Journal of Horticultural Research 2014, vol. 22(1): 93-100
DOI: 10.2478/johr-2014-0011

IDENTIFICATION OF FOUR NEW EST-BASED MARKERS ON THE APPLE (*MALUS* × *DOMESTICA*) GENETIC MAP

Sylwia KELLER-PRZYBYŁKOWICZ*, Małgorzata KORBIN
Research Institute of Horticulture
Konstytucji 3 Maja 1/3, 96-100 Skierniewice, Poland

Received: December 2, 2013; Accepted: May 30, 2014

ABSTRACT

The map of the linkage groups: LG2, LG12 and LG14, which are expected to contain QTLs related to fruit quality, was generated by analysis of 56 individuals of the cross: 'Retina' × 'Topaz'. Twenty three of the 27 SSR markers covered 225 cM in 'Retina' and 371 cM in 'Topaz' genome. High level of colinearity (~ 85%) was found between obtained map and the respective map regions of 'Fiesta', 'Discovery', 'Ralls Janet' and 'Delicious'. Only single inversions of marker positions were noted, predominantly in 'Topaz'. CAPS and SSCP/SNP markers in seven ESTs, chosen based on the metabolic pathways of ascorbic acids and sugar, were identified. Four of the CAPS markers, linked to the genes coding: *UDP* glucose : flavonoid 3-*o*-glucosyl transferase, ascorbate peroxidase, and two sugar transporters, were mapped on LG2 (GFglTra – both cultivars), LG12 (PGiso1B and PSTS – 'Topaz') and LG14 (PST – 'Retina'). According to our knowledge, loci of these markers have never been identified on the apple genome map.

Key words: comparative mapping, SSR transferability, ascorbic acid and sugar metabolism

INTRODUCTION

The domesticated apple (*Malus* × *domestica* Borkh.) is cultivated all across the temperate zone of the world. The annual world production of apples exceeds 73 million metric tons (FAOSTAT 2011). As a result of all evolutionary transformations within Amygdaloideae and Spiraeoideae subfamilies (Shulaev et al. 2008), the cultivated apple has 17 chromosomes (n = 17) and its genome size is about 740 Mb (Velasco et al. 2010, Han et al. 2011, Micheletti et al. 2011).

Various genetic maps of apple have been generated based on different cross populations (CP) of *M.* × *domestica* (Keller-Przybyłkowicz & Korbin 2013). The first linkage map covered approximately 950 cM and was created for 'Rome Beauty' and 'White Angel' (Hemmat et al. 1994). Improvement of the mapping technology resulted in maps for many other cultivars including: 'Wijcik McIntosh' (WM), NY 75441-67, NY 75441-58, 'Telamon', 'Braeburn', 'Prima', 'Fiesta', 'Discovery', 'Ralls Janet', 'Delicious', covering from 842 cM (Conner et al. 1997, Maliepaard et al. 1998, Kenis & Keulemans 2005, Igarashi et al. 2008) to almost 2000 cM in integrated maps (N'Diaye et al. 2008, Khan et al. 2012). The maps were constructed and saturated using RAPD (Random Amplified Polymorphic DNA), RFLP (Restriction Fragment Length Polymorphism), AFLP (Amplified Fragment Length Polymorphism) (Hemmat et al. 1994, Maliepaard et al. 1998, Liebhard et al. 2002, 2003), and more recently SSR (Simple Sequence Repeat), SNP (Single Nucleotide Polymorphism) (Silfverberg-Dilworth et al. 2006, Igarashi et al. 2008, Khan et al. 2012), cDNA microarray (Soglio et al. 2009) and diversity array technology (DArT) based markers (Schouten et al. 2012). Among them many sequences were linked to economically important traits such as plant resistance to pests and diseases, plant growth habit, fruit colour, acidity and sweet taste (Korban & Tartarini 2009). The conserved character of certain markers and their transferability between botanical taxa (Lewers et al. 2005, Sargent et al. 2007, Gasic et al. 2009) contributed to the progress in apple mapping (Gianfranceschi et al. 1998, Khan et al. 2012).

*Corresponding author:
e-mail: Sylwia.Keller@inhort.pl

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

This work is aimed at the generation of bin-map skeleton with SSR markers in order to identify genes controlling traits differentiating the apple cultivars ‘Retina’ and ‘Topaz’. We present the map of three linkage groups with four newly developed EST-based markers and discuss the efficiency of marker transferability.

MATERIALS AND METHODS

Plant material

The study was conducted on plants of the cultivars ‘Retina’ and ‘Topaz’, and 60 progeny of the cross between them. Plants were cultivated in the orchard of the Institute of Horticulture in Dąbrowice. Samples of young leaves (2 g) were collected separately from each plant. Tissues were grinded in liquid N_2 and stored in -70 °C until DNA extraction (Aldrich & Cullis 1993).

SSR (Single Sequence Repeat) markers

Ten microsatellite markers: CHO2a03, CHO3g07, CHO2c02a, CHO5dO4, CHO4dO2, CHO2gO4, CHO4gO4, CHO2cO6, CHO2fO6, CHO5dO8 (www.hidras.unimi.it) were applied to verify genetic authenticity of the progeny.

Additional 27 markers, distributed on three linkage groups of reference ‘Fiesta’ × ‘Discovery’ map as follows: LG2 – 7 SSRs LG12 – 10 SSRs and LG14 – 10 SSRs (Liebhard et al. 2002, 2003, www.hidras.unimi.it) (Table 1), were used to gene-rate the skeleton of ‘Retina’ and ‘Topaz’ genetic map. PCR was performed in Biometra Basic thermocycler according to the following thermal profile: 96 °C for 30 s, four steps with reduced annealing temperature, starting from 65 °C for 90 s, followed by 30 cycles with annealing temperature of 60 °C for 90 s. PCR products were electrophoretically size fractionated in 7% polyacrylamide gels, containing 0.4% urea and stained with 0.1% of silver nitrate.

EST (Expressed Sequence Tags)

Seven genes coding: dehydroascorbate reductase (*DHAR*), ascorbate peroxidase (*PGiso1B*), UDP-glucose 6-dehydrogenase (*UDP6Deh*), UDP-glucose glucosyl-transferase (*UDPglTra*), UDP glucose : flavonoid 3-*o*-glucosyl transferase (*GFglTra*), sugar transporters (*PST* and *PSTP*) were chosen based on the metabolic pathways of ascorbic acid and sugar, as well as based on KEGG and/or NCBI databases. Primers for amplification of these ESTs were synthesised using the Primer Select programme (Lasergene v. 7). The thermal profiles of the PCR contained 30 cycles as follows: 96 °C for 30 s, 60 °C for 60 s, 72 °C for 2 min for *UDP6Deh*, *UDPglTra*, *GFglTra*, *DHAR*, *PGiso1B* and 65 °C/60 s of annealing for *PST* and *PSTP* genes. Amplified products (500 ng of DNA) were digested with *Hae*III enzyme (Fermentas), according to the manufacturer protocol, to obtain CAPS markers (Cleaved Amplified Polymorphic Sequence). PCR-CAPS products were visualised under UV light after electrophoresis in agarose gel (1%) stained with ethidium bromide (50 $mg \cdot dm^{-3}$). Monomorphic ESTs were additionally assessed for SSCP (Single Strand Conformational Polymorphism) on polyacrylamide gels, containing 10% of glycerol. All polymorphic products were sequenced (CEQ8000, Beckman Coulter) and aligned using MagAlign software (Lasergen v. 7) for potential SNP identification.

Bin-map construction

The chromosome map was constructed using JoinMap v. 3.0 software (Kyazma, NL) (van Ooijen & Voorrips 2001). Statistical deviations from the expected Mendelian ratios were determined by χ^2 test. Only LOD (Logarithm Odd Ratio threshold) of 3.0 or higher were considered to represent linkage. Mapping distance was calculated using the Kosambi map function and drafted by the MapChart 2.1 software (Voorrips 2002).

RESULTS

Verification of the genetic status of the progeny

Patterns obtained in reactions with 10 specific SSR primers allowed for elimination of four ‘out-crosses’. Finally, population of 56 individuals derived from the ‘Retina’ × ‘Topaz’ cross was applied for mapping process.

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

Table 1. The SSR markers applied for the mapping of LG2, LG12 and LG14

Group	Primer name	5′ sequence	3′ sequence
LG 2	CHO2cO6	TGACGAAATCCACTACTAATGCA	GATTGCGCGCTTTTTAACAT
	CHO2f06	CCCTCTTCAGACCTGCATATG	ACTGTTTCCAAGCGATCAGG
	CHO2a04	GAAACAGGCGCCATTATTTG	AAAGGAGACGTTGCAAGTGG
	CHO2c02a	CTTCAAGTTCAGCATCAAGACAA	TAGGGCACACTTGCTGGTC
	CHO2b10*	CAAGGAAATCATCAAAGAT-TCAAG	CAAGTGGCTTCGGATAGTTG
	CHO3d10	CTCCCTTACCAAAAACACCAAA	GTGATTAAGAGAGTGATCGGGG
	CHO3d01*	CGCACCACAAATCCAACTC	AGAGTCAGAAGCACAGCCTC
LG 12	CHO5g07	CCCAAGCAA-TATAGTGAATCTCAA	TTCATCTCCTGCTGCAAATAAC
	CHO5d04	ACTTGTGAGCCGTGAGAGGT	TCCGAAGGTATGCTTCGATT
	CHO4g04	AGTGGCTGATGAGGATGAGG	GCTAGTTGCACCAAGTTCACA
	CHO1b12*	CGCATGCTGACATGTTGAAT	CGGTGAGCCCTCTTATGTGA
	CHO1g12	CCCACCAATCAAAAATCACC	TGAAGTATGGTGGTGCGTTC
	CHO5d11	CACAACCTGATATCCGGGAC	GAGAAGGTCGTACATTCCTCAA
	CHO4d02	CGTACGCTGCTTCTTTTGCT	CTATCCACCACCCGTCAACT
	CHO1d03	CCACTTGGCAATGACTCCTC	ACCTTACCGCCAATGTGAAG
	CHO1f02	TCACTATTTACGGGATCAAGCA	GTGCAGAGTCTTTGACAAGGC
	CHO3c02	TCACTATTTACGGGATCAAGCA	GTGCAGAGTCTTTGACAAGGC
LG 14	CHO3g04	ATGTCCAATGTAGACACGCAAC	TTGAAGATGGCCTAACCTTGTT
	CHO4c07	GGCCTTCCATGTCTCAGAAG	CCTCATGCCCTCCACTAACA
	CHO5d03	TACCTGAAAGAGGAAGCCCT	TCATTCCTTCTCACATCCACT
	CHO5e05	TCCTAGCGATAGCTTGTGAGAG	GAAACCACCAAACCGTTACAAT
	CHO1e01	GGTTGGAGGGACCAATCATT	CCCACTCTCTGTGCCAGATC
	CHO1g05	CATCAGTCTCTTGCACTGGAAA	GACAGAGTAAGCTAGGGCTAGGG
	CHO4f06	GGCTCAGAGTACTTGCAGAGG	ATCCTTAAGCGCTCTCCACA
	CHO3d08	CATCAGTCTCTTGCACTGGAAA	TAGGGCTAGGGAGAGATGATGA
	CHO3a02	TTGTGGACGTTCTGTGTTGG	CAAGTTCAACAGCTCAAGATGA
	CHO5g11*	GCAAACCAACCTCTGGTGAT	AAACTGTTCCAACGACGCTA

*Markers finally unmapped on analysed linkage groups of ‘Retina’ and ‘Topaz’

Construction of LG maps and assessment of their colinearity

Twenty three of the 27 SSR markers firstly characterised on LG2, 12 and 14 of the ‘Fiesta’ × ‘Discovery’ (Silfverberg-Dilworth et al. 2006) were identified in ‘Retina’ (15 SSRs) and ‘Topaz’ (18 SSRs). The markers covered 225 cM of ‘Retina’ and 371 cM of ‘Topaz’ genomes (Fig. 1). Linkage group 2 of both genotypes was constructed by four tightly linked markers (CHO2f06, CHO2c02a, CHO3d10, CHO2a04), and by CHO2c06 which was mapped only on LG2 of ‘Topaz’. Three SSRs (CHO1g12, CHO5d11 and CHO1f02) were identified on LG12 of both cultivars whereas CHO1d03 derived from ‘Retina’ and CHO5d04, CHO4d02, CHO5g07, CHO3c02, CHO4g04 from ‘Topaz’. CHO1e01 and CHO4c07 markers were mapped on LG14 of both cultivars but four SSRs: CHO5e05, CHO1g05, CHO3d08, CHO5d03 and three SSRs: CHO3g04, CHO3a02, CHO4f06 were found only in ‘Retina’ or ‘Topaz’, respectively.

The distances between the mapped SSRs varied from 1 to 70 cM while these distances on the reference maps varied from 0.001 to 40 cM, dependent on the marker and the map (Table 2). However, in many cases the distances between the SSRs were similar or even shorter comparing to the other maps (e.g. CHO1f02 – CHO1d03; the distance of 33.7 cM in ‘Discovery’ and 14 cM in ‘Retina’, CHO5g07 – CHO5d04; 20.7 cM/18.3 cM in ‘Fiesta’/‘Discovery’ and 1 cM in ‘Topaz’, CHO4d02 – CHO5d11; 20.5 cM/17.1 cM in ‘Fiesta’/‘Discovery’ and 4 cM in ‘Topaz’). The order of the SSRs on each tested chromosome showed high similarity to the reference

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

maps. In LG2 the exceptions were CHO2a04 and CHO2c06 in 'Topaz'. Putative inversions were noted for the marker pairs in LG12 (CHO1g12 – CHO5d11 of 'Retina', and CHO5g07 – CHO5d04 and CHO4d02 – CHO5d11 of 'Topaz') as well as in LG14 (CHO4c07 – CHO3d08 of 'Retina', and CHO3d08 – CHO1g05 and CHO3a02 – CHO3g04 of 'Topaz'). Moreover, inversion of the CHO4c07 – CHO1e01 between the female ('Retina') and male ('Topaz') maps was observed in the LG14 (Fig. 1).

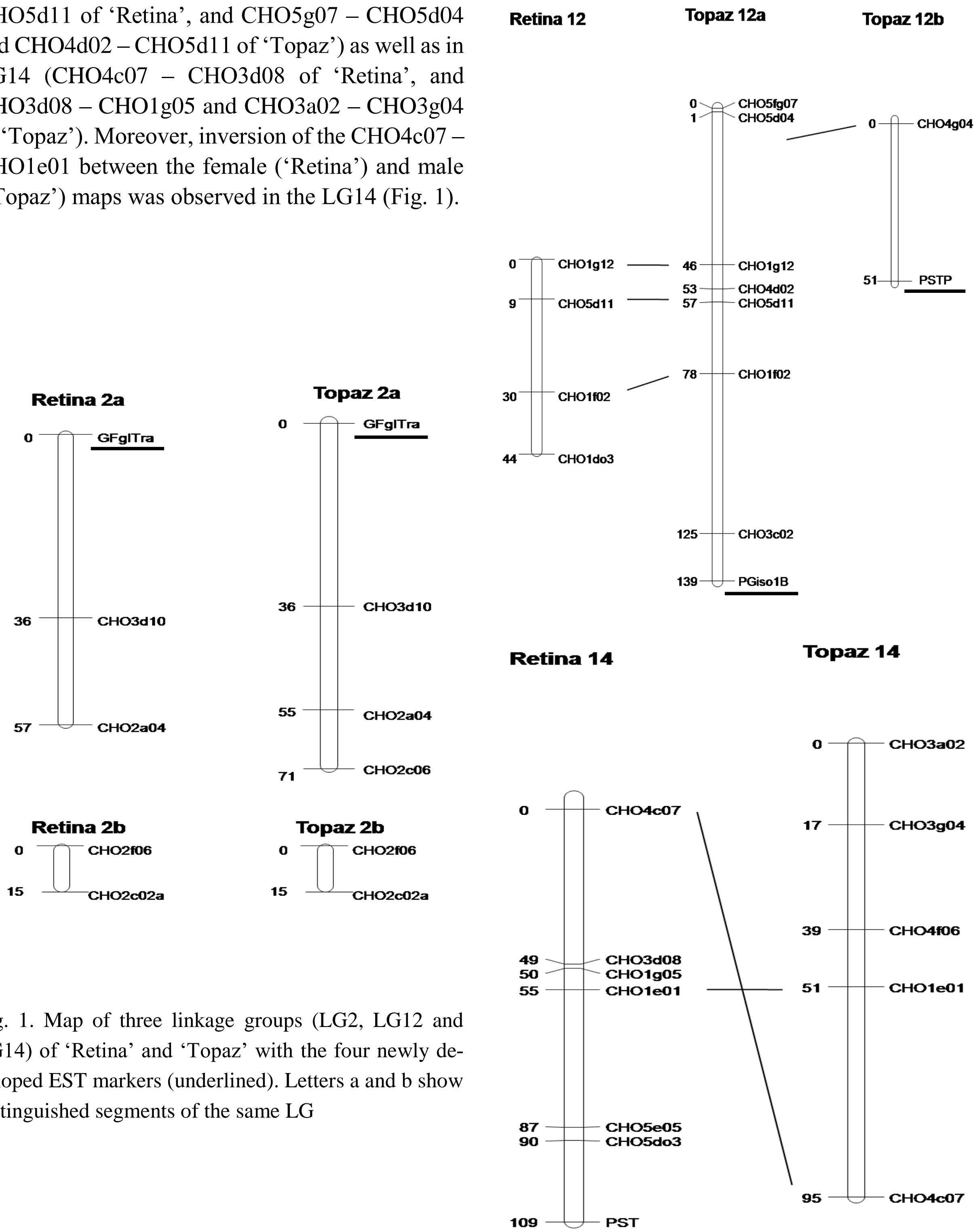

Fig. 1. Map of three linkage groups (LG2, LG12 and LG14) of 'Retina' and 'Topaz' with the four newly developed EST markers (underlined). Letters a and b show distinguished segments of the same LG

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

Table 2. Colinearity of LG2, LG12 and LG14 between ‘Retina’, ‘Topaz’, ’Fiesta’, ‘Discovery’, ‘Ralls Janet’ and ’Delicious’

Name of the marker pairs	Genetic distance between markers (cM)					
	LG 2					
	Retina	Topaz	Fiesta	Discovery	R. Janet	Delicious
GFglTra →CHO3d10	30	36	–	–		
GFglTra → CHO2a04	57	55	–	–		
CHO2f06 → CHO2c02a	15	15	4.0	5.3	6	6
CHO3d10 → CHO2a04	27	19	2.4	–		
CHO2a04 → CHO2c06	–	16^{inv}	3.9	–	3	1
CHO2CO6 → CHO3d10	–	–	1.5	4.6		
CHO3d10 → CHO2b10	–	–	1.7	–		
CHO2b10 → CHO2a04	–	–	0.7	–		
CHO2c06 → CHO3d10	–	–	18.1	24.9		
	LG 12					
	Retina	Topaz	Fiesta	Discovery	R. Janet	Delicious
CHO1g12 → CHO5d11	9^{inv}	11^{inv}	12.6	9.5		
CHO5d11 → CHO1f02	21	21	24.7	21.6		
CHO1f02 → CHO1d03	14	–	–	33.7		
CHO5g07 → CHO5d04	–	1	20.7	18.3		
CHO5d04 → CHO1g12	–	45	32.5	31.9		
CHO1g12 → CHO4d02	–	7	7.9	6.6		
CHO4d02 → CHO5d11	–	4^{inv}	20.5	17.1		
CHO5d11 → CHO3c02	–	68	–	39.6		
CHO3c02 → PGiso1B	–	14	–	–		
CHO4g04 → PSTP	–	51	–	–		
CHO3c02 → CHO1b12	–	–	–	18.4		
	LG 14					
	Retina	Topaz	Fiesta	Discovery	R. Janet	Delicious
CHO4c07 → CHO3d08	36	–	13.3	8.5		
CHO3d08 → CHO1g05	1	–	1.7	0.001		
CHO1g05 → CHO1e01	5	–	0.7	–		
CHO1g05 → CHO5e05	37	–	5.8	4.3		17
CHO1e01 → CHO5e05	32	–	5.1	–		
CHO5e05 → CHO5d03	3	–	6.5	8.6	13	4
CHO5d03 → CHO1g05	40	–	12.3	12.3		19
CHO5d03 → PST	19	–	–	–		
CHO3g04 → CHO3a02	–	17^{inv}	3.8	5.5		
CHO4f06 → CHO3g04	–	22^{inv}	8.5	5.5		
CHO4f06 → CHO1e01	–	12	3.1	–		
CHO1e01 → CHO4c07	–	44	8.5	–		

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

EST markers

PCR products of each of the seven genes were monomorphic between ‘Retina’ and ‘Topaz’. Digestion of the amplicons with *Hae*III resulted in generation of polymorphic fragments (120-590 bp) for *GFglyTra*, *PSTP*, *PST*, *PGiso1B* and *DHAR*. SSCP analysis and sequencing allowed for the identification of SNPs in *UDPglTra* (adenine : thymine, position 235) and *UDP6Deh* (adenine : cytosine, position 113).

Four of the SCAR markers were mapped as follows: GFglTra on LG2 (both cvs) PGiso1B and PST on LG12 (‘Topaz’) and PSTP on LG14 (‘Retina’) (Fig. 1). No SNP-based markers were located on the map.

DISCUSSION

Genetic maps play important role in modern agriculture due to their usefulness in marker-assisted crop improvement and gene introgression as well as in assessment of interactions between genes (Patocchi et al. 1999a, b). Each newly developed marker increases the knowledge about the genomes and practical significance of the map. Transfer of markers became useful and reliable for comparative mapping and colinearity assessment (Pierantoni et al. 2004). However, the efficiency of markers transferability is dependent on the genotype (Lewers et al. 2005, Varshney et al. 2005) and can be quite unsuccessful between distant genera (Gasic et al. 2009). It means that application of markers for other populations than originally described as a marker source always needs validation (Liebhard & Gessler 2000).

Our results demonstrate that 27 SSR markers of three linkage groups localised on ‘Fiesta’ and ‘Discovery’ maps (Liebhard et al. 2002, 2003, Silfverberg-Dilworth et al. 2006) are also present in ‘Retina’ and ‘Topaz’, cultivars that are characterised by high phenotypic diversity. The summer cultivar ‘Retina’ was developed in 1982 in Dresden-Pillnitz as a lineal offspring of ‘Apollo’ and clone BX 44/2. It is characterised by low firmness, medium size fruits, medium-high sweetness and perfumed flavour. The cultivar ‘Topaz’ was released in the Czech Republic in 1984 as a descendent of ‘Rubin’ (‘Lord Lambourne’ × ‘Golden Delicious’) and ‘Vanda’ (‘Jolana’ × ‘Lord Lambourne’). It is a middle-late cultivar with medium-large fruits having fairly sharp flavour and medium/low sugar content (Kruczyńska 2008).

The efficiency of our intra-species SSR transfer was relatively high (85%), similarly to the results of Gianfranceschi et al. (1998) who transferred markers from ‘Florina’ to ‘Iduna’ and A679/2 (in a success rate of 75%). The difference in SSR distance observed between the reference and ‘Retina’ × ‘Topaz’ maps could be consequence of the small number of progeny in our analysis. Small size of population results in detection of fewer recombination events, and thus in lower frequency of recombination and smaller map distances. In addition, it is quite possible that recombination frequencies between various loci could be different in various cultivars due to the impact of various genetic backgrounds. Differences in the order and the location of the loci can be also caused by inversions and translocations (Liebhard & Gessler 2000). Some rearrangement of markers in small regions of apple maps, indicated as single inversion events caused by local inconsistency in marker order, was reported by other authors too, and was explained as a result of differences in recombination frequencies between the parents of the mapping populations (Silfverberg-Dilworth et al. 2006, Igarashi et al. 2008, N’Diaye et al. 2008). The presence of many rearrangements detected in other *Rosaceous* species confirmed this theory (Klagges et al. 2013).

Comparative mapping is the manner to determine the level of colinearity of the genome of genetically distant plants (Han & Korban 2008) and predicts the location of genes coding an important trait in another species (Frary et al. 2008, Velasco et al. 2010).

On the basis of comparative SSR map of three LGs we determined the location of unmapped (until now) ETSs, which are associated with sugar and ascorbic acid metabolism. Two alleles of these ESTs were mapped in ‘Retina’ and three in ‘Topaz’. All mapped markers were developed as CAPS. Mapping of SNPs in the *UDP6Deh* and the *UDPglTra* sequences was not successful despite their identification in the genome of both analysed parental forms. In general, SNP markers are known

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

to have low level of transferability (Antanaviciute et al. 2012). It is also possible that these unmapped SNPs, as well as the CAPS-derived marker of *DHAR* gene were transferred during evolution of 'Retina' and 'Topaz' on genome segments which haven't been mapped by us.

REFERENCES

Aldrich J., Cullis C.A. 1993. RAPD analysis in flax: optimization of yield and reproducibility using KlenTaq 1 DNA polymerase, Chelex 100, and gel purification of genomic DNA. Plant Mol. Biol. Rep. 11: 128-141.

Antanaviciute L., Fernández-Fernández F., Jansen J., Banchi E., Evans K.M., Viola R. et al. 2012. Development of a dense SNP-based linkage map of apple rootstock progeny using the *Malus infinium* whole genome genotyping array. Genomics 13: 203. DOI: 10.1186/1471-2164-13-203.

Conner P.J., Brown S.K., Weeden N.F. 1997. Randomly amplified polymorphic DNA-based genetic linkage maps of tree apple cultivars. J. Amer. Soc. Hort. Sci. 122(3): 350-359.

FAOSTAT 2011. www.faostat.fao.org

Frary A., Doganlar S., Ratnaparkhe M.B. 2008. Comparative mapping. In: Kole C., Abbott A.G. (Eds.), Principles and practices of plant genomics, vol. 1. Genome mapping. Science Publishers, USA, pp. 205-228.

Gasic K., Han Y., Kertbundit S., Shulaev V., Iezzoni A.F., Stover E.W. et al. 2009. Characteristics and transferability of new apple EST-derived SSRs to other Rosaceae species. Mol. Breed. 23: 397-411. DOI: 10.1007/s11032-008-9243-x.

Gianfranceschi L., Seglias N., Tarchini R., Komjanc M., Gessler C. 1998. Simple sequence repeats for the genetic analysis of apple. Theor. Appl. Genet. 96: 1069-1076.

Han Y., Korban S.S. 2008. An overview of the apple genome through BAC end sequence analysis. Plant Mol. Biol. 67(6): 581-588. DOI: 10.1007/s11103-008-9321-9.

Han Y., Zheng D., Vimolmangkang S., Khan M.A., Beever J.E., Korban S.S. 2011. Integration of physical and genetic maps in apple confirms whole-genome and segmental duplications in the apple genome. J. Exp. Bot. 62(14): 5117-5130. DOI: 10.1093/jxb.err215.

Hemmat M., Weeden N.F., Manganaris A.G., Lawson D.M. 1994. Molecular marker linkage map for apple. J. Hered. 85: 4-11.

Igarashi M., Abe Y., Hatsuyama Y., Ueda T., Fukasawa-Akada T., Kon T., Kudo T., Sato T., Suzuki M. 2008. Linkage maps of the apple (*Malus* × *domestica* Borkh.) cultivars 'Ralls Janet' and 'Delicious' include newly developed EST markers. Mol. Breed. 22: 95-118. DOI: 10.1007/s11032-008-9159-5.

Keller-Przybyłkowicz S., Korbin M. 2013. The history of mapping the apple genome. Folia Hort. 25(2): 161-168. DOI: 10.2478/fhort-2013-0018.

Kenis K., Keulemans J. 2005. Genetic linkage maps of two apple cultivars (*Malus* × *domestica* Borkh.) based on AFLP and microsatellite markers. Mol. Breed. 15: 205-219. DOI: 10.1007/s11032-004-5592-2.

Khan M.A., Han Y., Zhao Y.F., Troggio M., Korban S.S. 2012. A multi-population consensus genetic map reveals inconsistent marker order among maps likely attributed to structural variation in the apple genome. PLOS ONE 7(11): 1-12. DOI: 10.1371/journal.pone.0047864.

Klagges C., Campoy J.A., Quero-Garcia J., Gratacos E., Silva H., Rosyara U.R. et al. 2013. Construction and comparative analyses of highly dense linkage maps of two sweet cherry intra-specific progenies of commercial cultivars. PLOS ONE 8(1): 1-12. DOI: 10.1371/journal.pone.0054743.

Korban S.S., Tartarini S. 2009. Apple structural genomics. In: Folta K.M., Gardiner S. (Eds.), Genetics and genomics of Rosaceae, vol. 6. Springer, pp. 85-119.

Kruczyńska D. 2008. Nowe odmiany jabłoni. Hortpress, 211 p. [in Polish]

Liebhard R., Gianfranceschi L., Koller B., Ryder C.D., Tarchini R., van de Weg E., Gessler C. 2002. Development and characterization of 140 new microsatellites in apple (*Malus* × *domestica* Borkh.). Mol. Breed. 10: 217-241. DOI: 10.1023/A:1020525906332.

Liebhard R., Koller B., Gianfranceschi L., Gessler C. 2003. Creating a saturated reference map for the apple (*Malus* × *domestica* Borkh.) genome. Theor. Appl. Genet. 106: 1497-1508. DOI: 10.1007/s00122-003-1209-0.

Liebhard R., Gessler C. 2000. Possible errors in genome mapping. IOBC/WPRS 23(12): 127-135.

Lewers K.S., Styan S.M.N., Hokanson S.C. 2005. Strawberry gen-Bank-derived and genomic simple sequence repeat (SSR) markers and their utility with strawberry, blackberry, and red and black raspberry. J. Amer. Soc. Hort. Sci. 130(1): 102-115. DOI: 10.1186/1471-2229-8-69.

Maliepaard C., Aston F.H., van Arkel G., Brown L.M., Chevereau E., Dunemann F. et al. 1998. Aligning

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM

male and female linkage maps of apple (*Malus pumila* Mill.) using multi-allelic markers. Theor. Appl. Genet. 97: 60-73.

Micheletti D., Troggio M., Salamini F., Viola R., Velasco R., Salvi S. 2011. On the evolutionary history of the domesticated apple. Nat. Genet. 43: 1044-1045. DOI: 10.1038/ng.983.

N'Diaye A., van de Weg W.E., Kodde L.P., Koller B., Dunemann F., Thirmann M. et al. 2008. Construction of an integrated consensus map of the apple genome based on four mapping populations. Tree Genet. Genomes 4: 727-743. DOI: 10.1007/s11295-008-0146-0.

van Ooijen J.W., Voorrips R.E. 2001. JoinMap 3.0. Software for the calculation of genetic linkage maps. Plant Research International, Wageningen, Netherlands, 78 p.

Patocchi A., Vinatzer B.A., Gianfranceschi L., Tartarini S., Zhang H.B., Sansavini S., Gessler C. 1999a. Construction of a 550 kb BAC contig spanning the genomic region containing the apple scab resistance gene *Vf*. Mol. Gen. Genet. 262: 884-891.

Patocchi A., Gianfranceschi L., Gessler C. 1999 b. Towards the map-based cloning of *Vf*: fine and physical mapping of the *Vf* Region. Theor. Appl. Genet. 99: 1012-1017.

Pierantoni L., Cho K.H., Shin I.S., Chiodini R., Tartarini S., Dondini S.J., Sansavini S. 2004. Characterization and transferability of apple SSRs to two European pear F_1 populations. Theor. Appl. Genet. 109: 1519-1524. DOI: 10.1007/s00122-004-1775-9.

Sargent D.J., Rys A., Nier S., Simpson D.W., Tobutt K.R. 2007. The development and mapping of functional markers in Fragaria and their transferability and potential for mapping in other genera. Theor. Appl. Genet. 114: 373-384. DOI: 10.1007/s00122-006-0441-9.

Schouten H.J., van de Weg W.E., Carling J., Khan A.S., Mckay S.J., van Kaauwen M.P.W. et al. 2012. Diversity arrays technology (DArT) markers in apple for genetic linkage maps. Mol. Breed. 29: 645-660. DOI: 10.1007/s11032-011-9579-5.

Silfverberg-Dilworth E., Matasci C.L., van de Weg W.E., van Kaauwen M.P.W., Walser M., Kodde L.P. et al. 2006. Microsatellite markers spanning the apple (*Malus* × *domestica* Borkh.) genome. Tree Genet. Genomes 2: 202-224. DOI: 10.1007/s11295-006-0045-1.

Shulaev V., Korban S.S., Sosinski B., Abbot A.G., Aldwinckle H.S., Folta K.M. et al. 2008. Multiple models for Rosaceae genomics. Plant Physiol. 147: 985-1003. DOI: 10.1104/pp.107.115618.

Soglio V., Costa F., Molthoff J.W., Mieke W., Weemen-Hendriks J., Schouten H.J., Gianfranceschi L. 2009. Transcription analysis of apple fruit development using cDNA microarrays. Tree Genet. Genomes 5(4): 685-698. DOI: 10.1007/s11295-009-0219-8.

Varshney R.K., Sigmund R., Borner A., Korzun V., Stein N., Sorrells M.E., Langride P., Graner A. 2005. Interspecific transferability and comparative mapping of barley EST-SSR markers in wheat, rye and rice. Plant Sci. 168: 195-202. DOI: 10.1016/j.plantsci.2004.08.001.

Velasco R., Zharkikh A., Affourtit J., Dhingra A., Cestaro A., Kalyanaraman A. et al. 2010. The genome of the domesticated apple (*Malus* × *domestica* Borkh.). Nat. Genet. 42(10): 833-841. DOI: 10.1038/ng.654.

Voorrips R. 2002. MapChart. Software for the graphical presentation of Linkage maps and QTLs. J. Hered. 93: 77. DOI: 10.1093/jhered/93.1.77.

www.hidras.unimi.it

Brought to you by | Uniwersytet Przyrodniczy w Poznaniu
Authenticated
Download Date | 2/23/18 11:33 AM