group 1 are located on strawberry chromosome 7. However few rearrangements exist between both genomes. 15 markers on rose LG2 are located on strawberry chromosome 1 and 16 markers on chromosome 6, whereas 14 markers on rose LG 3 are located on strawberry chromosome 6 (Table 3). The synteny can be used to clone genes as recently demonstrated for the continuous flowering gene in rose and strawberry (Iwata et al., 2012). The micro-synteny was studied at the *Rdr1* locus (Terefe-Ayana et al., 2012). The *Rdr1* locus corresponds to a cluster of TIR-NBS-LRR genes. By sequencing, the authors demonstrated that the cluster was conserved within the genus *Rosa* (between *R. multiflora* and *R. rugosa*) but also between *Rosa* and *Fragaria vesca*. A similar region exists on chromosome 7 in woodland strawberry even if numerous inversions and translocations were detected between rose and strawberry (Terefe-Ayana et al., 2012).

CONCLUSION

The rose genome sequence will open a new area for research in rose genetics and genomics. Concerning functional genomics, resources now exist to follow gene expression during developmental processes or in response to biotic or abiotic stresses by RNA Seq (Dubois et al., 2012). It will allow the identification of important genes in these processes. With the rose genome sequence, epigenomic modifications can be studied to detect modifications of the chromatin as DNA methylation or histone acetylation (Rivera and Ren, 2013). Concerning genetic studies, new technologies are now available to develop high-density genetic maps. In crops, re-sequencing (as Genotyping-By-Sequencing, GBS (Elshire et al., 2011)) is already used in routine and should be soon available for species as roses. The anchorage of genetic maps and rose genome should accelerate the cloning of major genes and QTL, by identifying rapidly candidate genes under the studied locus. In rose, till now, all genetic studies have been done on F_1 progeny, with a restricted genetic diversity (Byrne, 2009). With new genotyping technologies, genome-wide association studies are now possible in rose, even if studies on linkage disequilibrium are still necessary to define the best strategy: candidate gene vs. genome-wide approach (Hall et al., 2010). The rose genome sequence will give new insights concerning the genetic diversity and the genome evolution within the genus *Rosa* but also within the *Rosaceae* family. Genomic comparisons with already sequenced genomes, as apple, peach or strawberry, will help to understand the origin and evolution

of the *Rosaceae* genome.

The rose genome will be also an important resource for rose breeders. Markers, associated with a locus, can be rapidly obtained and transferred for molecular assisted selection. Furthermore, with the high density of SNP markers and the decreasing cost of genotyping, it could become feasible to do genomic selection in rose. Genomic selection is used routinely in animals (Meuwissen et al., 2013) and important studies are done to develop this approach in crops. The marker effects are estimated in a genotyped and phenotyped training population and then are used for the estimation of breeding values of interest genotypes. For instance in rose, the selection of adult traits can be done at the seedling stage and therefore greatly accelerating the process of plant selection.

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Tables

Table 1. Unigene discovery in rose using NGS technologies.

Dubois et al., 2012. (*R. chinensis* 'Old Blush').			
	Reads	Lenght (Mb)	Contigs
454	1,043,748	288	80,714
Illumina	9,332,571	300	
dB: http://iant.toulouse.inra.fr/R.chinensis.			
Kim et al., 2012. (*R. hybrida* 'Vital', 'Maroussia', 'Sympathy', *R. rugosa* 'Heading').			
	Reads	Lenght (Mb)	Contigs
454	508,403	108	
(value / librairie)	127,100	27	13,609
dB: http://210.218.199.249/rose/.			
Pei et al., 2013. dB: http://bioinfo.bti.cornell.edu/rose.			

Table 2. Micro RNA discovery in rose.

Kim et al. (2012). From 4 different cultivars ('Vital', 'Maroussia', 'Sympathy', *R. rugosa* 'Heading').			
	sRNA	Predicted miRNA against *F. vesca* genome	Predicted miRNA against miRNA dB
454	2,574,444	192 (with 33 new)	137
Pei et al. (2013) (studied by family) From 4 different libraries from the cultivar 'Samantha'			
	sRNA	Predicted miRNA against *F. vesca* genome	Predicted miRNA against miRNA dB
Illumina	5,309,191	47 new miRNA	33

Table 3. Macro-synteny between rose and woodland strawberry. The results presented are based on unpublished data from Angers (L. Hibrand-Saint Oyant, INRA) and Bordeaux (B. Desnoye, INRA) and published data from Israeli group (Gar et al., 2011). The figures in the table represent common genetic markers between the 7 rose linkage groups (RG) and the 7 *F. vesca* chromosmes (FvChr).

	RG1	RG2	RG3	RG4	RG5	RG6	RG7
FvChr1		15		1	3		
FvChr2	1			1	1	22	
FvChr3			2	3	12		
FvChr4				7	1	1	
FvChr5					1		16
FvChr6	1	16	14	1			
FvChr7	16		1	1	1	1	