POLISH SOCIETY FOR HORTICULTURAL SCIENCE

Folia Hort. 25/2 (2013): 161-168

DOI: 10.2478/fhort-2013-0018

FOLIA HORTICULTURAE

Published by the Polish Society for Horticultural Science since 1989

REVIEW | Open access | http://www.foliahort.ogr.ur.krakow.pl

The history of mapping the apple genome

Sylwia Keller-Przybyłkowicz, Małgorzata U. Korbin*

Department of Fruit Plant Breeding
Laboratory of Unconventional Breeding Methods
The Research Institute of Horticulture
Konstytucji 3 Maja 1/3, 96-100 Skierniewice

ABSTRACT

This review summarises the research projects that have been conducted with the goal of mapping the apple (*Malus* × *domestica*) genome. The generation of apple linkage and physical maps, which was started at the end of the 20th century by many scientific teams, has resulted in rich data useful for further fundamental and applied studies. The mapping efforts mainly contained the choice of mapping populations as well as the choice of types and number of markers. Over the years, scientists have achieved major successes and faced major obstacles. Many economically important traits have been mapped in the apple genome, which has a total length of 2000 cM. The recently published integrated genetic and physical maps summarise the data and will be helpful to modern breeding programs, with a special focus on resistance to various diseases, as well as on fruit quality and other desired apple traits.

Key words: linkage map, *Malus* × *domestica*, physical map

INTRODUCTION

Genome mapping establishes the "road map" of the genome (Kole and Abbott 2008). The mapping of chromosomes helps to locate important genes and identify the molecular environment of coding and non-coding DNA sequences. Based on the manner of their generation, two types of maps are featured: the genetic map and the physical map. The first one shows the order of genes and the distance between them (expressed as the percentage of recombination) and is measured in centiMorgans (cM). The physical maps present the actual physical position of genes with distances measured in base pairs (bp). Both the genetic and physical maps can be applied for crop improvement. For instance, markers linked to genes and/or QTL can be used for the introgression of favourable alleles of genes, for selection in breeding programs, and for screening germplasm for targeted traits (Kole and Abbott 2008). Thus, maps are considered a valuable tool for contemporary agriculture, particularly for present-day breeding.

The domesticated apple (*Malus* × *domestica* Borkh., family Rosaceae, subfamily Maloideae) (Hummer and Janick 2008) is cultivated all across the temperate world and the annual world production of this fruit exceeds 73 million metric tons (FAOSTAT 2011). The apple has long been considered a result of allopolyploidization between species related to the subfamilies Spiraeoideae (n = 9) and Amygdaleoideae (n = 8), with possible autopolyploidization events (Evans and Campbell 2002). More recently, genome-wide duplications have been suggested as the cause of the transition

*Corresponding author.
Tel.: +48 46 834 52 69; fax: +48 46 834 52 69;
e-mail: malgorzata.korbin@inhort.pl (M. Korbin).

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from nine ancestral chromosomes to 17 (Velasco et al. 2010). The size of the *Malus* genome is relatively small (742.3 Mbp/1C) and comparable in length to that of the tomato (Shulaev et al. 2008).

Over the years, many apple maps have been generated. The Genome Database of Rosaceae (www.rosaceae.org) and databases derived from European *Malus* projects such as HiDRAS (www.hidras.unimi.it) display several reference maps of the apple genome, allowing users to focus on regions of interest, or align maps for comparative purposes (Jung et al. 2008).

In this review the authors would like to present the history of apple genome mapping by emphasising the successes and the obstacles of these research efforts.

Mapping populations

The choice of mapping population is critical for successful map construction. Self-incompatibility and the long juvenile period of *M.* × *domestica* (3-10 years) limit the generation of segregating populations such as F_2, $F_{2:3}$, BC or RIL, which are commonly used for the mapping of other plant species. Therefore, the apple maps were built on F_1 obtained from inter/intraspecific cross pollination (CP) of various cultivars characterised by high heterozygosity (Maliepaard et al. 1998).

The first segregating population resulted from the cross 'Rome Beauty' × crabapple 'White Angel' contained only 56 genotypes (Hemmat et al. 1994). Later on, the number of progeny extended from 100 to 200 genotypes ('Wijcik McIntosh' × NY 75441-67, 'Wijcik McIntosh' × NY 75441-58; 'Ralls Janet' × Mitsubakaido, 'Delicious' × Mitsubakaido) (Conner et al. 1997, Igarashi et al. 2008), and from 250 to 300 progeny ('Prima' × 'Fiesta', 'Fiesta' × 'Discovery', 'Telamon' × 'Braeburn', 'Florina' × 'Nova Easygro') (Maliepaard et al. 1998, Liebhard et al. 2002, 2003a, Kenis and Keulemans 2005, Le Roux et al. 2010). In the last decade, numerous subsets of these previously described populations were re-used in order to increase the saturation level of individual maps (Calenge et al. 2004, 2005, Silfverberg-Dilworth et al. 2006). On the other hand, 60 progeny were applied at the beginning of the study on the 'Retina' × 'Topaz' bin-map (Keller-Przybyłkowicz 2011) and further analysis, including searches for specific QTLs, has been continued on new sub-populations derived from the same cross (unpublished data).

Using CarthaGene software, marker data generated earlier for 676 progeny of the crosses 'Discovery' × TN10-8, 'Fiesta' × 'Discovery', 'Discovery' × 'Prima' and 'Durello di Forli' × 'Fiesta' were applied for the construction of an integrated map of the apple genome (N'Diaye et al. 2008). Recently, Khan et al. (2012) built a global "virtual" consensus map using the GoldenGate genotyping platform (HTS) and data that had been obtained from several mapping populations, containing over 500 individuals in total.

Molecular markers and linkage map construction

The first skeletons of apple maps were built based on RAPD (*Random Amplified Polymorphic DNA*), RFLP (*Restriction Fragment Length Polymorphism*) and AFLP (*Amplified Fragment Length Polymorphism*) markers (Hemmat et al. 1994, Conner et al. 1997, Maliepaard et al. 1998, Kenis and Keulemans 2005). However, these markers have many disadvantages such as laborious genotyping (RFLP), dominant inheritance (AFLP, RAPD), low reliability (RAPD), and low level of polymorphism (RFLP, RAPD). The usefulness of some of the RAPD and RFLP markers for apple mapping increased after their conversion to SCAR markers (*Sequence Characterized Amplified Regions*) (Tartarini et al. 1999, Bus et al. 2005, Boudichevskaia et al. 2006).

In parallel, apple-specific microsatellites (SSR, *Simple Sequence Repeat*), which are highly polymorphic, transferable, easy to amplify and very reliable (Hokanson et al. 1998), became the marker of choice in the generation and saturation of apple maps (Gianfranceschi et al. 1998, Liebhard et al. 2002, Silfverberg-Dilworth et al. 2006, Keller-Przybyłkowicz 2011). Lately, SNPs (*Single Nucleotide Polymorphism*), have become very useful in apple mapping due to their high abundance and high throughput genotyping as well as their transferability not only between apple cultivars but even between *Malus* and *Pyrus* genomes (Antanaviciute et al. 2012). Moreover, the development of EST and SNP arrays provides high throughput genotyping for further linkage map construction and will greatly facilitate future QTL and association analysis (Antanaviciute et al. 2012).

In recent years, cDNA microarrays have become the source of new types of markers (Soglio et al. 2009). As a continuation of whole-genome profiling, diversity array technology (DArT) has also been applied in the mapping of the apple genome (Schouten et al. 2012).

Seventeen linkage groups (LGs) for the maternal 'Rome Beauty' and 24 LGs for the paternal 'White

Angel' were described for the first apple map by Hemmat at al. (1994). Other early maps, based on the cross between 'Wijcik McIntosh' and NY 75441-67 / NY 75441-58, characterised 19 linkage groups for 'Wijcik McIntosh' (1206 cM in length), 16 linkage groups for NY 75441-67 (692 cM) and 18 linkage groups for NY 75441-58 (898 cM) (Conner et al. 1997).

The next genetic maps described 17 linkage groups, with total lengths of 843 cM and 984 cM for 'Prima' and 'Fiesta', respectively (Maliepaard et al. 1998), 1082 cM and 1031 cM for 'Ralls Janet' and 'Delicious' (Igarashi et al. 2008), 1039 cM and 1245 cM for 'Telamon' and 'Braeburn' (Kenis and Keulemans 2005), 1143 cM and 1454 cM for 'Fiesta' and 'Discovery' (Liebhard et al. 2003a) to 1991 cM for the integrated *M.* × *domestica* map (Khan et al. 2012). The differences between the various maps were related to the type and number of the DNA markers. For instance, genotyping the progeny of the cross 'Rome Beauty' × 'White Angel' was carried out by 409 markers (Hemmat at al. 1994) whereas the linkage mapping of 'Fiesta' × 'Discovery' was carried out by 840 markers (Liebhard et al. 2002, 2003a), by 938 markers (Silfverberg-Dilworth et al. 2006) and by 1046 markers (N'Diaye et al. 2008). Almost 800 newly developed DArT markers increased the genome saturation from 55% to 76% for 'Prima' and from 60% to 74% for 'Fiesta' (Schouten et al. 2012). The newest integrated map based on 2875 SSRs and SNPs resulted in intervals between markers even smaller than 1 cM (Khan et al. 2012).

Gene loci and QTL regions on the M. × domestica maps

The majority of major genes, gene markers and quantitative trait loci (QTL) located on the genetic maps are linked with plant resistance to economically important apple diseases.

Several SCAR markers related to the *Rvi6* locus (formerly *Vf*), primarily originating from *M. floribunda* Sieb. 821, which is monogenically resistant to apple scab caused by *Venturia inaequalis* (race 6), were identified on LG1 (Huaracha et al. 2004). The *Rvi1* gene (formerly *Vg*), originally described in 'Golden Delicious', which is resistant to race 1 of *V. inaequalis*, was localised on LG12 of 'Prima' (Durel et al. 2000). Further work on *M.* × *domestica* resistance to *V. inaequalis*, exploited by Bus et al. (2005) and Boudichevskaia et al. (2006), allowed the identification of two different *R* genes: *Rvi2* (*Vh2*) and *Rvi4* (*Vr1/Vh4*) carrying *Vr* regions on LG2 of Russian Seedling (*Malus pumila* R12740-7A). The apple scab resistance gene *Rvi5* (*Vm*), originally derived from *M. micromalus*, was located on linkage group 17 of 'Murray' (Cheng et al. 1998, Patocchi et al. 2005). The analysis of various mapping populations allowed the identification of further *R* genes: *Rvi10* and *Rvi17* (formerly *Va,* scab resistance derived from 'Antonovka') on LG1 (Hemmat et al. 2003, Dunemann and Egerer 2010), *Rvi11* (*Vbj*, apple scab resistance derived from *Malus baccata jackii*) on LG2 (Gygax et al. 2004) and *Rvi12* (*Vb,* scab resistance from Hansen's baccata #2) on LG12 (Hemmat et al. 2003, Erdin et al. 2006). Likewise, the *Rvi13* gene (*Vd,* scab resistance from 'Durello di Forli') was located on LG10 (Tartarini et al. 2004, Soriano et al. 2009). In addition to *R* genes, several QTL impacting scab resistance and a number of RGA (resistance gene analogues) have been identified from different apple cultivars (Liebhard et al. 2003b, Durel et al. 2003, Calenge et al. 2004, Gessler et al. 2006, Soufflet-Freslon et al. 2008).

The regions linked to polygenic apple resistance to fire-blight (caused by *Erwinia amylovora*) were detected on linkage group 3, 7 and 12 of 'Prima', 'Fiesta', 'Idared', *M. robusta* 5, 'Discovery', TN10-8, 'Evereste' and *M. floribunda* 821 (Calenge et al. 2005, Peil et al. 2007, Khan et al. 2006, 2007, Durel et al. 2009). Moreover, additive interactions of several additional resistance regions in the same genotype were identified (Calenge et al. 2005).

Several genes of resistance to powdery mildew (caused by *Podosphaera leucotricha*) were mapped on different apple chromosomes such as LG12 (*Pl-1,* resistance derived from *Malus robusta*) (Dunemann et al. 2007), LG11 (*Pl-2*, derived from *Malus zumi* and *Pl-mis* from Mildew Immune Selection) (Alston et al. 2000, Gardiner et al. 2003), LG8 (*Pl-w,* derived from crabapple 'White Angel') (Evans et al. 2003), and LG12 (*Pl-d*, derived from 'D12') (James et al. 2004). The analysis of 'Discovery' × TN10-8 progeny allowed for the mapping of additional QTL regions connected with powdery mildew resistance on LGs 2, 8, 13, 14, and 17 (Calenge and Durel 2006). Genes conferring resistance toward the woolly apple aphid (*Eriosoma lanigerum*) such as *Er1* (originated from 'Northern Spy') and *Er3* (from *Malus sieboldii*) were mapped on LG8, whereas *Er2* gene (from *M. robusta*) was located on LG17 (Bus et al. 2007). The gene *Dp-fl* conferring resistance toward the rosy apple aphid (*Dysaphis plantaginea* Passerini) was mapped on LG8 (Dapena et al. 2009). Moreover, leaf curling aphid (*Dysaphis*

devecta Wlk) resistance gene (*Sd1*), described firstly by Roche et al. (1997), was revealed on LG7 of the cultivar 'Florina' (Cevik and King 2002).

Studies on genes and regions controlling many other plant traits have also been conducted from the beginning of apple mapping. Putative QTL regions controlling blooming behaviour were expected on LG7, 8, 10, 15, 17, sugar content on LG3, 6, 8, 9, 14, acidity on LG8 and LG16, and the juvenile period on LG3 and LG15 of the first 'Fiesta' × 'Discovery' – based map (Liebhard et al. 2003c). Maliepaard et al. (1998) localised putative QTL of fruit acidity (LG16) and juvenile period (LG3 and LG15) of 'Prima' × Fiesta'. The position of these QTL was confirmed in more recent investigations carried out on 'Telamon' × 'Braeburn' progeny (Kenis and Keulemans 2004, 2007, 2008). In a study on the same progeny, QTLs of fruit harvest (LG3, LG9, LG16), yield (LG5, LG15, LG16), fruit weight (LG2, LG6, LG10), fruit browning (LG17) (Kenis et al. 2008), and the content of fruit vitamin C (LG6, 10, 11 and 17) (Davey et al. 2006) were identified. However, despite such a broad spectrum of research on the location of QTL regions on the apple map, so far only some aspects of this knowledge have found applications in the practical breeding of this species.

Recently, functionally characterised markers that diversify phenotypical variations in regard to sequence motifs have become very reliable for genetic map saturation (Andersen and Lübberstedt 2003). For instance, the functional markers adequate to sequences of genes associated with the regulation of ethylene synthesis and fruit firmness such as *ACO* (1-aminocyclopropane-1-carboxylate oxydase) and *ACS* (1-aminocyclopropane-1-carboxylate synthase) were mapped on LG10 and LG15, respectively (Harada et al. 2000, Costa et al. 2005, Soglio et al. 2009). Han et al. (2007, 2008) and Fernandez-Fernandez et al. (2008) described additional functional markers: sequences coding β-cyanoalanin synthase and ubiquitin F_1 related protein *MdFBCP1*, neighbouring the *ACO* alleles on LG10, and the Ethylene Receptor gene (*ETR1)* regulating fruit ripening, near the *ACS* alleles (Fernandez-Fernandez et al. 2008). The study of EST homologues to expansine (*Exp*7) and polygalacturonase (*MdPG1*) genes, both controlling fruit softness, allowed the localisation of these sequences on the first linkage group of 'Prima' (Costa et al. 2008) and LG10 of 'Mondial Gala' (Costa et al. 2010), respectively. The markers related to sequences of *Gfc* and *Rni* genes associated with fruit flesh colour and the *MdMYB10* gene (anthocyanin biosynthesis regulator) were mapped on chromosome IX in the progeny of the crosses 'Sciros' × 91.136 B6-77, 'Geneva' × 'Beaeburn' and 'Fiesta' × 'Totem' (Chagne et al. 2007, Fernandez-Fernandez et al. 2008).

The analysis of selected segments of 'Retina' and 'Topaz' genome allowed the mapping of four genes responsible for plant defence: defensin peroxidase (*DefPerox*) on LG14 of 'Retina', glutathione S-transferase class-phi (*GluStra*) on LG3 of 'Retina' and the metallothionein-like protein type 3 and 2 (*MALDO3*, *MALDO2*) on LG3 and LG12 of 'Topaz', respectively. Other markers derived from ESTs of genes responsible for sugar metabolisms, including *GFglyTra* – UDP glucose: flavonoid 3-o-glucosyl transferase, *PSTP* – putative sugar transporter protein, and *PST* – putative sugar transporter, were mapped on LG2 of 'Retina' and 'Topaz', on LG12 of 'Topaz' and on LG14 of 'Retina'. Ascorbate peroxidase (homolog *APX* – *PGiso1B*) locus was identified on LG12 of the 'Topaz' genome (Keller-Przybyłkowicz 2011).

Generation of a genetic apple map – obstacles and errors

The major critical points in apple map generation include: the choice of appropriate parental forms and progeny set for efficient mapping, the selection of flanking markers, as well as the proper screening methodology for QTL analysis (Liebhard and Gessler 2002). In general, high heterozygosity of the parents results in a segregation of the markers and allows for the determination of the distance between them and the genes of interest, by measuring the recombination frequency using the formula: 1% of recombination equals 1 cM (Lander and Botstein 1989). The statistical significance of the results is estimated by a LOD Score (*Logarithm of the ODD*) and ML (maximum likelihood) (Van Ooijen 1999, 2001). Various QTL mapping software programs are available, including fixed model (Xu and Atchley 1995), individual marker locus model (Knapp et al. 1990), segmental mapping (Perez-Enciso et al. 2000) and functional mapping (Ma et al. 2002). The various methodologies consider factors such as segregation type, input files, mapping function and thresholds setups, which affect the quality and the reliability of the map. It is noteworthy that problems arising from the incorrect scoring of markers, an improper assembly of the mapping results (after the calculation of the "goodness of fit" for each marker), as well as unsuitable software setups

have been reported since the beginning of genetic mapping (Lander and Botstein 1989, Liebhard and Gessler 2000, Van Ooijen 2001).

Physical maps of the apple genome

The first *M.* × *domestica* physical maps were based on a partial sequencing of regions controlling the resistance to apple scab, using BAC-libraries constructed for 'Florina' (Vinatzer et al. 1998) and for *M. floribunda* 821 (Patocchi et al. 1999a,b, Xu et al. 2001). A more developed physical map was obtained by screening 3,744 BAC contigs (Han et al. 2008, 2009). The predicted genes covered a broad range of functional categories, such as cellular components, signal transduction, metabolism and stress response (32,250 genes). Han et al. (2008) determined the total coding region of the apple genome in the physical map of 'GoldRush' to be 64.5 Mbp.

Recently, physical mapping strongly supported by new computational tools and evolved by advanced high-throughput sequencing technologies has resulted in the recognition of a sequence of the entire apple genome (Velasco et al. 2010). After assembling and anchoring, the 'Golden Delicious' genome was found to contain 17 chromosomes (with 98% coverage of the apple genome), in a total length of 742.3 Mbp. This physical map contained 57,386 putative genes (including 11,444 genes specific for apple), 31,678 transposable elements and numerous repeated sequences. Simultaneously, a physical map of 'Royal Gala' with 19,732 sequences, representing about 60% of the total genome, was generated by Sanzol (2010). Both groups showed high levels of genome duplications followed by translocation and deletion events (Sanzol 2010, Velasco et al. 2010). Velasco et al. (2010) suggested that each doublet in the original set of eight chromosomes originated from one ancestor via inter-chromosomal rearrangements between chromosomes III and XI, V and X, IX and XVII and XII and XVI. Based on the physical maps, Han et al. (2011) concluded that the homology between pairs of linkage groups I and VII, II and XV, III and XI, IV and XII, V and X, VI and XIV, VIII and XV and IX and XVII demonstrates a large number of duplications in the apple genome.

SUMMARY

The generation of both the genetic and physical maps of apple widen the knowledge regarding the structure and origin of the *M.* × *domestica* genome. Further generation maps have become important for marker-assisted crop improvement, for the introgression of single genes and pyramiding breeding in the case of complex and polygenic traits. In addition, these maps are useful for the dissection of gene interactions and the identification of favourable alleles in segregating populations. However, before the application of this knowledge (and especially to new apple cultivars), one must validate the data.

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HISTORIA MAPOWANIA GENOMU JABŁONI

Streszczenie: Prace nad uzyskiwaniem genetycznych oraz fizycznych map genomu jabłoni (*M.* × *domestica*), rozpoczęte w końcu XX wieku, znacząco poszerzyły wiedzę dotyczącą ewolucji i struktury genomu tego gatunku. Mapy nowej generacji, zawierające pełną sekwencję nukleotydową stały się cennym narzędziem podczas tworzenia programów krzyżowań ukierunkowanych na introgresję genów kodujących lub modulujących ważne gospodarczo cechy i gromadzenie wielu z nich w genomach nowych odmian. Istniejące mapy genomów odmian jabłoni umożliwiają nie tylko rozpoznanie mechanizmów współdziałania genów, ale również identyfikację pożądanych alleli w populacjach potomnych. Baza danych, wygenerowana podczas sporządzania map stanowi 'kamień milowy' dla rozwoju hodowli jabłoni. Niemniej przed skorzystaniem z tych danych winny być one poddane dogłębnej weryfikacji.

Received November 5, 2013; accepted November 20, 2013