Review

Genomics of pear and other Rosaceae fruit trees

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The family Rosaceae includes many economically important fruit trees, such as pear, apple, peach, cherry, quince, apricot, plum, raspberry, and loquat. Over the past few years, whole-genome sequences have been released for Chinese pear, European pear, apple, peach, Japanese apricot, and strawberry. These sequences help us to conduct functional and comparative genomics studies and to develop new cultivars with desirable traits by marker-assisted selection in breeding programs. These genomics resources also allow identification of evolutionary relationships in Rosaceae, development of genome-wide SNP and SSR markers, and construction of reference genetic linkage maps, which are available through the Genome Database for the Rosaceae website. Here, we review the recent advances in genomics studies and their practical applications for Rosaceae fruit trees, particularly pear, apple, peach, and cherry.

Key Words: apple, co-linearity, genome sequence, peach, pear, reference map.
showed that a relatively recent (ca. 50 million years ago) genome-wide duplication resulted in the transition from nine ancestral chromosomes to 17 chromosomes in apple, based on whole-genome sequencing analysis.

In recent years, international collaborative studies by the Rosaceae research community have hastened progress in developing genetic and genomic resources for representative crops such as apple (*M. × domestica*), peach (*P. persica*), and strawberry (*Fragaria* spp.) (Shulaev et al. 2008); this strategy was based on a consensus that there are multiple Rosaceae model species (Dirlewanger et al. 2009b). These resources, including expressed sequence tags (ESTs), bacterial artificial chromosome (BAC) libraries, physical and genetic maps, and molecular markers and bioinformatics tools, are available through the Genome Database for the Rosaceae (GDR; http://www.rosaceae.org). The availability of this database has rendered various rosaceous crops highly amenable to functional and comparative genomics studies. Here we review recent progress in genomics studies on Rosaceae fruit trees such as apple, pear, peach, and cherry, and discuss the newly accumulated knowledge and resources for comparative genomics studies on this family.

**Genome sequences of Rosaceae fruit crops**

Whole-genome sequences have been reported for Chinese pear (Wu et al. 2013), European pear (Chagné et al. 2014), apple (Velasco et al. 2010), peach (Verde et al. 2013), Japanese apricot (Zhang et al. 2012), wild strawberry (Shulaev et al. 2011) and cultivated strawberry (Hirakawa et al. 2014) (Table 1). The draft genome of the Chinese pear ‘Dangshansuli’ (*P. bretschenederi*) is now available (Wu et al. 2013). A total of 2103 scaffolds span 512.0 Mb (97.1% of the estimated genome size, 527 Mb) and are not anchored to the 17 chromosomes. The Chinese pear genome assembly contains 42,812 protein-coding genes, and about 28.5% of them encode multiple isoforms. The identified repetitive sequences (271.9 Mb in total) account for 53.1% of the genome. The difference in size between the pear and apple genomes is mainly due to the presence of repetitive sequences (predominantly transposable elements), whereas genic regions and protein-coding genes are similar in both species. A draft genome assembly of European pear ‘Bartlett’ (Chagné et al. 2014) contains 142,083 scaffolds and covers a total of 577.3 Mb (96.2% of the estimated genome size, 600 Mb). A total of 43,419 putative genes were predicted, of which 1219 are unique to European pear and are not found in other dicots plant genomes sequenced. Analysis of the expansin gene family and other cell wall-related genes showed their involvement in fruit softening in both European pear and apple. It is expected that pear genome sequences of Chinese and European pears will be assigned to 17 pseudo-chromosomes, which will greatly help us to conduct genetics and genomics studies in pears.

An international consortium has published a draft genome sequence of the domesticated apple ‘Golden Delicious’, a common founder cultivar in many breeding programs (Velasco et al. 2010). The genome assembly of ‘Golden Delicious’ consists of 122,146 contigs spanning a total of 603.9 Mb (81.3% of the estimated genome, 742.3 Mb). Seventeen pseudo-chromosomes (GDR, *Malus × domestica* Genome v1.0) were obtained from these contigs. A total of 57,386 putative protein-coding genes were predicted. The MADS-box gene family involved in flower and fruit development is expanded in apple to 15 members. The other gene families related with transport and assimilation of sorbitol are also expanded, and are involved in Rosaceae-specific metabolism.

A high-quality draft reference genome sequence, Peach v1.0, of the doubled haploid genotype of the peach cultivar ‘Lovell’ has been reported (Verde et al. 2013). Since ‘Lovell’ is completely homozygous, its genome assembly has facilitated obtaining a reliable and unbiased reference genome. Using 827 markers from an updated *Prunus* reference map (Howad et al. 2005), Verde et al. (2013) organized 215.9 Mb of the Peach v1.0 genome into eight pseudomolecules covering 81.5% of the estimated genome (265 Mb). A total of 27,852 protein-coding genes were predicted. Furthermore, comparative analyses showed that the ancestral triplicated blocks in peach are detected, and that putative paleoancestor regions are detectable.

The genome of Japanese apricot or mei (*P. mume*) was one of the first genomes to be sequenced in the subgenus *Prunus* of the genus *Prunus* (Zhang et al. 2012). Japanese apricot was domesticated in China more than 3000 years ago as an ornamental plant and fruit tree. A 237-Mb genome assembly was generated from 29,989 scaffolds, 84.6% of which were further anchored to eight chromosomes in a

| Common name                | Pyrus bretschneideri | Pyrus communis | Malus × domestica | Prunus persica | Prunus mume | Fragaria vesca |
|----------------------------|----------------------|----------------|-------------------|---------------|-------------|---------------|
| Cultivar name              |                      |                |                   |               |             |               |
| No. of contigs             | 25,312               | 182,196        | 122,146           | –             | –           | –             |
| No. of scaffolds           | 2103                 | 142,083        | –                 | 391           | 45,592      | –             |
| Genome assembly size (Mb)  | 512.0                | 577.3          | 603.9             | 215.9         | 45,592      | 29,989        |
| Coverage (%)               | 97.1                 | 96.2           | 81.3              | 81.5          | 84.6        | 84.6          |
| Estimated genome size (Mb) | 527                  | 600            | 742.3             | 265           | 280         | 280           |
| No. of pseudo genes        | 42,812               | 43,419         | 57,386            | 27,852        | 31,390      | 34,809        |
| No. of pseudo-chromosomes  | 17                   | 8              | 8                 | 8             | 7           |               |
| Reference                  | Wu et al. 2013       | Chagné et al. 2014 | Velasco et al. 2010 | Verde et al. 2013 | Zhang et al. 2012 | Shulaev et al. 2011 |
genetic map constructed by restriction-site-associated DNA sequencing (RADseq); 31,390 protein-coding genes were annotated and integrated using ab initio gene prediction methods. By comparison of the P. mume genome with the available data, nine ancestral chromosomes of the Rosaceae family were reconstructed (Zhang et al. 2012).

Strawberry is one of the most important Rosaceae crops, and genomes were sequenced for wild woodland strawberry (Shulaev et al. 2011) and cultivated octoploid strawberry (Hirakawa et al. 2014). The woodland strawberry F. vesca (2n = 2x = 14), a diminutive herbaceous perennial, has a small genome (240 Mb) that shares substantial sequence identity with the genomes of the cultivated strawberry (F. × ananassa) and other economically important rosaceous plants. A total of 209.8 Mb (>95%) of the genome sequence were included in 272 representative scaffolds out of 3262 scaffolds, which were anchored to seven pseudo-chromosomes in the genetic linkage map. Gene prediction modeling identified 34,809 putative protein-coding genes. Macrosyntetic relationships between Fragaria (x = 7) and Prunus (x = 8) predict a hypothetical ancestral Rosaceae genome that had nine chromosomes. Furthermore, the whole genome sequences of peach, apple and strawberry were analyzed and compared by using 1399 orthologous regions between the three genomes, suggesting the ancestral genome (x = 9) to the extant Fragaria, Prunus and Malus genomes (Illa et al. 2011, Jung et al. 2012).

### Genome-wide molecular markers

**SSR markers**

Simple sequence repeat (SSR) markers, or microsatellites, provide a reliable method for evaluation of genetic diversity and construction of genetic maps because of their co-dominant inheritance and the allelic abundance (Weber and May 1989). More than 1000 SSR markers have been developed in Japanese and European pears from genome sequences (Fernández-Fernández et al. 2006, Inoue et al. 2007, Sawamura et al. 2004, Yamamoto et al. 2002a, 2002b, 2002c), ESTs (Nishitani et al. 2009, Zhang et al. 2014), and next-generation sequencing (NGS) data (Yamamoto et al. 2013). Recently, a large number of SSR markers have been developed from the whole-genome sequence of Chinese pear ‘Dangshansuli’ (Chen et al. 2015). SSR markers developed in pear have been often used as anchor loci for reference genetic linkage maps of pear (Chen et al. 2015, Yamamoto et al. 2007).

In apple, hundreds of SSR markers have been developed (Celton et al. 2009, Gianfranceschi et al. 1998, Guilford et al. 1997, Liebhard et al. 2002, 2003, Moriya et al. 2012, Silfverberg-Dilworth et al. 2006, van Dyk et al. 2010) and used to construct high-quality genetic linkage maps with high marker density. Among Prunus spp., a large number of SSR markers have been developed for peach and almond (Aranzana et al. 2002, 2003, Cipriani et al. 1999, Dirlewanger et al. 2002, Howat et al. 2005, Nishitani et al. 2007, Sosinski et al. 2000, Testolin et al. 2000, Yamamoto et al. 2002d, 2003, 2005), cherries (Cantini et al. 2001, Downey and Iezzoni 2000, Joobeur et al. 2000, Struss et al. 2002), and apricot (Lopes et al. 2002).

**SNP markers**

Although at present SSR markers seem to be the best choice for genetics and genomics studies, marker systems with even higher throughput, such as single-nucleotide polymorphisms (SNPs), have been developed based on whole-genome sequencing data. Using NGS technology, Montanari et al. (2013) have developed 1096 SNPs from three European pear cultivars. A total of 857 polymorphic SNP markers were validated and mapped using a segregating population of European pear ‘Old Home’ × ‘Louise Bon Jersey’ and interspecific breeding families derived from Asian (P. pyrifolia and P. bretschneideri) and European pear pedigrees. Japanese pear ‘Housui’ (syn. ‘Hosui’) has also been used for EST sequencing of 185 Mb and genome sequencing of 529 Mb (Terakami et al. 2014). Using the GoldenGate assay, Terakami et al. (2014) evaluated 1536 SNPs detected in EST and genome sequences of ‘Housui’, and mapped 609 SNPs on its linkage map. Using RADSeq, Wu et al. (2014) have genotyped Chinese pear SNPs by NGS and mapped 3143 SNPs on a linkage map.

The 8K apple Infinium SNP chip has been developed by the USA-based international research program RosBREED (Chagné et al. 2012). To discover genome-wide SNPs, 27 apple cultivars were chosen to represent worldwide breeding germplasms and were re-sequenced at low coverage by NGS technology. Of 2,113,120 SNPs detected, 7867 were selected for the apple 8K SNP array; after evaluation in segregating families and a germplasm collection, 5554 were found to be polymorphic (Chagné et al. 2012). Despite this progress, the number of robust and evenly distributed SNP markers in the 8K array was not sufficient. Recently, a 20K SNP array has been developed by the European research program FruitBreedomics, which focuses on bridging the gap between breeding and genomics (Bianco et al. 2014). This SNP array has been developed to enable high-precision genome-wide association analyses and pedigree-based analysis because of rapid decay of linkage disequilibrium. The SNPs included in this array were predicted from re-sequencing data derived from the genome sequences of 13 apple cultivars and one accession of crab apple (M. micromalus).

Using NGS technology, the International Peach SNP Consortium has re-sequenced the whole genomes of 56 peach breeding accessions (Verde et al. 2012, 2013) and developed a 9K SNP array (Verde et al. 2012). Using the GoldenGate assay, Martínez-Garcia et al. (2013) have evaluated a set of 1536 SNPs of peach (P. persica) developed from the whole-genome sequences of three cultivars. The RosBREED Consortium has also developed a 6K SNP array for diploid sweet cherry (P. avium) and allotetraploid sour cherry (P. cerasus) (Peace et al. 2012).
High-density reference genetic linkage maps constructed with genome-wide molecular markers are important for many genetic and breeding applications in Rosaceae fruit trees including marker-assisted selection (MAS), mapping of quantitative trait loci (QTLs), identifying DNA markers for fingerprinting, and map-based gene cloning. Because good, comprehensive books and reviews have been produced that describes mendelian traits and QTLs in Rosaceae fruit trees (Dirlewanger et al. 2009a, Korban and Tartarini 2009, Salazar et al. 2014), it would be impractical to repeat that information. Instead we describe high-density reference genetic linkage maps in pear, apple and Prunus.

Pear reference maps

Among Pyrus spp., integrated high-density genetic linkage maps are available for the European pear cultivars ‘Bartlett’ and ‘La France’ and the Japanese pear cultivar ‘Housui’; these maps are based on SSRs from pear, apple, and Prunus, amplified fragment length polymorphisms (AFLPs), isozymes, and phenotypic traits (Terakami et al. 2009, Yamamoto et al. 2002c, 2004a, 2007). The linkage maps of ‘Bartlett’, ‘La France’, and ‘Housui’ consisted of 447, 414, and 335 marker loci, respectively, and covered 17 linkage groups (LGs), which matched the basic chromosome number of pear (x = 17). Recently, Terakami et al. (2014) established a SNP assay to evaluate 1536 SNPs detected in the EST and genome sequences of ‘Housui’, and mapped 609 SNPs on a linkage map of ‘Housui’. After all available SNP and SSR markers were integrated, the latest version of updated reference genetic linkage map of ‘Housui’ was reconstructed (Fig. 1), which consists of 1033 loci, including 609 SNPs from transcriptome and genome analyses, 61 SNPs from potential intron polymorphism markers (Terakami et al. 2013), 202 pear SSRs, 141 apple SSRs, and 20 other markers. Montanari et al. (2013) evaluated a set of 1096 European pear SNPs and 7692 apple SNPs, and mapped 857 and 1031 SNPs, respectively, on pear genetic maps. On the basis of whole-genome sequencing of P. bretschneideri, Chen et al. (2015) constructed a consensus genetic map consisting of 734 SSR loci derived from 1341 newly designed SSRs. Using RADseq, Wu et al. (2014) mapped 3143 SNPs on linkage maps of Chinese pear.

Apple reference maps

Several apple reference genetic linkage maps have been published. The first RFLP-based reference maps for ‘Prima’ and ‘Fiesta’ were constructed using 152 F1 individuals and the two maps were aligned using 67 multi-allelic markers (Maliepaard et al. 1998). SSR-based integrated genetic linkage maps for ‘Fiesta’ and ‘Discovery’ were constructed using 840 molecular markers including 129 SSRs (Liebhard et al. 2002, 2003). A new set of 148 apple microsatellite markers has been developed and mapped on the reference linkage maps of ‘Fiesta’ and ‘Discovery’ (Silfverberg-Dilworth et al. 2006). Recently, the 8K Infinium SNP chip described above was used to construct a high-density genetic linkage map in apple (Chagné et al. 2012). In the FruitBreedomics project, 21 full sib families were SNP-genotyped, resulting in the genetic mapping of approximately 15,800 SNP markers (Bianco et al. 2014).

Prunus reference maps

The framework Prunus mapping population for construction of the reference map was an F2 population (referred to as the T × E population) produced by crossing almond (Prunus dulcis) ‘Texas’ × peach (P. persica) ‘Earlygold’ and selfing a single F1 plant (MB 1-73) (Joobeur et al. 1998). The T × E map contained 562 marker loci (Dirlewanger et al. 2004a). Howad et al. (2005) established a Prunus reference map using a set of six F2 plants, one F1 hybrid, and one parent of the F1 hybrid, which could jointly define 65 possible different genotypes by the markers mapped on the T × E map. Howad et al. (2005) identified and mapped 264 SSR markers from 401 different SSR primer pairs. Recently, Verde et al. (2013) have aligned the eight main scaffolds (pseudo-chromosomes) against the updated version of the Prunus reference map constructed by Howad et al. (2005).

A consensus cherry genetic linkage map has been developed using 94 individuals from an interspecific cross, ‘Napoleon’ (P. avium) × P. nipponica accession F1292; this map consisted of 174 loci, including 160 SSR loci and 6 gene-specific markers, and covered 680 cM (Clarke et al. 2009). Cabrera et al. (2012) developed a sweet cherry (P. avium) reference linkage map using Rosaceae Conserved Orthologous Set (RosCOS) markers and SSR markers. RosCOS markers were identified from 3818 rosaceous unigenes comprised of two or more ESTs corresponding to single-copy genes in Arabidopsis (Cabrera et al. 2009, 2012). Of the 627 RosCOS markers, 81 SNPs representing 68 genome-wide RosCOS were mapped in four F1 populations and placed on the consensus sweet cherry linkage map that included previously reported SSRs, indel, and S-RNase markers and spanned 779.4 cM. Klugges et al. (2013) constructed SNP-based high-density genetic maps of sweet cherry using intraspecific progenies from crosses between parental lines ‘Black Tartarian’ × ‘Kordia’ (BT × K) and ‘Regina’ × ‘Lapins’ (R × L). Of 5686 SNP markers tested, 723 and 687 were mapped onto eight LGs in BT × K and R × L, respectively. The obtained maps spanned 752.9 and 639.9 cM, with an average distance between markers of 1.1 and 0.9 cM, respectively. Very recently, genotyping-by-sequencing (GBS), a new methodology based on high-throughput sequencing, was applied for genome mapping in sweet cherry (Guajardo et al. 2015).

Marker-assisted selection in Japanese pear

MAS can accelerate selection and reduce the progeny size and the cost of raising individuals to maturity in the field, especially in fruit trees (Luby and Shaw 2001). In Japanese
Fig. 1. The latest version of integrated reference genetic linkage map of Japanese pear ‘Housui’ based on SNP and SSR markers. A total of 81 SSR loci including 67 from pear ESTs or 454 genome sequencing analysis and 14 from apple, which were included in the ‘Housui’ map of Yamamoto et al. (2013), were added to the recently published SNP-based map (Terakami et al. 2014). Linkage groups are designated as Ho1 to Ho17, HoX1 and HoX2. The number to the left of each marker indicates genetic distance (cM). SSR markers (green, underlined) were developed from pear. SSR markers (red, italicized) were developed from apple. SNP markers developed by transcriptome analysis are denoted by JPsnpHou and SNP markers developed from potential intron polymorphism markers are denoted by TsuSNP. Distorted segregation is indicated by a significant P value of the χ² test: *P  = 0.05, **P  = 0.01, ***P  = 0.005.
Pear, several molecular markers associated with genes of interest traits have been identified and used for MAS in practical breeding programs of the National Agriculture and Food Research Organization (NARO) Institute of Fruit Tree Science, Japan (Table 2). Since several characteristics were already analyzed by genome mapping, QTL analysis, or both, the positions of responsible genes (loci) were identified in genetic linkage maps and tightly linked molecular markers were identified; these data are deposited in the public database of the Applied Crop Genomics Research Center (http://www.naro.affrc.go.jp/genome/index.html). DNA markers have been identified that are associated with genes for resistance to scab disease caused by Venturia nashicola (Gonai et al. 2012, Iketani et al. 2001, Terakami et al. 2006) and for resistance (or susceptibility) to black spot disease caused by a Japanese pear pathotype of Alternaria alternata (Banno et al. 1999, Iketani et al. 2001, Terakami et al. 2007). Self-incompatibility in Japanese pear is controlled by a single multi-allelic S-locus, and S-genotype identification is important for breeding and selection of pollen donors for fruit production. Several molecular assays for rapid and reliable S-genotype determination have been established, such as polymerase chain reaction–restriction fragment length polymorphism (PCR-RFLP) analysis (Ishimizu et al. 1999) and allele-specific PCR amplification (Nashima et al. 2015). The S<sub>4</sub>sm allele of the self-compatible cultivar ‘Osa-Nijisseki’ (a mutant of the self-incompatible cultivar ‘Nijisseki’) has been identified and found to lack a 236-kbp genomic region that includes the S<sub>4</sub>-RNase coding region (Okada et al. 2008). Molecular markers associated with the following fruit-related traits were also revealed: fruit storage potential controlled by ethylene production (the 1-aminocyclopropane-1-carboxylate (ACC) synthase gene; Itai et al. 2003), fruit skin color (Inoue et al. 2006, Yamamoto et al. 2014), and harvest time (Yamamoto et al. 2014). These markers can be used for MAS in Japanese pear breeding programs.

**Synteny in Rosaceae fruit trees**

It is expected that comparative genomics in Rosaceae fruit trees

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**Table 2.** Molecular markers associated with genes of interest in Japanese pear and their positions in genetic linkage maps

| Characteristics          | Gene symbol | Gene sources | Linkage group nos. | Associated molecular markers (Accession nos.) | F-primer sequences (5′-3′) | R-primer sequences (5′-3′) | References |
|--------------------------|-------------|--------------|--------------------|------------------------------------------------|---------------------------|---------------------------|------------|
| Scab resistance to V. nashicola | Vnk         | Kinchaku     | 1                  | TsuENH184 (AB621908)                             | ccctccctgactaccctcaaa     | gtctcattgaaagggctctctagac    | Gonai et al. 2012, Terakami et al. 2006 |
|                          |             |              |                    | TsuENH101 (AB621905)                             |                           |                           |                        |
| Black spot susceptibility | A           | Osa Nijisseki | 11                 | CMNB41/235                                      | gcagctgctcaagtgagtgaag    | aaaccttcatctcaccacagcctgacte | Banno et al. 1999, Terakami et al. 2007 |
|                          | Ani         | Osa Nijisseki | 11                 | CH04h02                                         | gcagctgctcaagtgagtgaag    | aaaccttcatctcaccacagcctgacte | Terakami et al. 2007 |
|                          | Ana         | Nansui       | 11                 | CH03d02                                         | gcagctgctcaagtgagtgaag    | aaaccttcatctcaccacagcctgacte |                        |
| Self-incompatibility S   |             | Japanese pear | 17                 | S-RNase                                         | ttacgctgaatcatcact     | acgttgcacactaatg            | Ishimizu et al. 1999, Nashima et al. 2015 |
| Self-compatibility S<sup>4</sup>sm |         | Osa Nijisseki | 17                 | SM                                              | tgcgtctgaaggatcaaatcgg    | gccttgcaggtctggg            | Okada et al. 2008 |
| Fruit skin color         | PruC        | Niitaka Akiikari | 8                 | OPH-19-425                                      | tgcagcagctccagatcctct    | caaaacttcatctcaccacagcctgacte | Inoue et al. 2006, Yamamoto et al. 2014 |
|                          |             |              |                    | Mdo.ch.8.10 CH04g12                              | tgcagcagctccagatcctct    | caaaacttcatctcaccacagcctgacte |                        |
| Fruit storage             | PpACS2      | Japanese pear | 15                 | ACC synthase                                    | gtcagactgacagcaaaatc     | agtagagcgaggaanaaatc         | Itai et al. 2003 |
| Harvest time              | HarT-1 (QTL) | Taikoku       | 3                  | BGA35 (AB219799)                                | agtagagcgaggaanaaatc     | gtcagactgacagcaaaatc         | Yamamoto et al. 2014, Yamamoto et al. 2014 |
|                          | HarT-2 (QTL) | Taikoku       | 15                 | PPACS2                                          | agtagagcgaggaanaaatc     | gtcagactgacagcaaaatc         |                        |

<sup>a</sup> GTTCTTG: pig tail sequence for DNA sequencer analysis.
trees will be able to integrate conserved candidate genes, molecular markers associated with interest traits, and QTLs, in order to verify how the genetic and molecular factors control traits like fruit quality and texture across species and genera. Therefore, synteny or comparative genome mapping is an important approach, which determines the homologous genes of related species, as well as the co-linearity (conservation of the gene order) among conserved genomic regions.

**Co-linearity between Pyrus and Malus**

Yamamoto et al. (2001) applied apple SSR markers inter-generically for the characterization of several pear species (P. pyrifolia, P. bretschneideri, P. ussuriensis, P. communis, and P. calleryana). Nucleotide repeats were detected in the amplified fragments of pear and apple by both sequencing and Southern blot analyses, and the differences in fragment sizes between pear and apple were due mainly to the differences in the number of such repeats. The SSR markers are applicable across genera in the tribe Pyreae, subtribe Pyrinae, which includes apple, pear, quince (Cydonia oblonga Mill.), and loquat (Liebhard et al. 2002, Soriano et al. 2005, Yamamoto et al. 2001, 2004a, 2004b). When pear genetic linkage maps (‘Bartlett’ and ‘La France’) were compared with the apple reference maps (‘Discovery’ and ‘Fiesta’), 66 apple SSR loci could be positioned onto the homologous LGs of pear (Yamamoto et al. 2007). Furthermore, SSR locus positions within LGs were almost identical in pear and apple, indicating good co-linearity in all 17 LGs. Gisbert et al. (2009) used SSR markers from apple and pear to construct genetic linkage maps of loquat cultivars ‘Algerie’ and ‘Zaozhong-6’; the loquat maps showed a high syntenic relationship with apple maps when anchored SSR markers were used. Fukuda et al. (2014) identified almost perfect co-linearity of LG10 among loquat, pear, and apple. These findings suggest that all chromosomes of the genera in the tribe Pyreae show co-linearity despite considerable differences in the genome sizes, which range from 1.11 pg/2C to 1.57 pg/2C (Dickson et al. 1992, Dirlewanger et al. 2009b).

**Co-linearity within Prunus**

The marker transferability is extremely high within *Prunus*. For example, among 277 *Prunus* SSRs, including 141 from peach (P. persica), 58 from apricot (P. armeniaca), 31 from almond (P. dulcis), 9 from sweet cherry (P. avium), 4 from sour cherry (P. cerasus), and 6 from Myrobalan plum (*Prunus cerasifera* Ehrh.), 95.3% showed PCR amplification in Myrobalan plum (Dirlewanger et al. 2004a). Furthermore, Mnejja et al. (2010) examined *Prunus* SSR markers for transferability across rosaceous crops using nine species, almond (P. dulcis), peach (P. persica), apricot (P. armeniaca), Japanese plum (*Prunus salicina* Lindl.), European plum (*Prunus domestica* L.), sweet cherry (P. avium), apple (M. × domestica), pear (P. communis), and strawberry (F. ×ananassa). Of the 145 SSRs derived from *Prunus* species, 83.6% of amplified bands of the expected size range were identified in other *Prunus* species, and the proportion of SSRs showing polymorphism was also high (63.9%) (Mnejja et al. 2010). In contrast, only 16.3% of the *Prunus* SSRs were transferable across species of other Rosaceae genera such as apple, pear, and strawberry (Mnejja et al. 2010).

SSR markers developed for various *Prunus* species have been intensively used to compare *Prunus* linkage maps (Dirlewanger et al. 2004b). Detailed map comparisons were performed using common SSR markers between the reference genetic linkage map T × E (Joobeur et al. 2000) and the maps of *P. armeniaca* (Lambert et al. 2004), P. davidiana (Fouloungne et al. 2003), and P. cerasifera (Dirlewanger et al. 2004a). The distribution and order of SSR markers in all *Prunus* species show complete synteny except for a reciprocal translocation between LGs 6 and 8 detected in peach and almond (Dirlewanger et al. 2004b, Jáuregui et al. 2001). The SNP-based sweet cherry maps displayed high synteny and co-linearity of all eight LGs with the *Prunus* reference map and with the peach genome v1.0 (Klagges et al. 2013).

**Synteny between Pyrus (Malus) and Prunus**

Transferability of SSR markers is very low between tribes, as shown by comparing *Pyrus* and *Malus* (M. et al. 1999) found that only 18% of peach SSRs showed amplified bands in apple. Similarly, Yamamoto et al. (2004a) observed that only 10% of the *Prunus* SSRs could be transferred to the genetic linkage maps of *Pyrus* (‘Bartlett’ and ‘Hou sui’). Only one out of 15 apple SSR markers was transferable to *Prunus* (Liebhard et al. 2002). A total of 613 RosCOS markers were successfully amplified and mapped on the *Prunus* T × E reference map. These RosCOS markers will be useful for further investigations of syntenic relationships between *Pyrus* (Malus) and *Prunus*. Furthermore, several other reports have showed synteny within Rosaceae plants (Sargent et al. 2009, Vilanova et al. 2008) and Rosaceae vs. other family (Staton et al. 2015).

**Conclusion and perspectives**

In this manuscript, we describe to focus recent progress on whole-genome sequences, genome-wide SNP and SSR markers, construction of reference genetic linkage maps, and synteny studies in Rosaceae fruit trees, which will help us to develop new cultivars with desirable traits by MAS and new genomic-based strategies in breeding programs.

Genetic improvement of Rosaceae fruit trees is strongly hampered by their large tree size, long generation, an extended juvenile phase for seedling (Luby and Shaw 2001, Rikkerink et al. 2007). Therefore, it is considered that MAS and marker-assisted breeding can accelerate selection and reduce the progeny size and the cost of raising individuals to maturity in the field (Luby and Shaw 2001, Rikkerink et al. 2007). However, attempts to MAS in fruit tree breeding programs remain limited for a few simply inherited traits, because marker development for MAS via bi-parental QTL mapping is also hindered by the same complications. Newly
developed high-throughput genotyping technologies such as SNP chips and genotyping using NGS have enabled new genomic-based strategies such as genome-wide association studies (GWAS), which are an alternative to bi-parental QTL mapping in long-lived perennials. Selection based on genomic predictions of breeding values, i.e., genomic selection (GS, Meuwissen et al. 2001) is another alternative for MAS. The robust and evenly distributed genome-wide SNP markers combined with reference genetic linkage maps, help us to use new genomic-based strategies such as GWAS and GS, which are now emerging as powerful tools in pear, apple, and forest tree breeding programs (Grattaglia and Resende 2011, Iwata et al. 2013a, 2013b, Kumar et al. 2012, 2013).

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