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APPLICATION OF MOLECULAR MARKERS IN APPLE BREEDING

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Apple is economically the most important species of genus *Malus* Miller. In respect of production, trade and consumption, it ranks first among deciduous fruit and third on a global scale among all fruit species. Apple breeding is carried out on a large scale in several scientific institutes throughout the world. Due to this activity, apple is a fruit species with the highest number of described monogenic traits; 76 genes, encoding morphological traits, pest and disease resistance, as well as 69 genes encoding enzymes. The development of molecular markers (RFLPs, AFLPs, SCARs and SSRs) has allowed the mapping of the apple genome

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and the development of several saturated genetic maps, to which genes controlling important traits are assigned. Markers flanking these genes not only play an important role in selecting parental combinations and seedlings with positive traits, but they are also particularly important in detecting recessive traits, such as seedless fruit. In addition they enable pre-selection for polygenic quantitative traits. In recent years, particular attention has been paid to biochemical and physiological processes involved in the pathway of important traits e.g., ripening and the storage capability of apple fruit.

Key words: apple, marker, genetic map, QTL

INTRODUCTION

Apple (*Malus x domestica* Borkh.) ranks third in terms of total global production of all fruit crops, with just over 60 million tonnes in 2005 and an export value exceeding 6.5 billion US dollars. The production quantity even increased by 27% between 1995 and 2006 (http://faostat.fao.org). Apple breeding is carried out on a large scale in several scientific institutes throughout the world. More than 10,000 cultivars have been named and released. Breeders worldwide intensively develop new selections annually, though only a few dozen types are widely produced in commerce today (JANICK *et al*., 1996; HAMPSON and KEMP, 2003). Approaches to the improvement of apple breeding have changed markedly in the past two decades. This review will focus on the genetic improvement of apple, for which the identification and use of molecular markers and marker-assisted selection with genetic maps for important cultivars and advanced selections, have been used.

Apple genetic maps

The first genetic map of apple was published in 1994 from the cross 'Rome Beauty' x 'White Angel' (HEMMAT *et al*., 1994) that combined the isoenzyme, RFLP (fragment length polymorphisms) and RAPD (random amplified polymorphic DNA) markers distributed over 21 and 24 linkage groups (LG), respectively. CONNER *et al*. (1997) developed the second set of more saturated maps for 'Wijcik McIntosh' and advanced scab-resistant selections from the Cornell breeding programme (NY 75441-67 and NY 75441-58). The number of linkage groups has been reduced (19, 16 and 18, respectively) closer to the haploid chromosome number of apple ($n = 17$).

Highly polymorphic and transferable markers called microsatellites (simple sequence repeats or SSRs) have been developed for apple by several research groups. The use of these markers, a number of isoenzymes, RFLPs, RAPDs, AFLPs (amplified fragment length polymorphisms) and SCARs (sequence characterised amplified regions) in the population of 152 seedlings, allowed the construction of linkage maps with 17 linkage groups for the cultivars 'Prima' and 'Fiesta' (MALIEPAARD *et al*., 1998). Map positions were provided for resistance genes to *Venturia inaequalis* (Cooke.), Wint. and *Disaphis devecta* Wlk. (*Vf* and Sd_1, respectively), for the fruit acidity gene *Ma* and for the self-incompatibility locus *S*.

Table 1. Genetic maps of apple

Cross	Pop. size	Marker Type						References	Traits
		Isoenzyme	RFLP	RAPD	AFLP	SSR	Others		
'Rome Beauty' x 'White Angel'	56	34	8	367	-	-	-	HEMMAT *et al*., 1994	*Pl-w*
'Wijcik McIntosh' x NY 75441-67	114	6	-	138	-	-	-	CONNER *et al*., 1997	*Rf*, *Vf*, *Co*, *Ma*
'Wijcik McIntosh' x NY 75441-58	172	6	-	266	-	-	-	CONNER *et al*., 1997	
'Prima' x 'Fiesta'	152	17	124	133	9	10	SCAR - 1	MALIEPAARD *et al*., 1998	*Vf*, *Sd-1*, *Ma*, *S*
'Fiesta' x 'Discovery'	112	-	-	217	-	118	-	LIEBHARD *et al*., 2002	
'Fiesta' x 'Discovery'	267	-	-	235	475	129	SCARs – 1	LIEBHARD *et al*., 2003	
'Fiesta' x 'Discovery'	44 (subset of 112)	-	-	-	-	-	ARGHs - 18	BALDI *et al*., 2004	ARGHs
'Fiesta' x 'Discovery'	44 (subset of 267)	-	-	-	-	156	-	SILFVERBERG–DILWORTH *et al*., 2006	
'Discovery' x TNR10-8	149	13	-	-	102	62	RGHs - 22	CALENGE *et al*., 2004; 2005	*Vg*, scab QTL, RGHs
'Telamon' x 'Braeburn'	257	-	-	-	463	21	-	KENIS and KEULEMANS, 2005	For QTL analysis grow habit and fruit quality
'Fiesta' x 'Totem'	85	-	-	-	-	247	SCARs – 4; 8 known-function genes	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008	*Vf*, *Pl-2*, *Co*, *Rt*, *Gfc*

Additional apple maps have been published in recent years (Tab. 1). The progeny from a cross 'Discovery' x TN10-8 was used to produce apple map by researchers at INRA Angers, France; 'Durello di Forli' x 'Fiesta' progeny was investigated at the University of Bologna in Italy, in partnership with the NAGREF in Naoussa, Greece; the cross 'Prima' x 'Discovery' was researched at BAZ in Ahrensburg, Germany (BROWN, 2003). The cross 'Fiesta' x 'Discovery' was studied by LIEBHARD *et al*. (2003) whereby the map included 475 AFLPs, 235 RAPDs and 130 STS markers to which 157 SSRs were added by SILFVERBERG-DILWORTH *et al*. (2006). FERNÁNDEZ-FERNÁNDEZ *et al*. (2008) described the development of a map of 259 STS loci - 247 SSRs, 4 SCARs and 8 known-function genes, as well as 5 genes

for agronomic traits (scab resistance - *Vf*, mildew resistance - *Pl-2*, columnar growth habit - *Co*, red tissues - *Rt* and green flesh background colour - *Gfc*) in the interspecific F_1 apple progeny, from the cross 'Fiesta' (cultivated) x 'Totem' (ornamental). Ninety SSR loci and three genes including *ETR1* (ethylene receptor), *Rt* and *Gfc* were mapped for the first time in apple.

Saturated and high-density genetic linkage maps are very useful in both fundamental and applied genetic research. These maps should be taken as references for future mapping in apple, as the large number of SSR markers can be transferred to any apple cultivar and can provide a frame which can be quickly saturated with e.g., AFLPs (LIEBHARD *et al*., 2003). The maps allow studies of the genome structure, the localisation of genes of interest, the identification of quantitative trait loci (QTLs) and enable marker-assisted selection (MAS).

Markers linked to monogenic traits in apple

Apple is a fruit species with the highest number of monogenic traits described; 76 genes encoding morphological traits, pest and disease resistance as well as 69 genes encoding enzymes (ALSTON *et al*., 2000). Most markers identified so far are linked to major gene traits, i.e. mainly for resistance to economically significant pests and diseases of apple, as most breeding programmes aim to develop resistant cultivars. Identification of genetic markers for resistance genes (e.g. apple scab, powdery mildew, and rosy and woolly apple aphid) has been simplified, as many of these traits are controlled by major genes. The mapping of resistance genes loci shows that they are often linked or residing in clusters (BUS *et al*., 2005a; XU and KORBAN, 2002). The primary use of genetic markers in resistance breeding has been in the application of the MAS for pyramiding resistance genes in seedling progenies, as well as for germplasm screening for sources of resistance.

In apple the best studied are scab resistance genes as scab is economically very important and it is relatively easy to identify markers for major genes. Fifteen apple scab resistance genes have been identified and twelve mapped so far. Table 2 presents the identified genes with LG groups, within which they were mapped, as well as the markers linked to these genes and could be applied for MAS. The new nomenclature of the apple scab resistance genes was proposed by BUS *et al*. (2009), e.g. *Rvi1*, *Rvi2*, *Rvi4*, *Rvi5*, *Rvi6*, *Rvi10*, *Rvi11*, *Rvi12*, *Rvi13* and *Rvi15*, respectively *Vg*, *Vh2*, *Vh4*, *Vm*, *Vf*, *Va*, *Vbj*, *Vb*, *Vd* and *Vr2* according to the old apple scab resistance gene nomenclature; (please note that in the manuscript we use the old nomenclature). The most widely used is *Vf* from *Malus floribunda*, therefore almost all commercial apple scab resistant cultivars carry this gene. In the meantime, *V. inaequalis* strains able to overcome the *Vf* resistance (PARISI *et al*., 2006) have been detected. Other genes, e.g. *Va*, *Vbj*, *Vb* and *Vm* have been known for half a century, but until now only two cultivars that carry one of these genes have been released ('Murray' and 'Rouville' carrying *Vm*). More recently, other major scab resistance genes e.g. *Vg*, *Vh2*, *Vh4*, *Vd* and *Vr2* have been identified and mapped, and two cultivars carrying these genes have been released ('Regia' carrying *Vh4*; 'Durello di Forlì', carrying *Vd*) (PATOCCHI *et al*., 2009). Thus, molecular markers for nearly all

major resistance genes, which can be alternatives to the *Vf* gene and suitable for MAS, are available for breeding new cultivars with durable resistance. One of the strategies that can be used is the pyramiding of several major genes in an individual plant. To facilitate breeding of new cultivars with pyramided resistance genes, PATOCCHI *et al*. (2009) presented the current status of an initiative to monitor the geographic distribution of *V. inaequalis* virulences and a proposal to standardise reporting of the size of the SSR marker alleles in coupling with all new and already reported apple scab resistance genes.

Another important disease of apple is powdery mildew caused by *Podosphaera leucotricha*, for which several sources of resistance are known. Seven powdery mildew resistance genes have been identified and four have been mapped so far. Mapping of resistance to *P. leucotricha* is much more time consuming than the mapping of *V. inaequalis* resistance, since phenotypic screening of seedling populations takes several years (GARDINER *et al*., 2007). Major genes such as *Pl-1* and *Pl-2* from *M. robusta* and *M. zumi* respectively have been widely used in apple breeding programmes. Other major genes with increasing importance are *Pl-w* from 'White Angel' (BATLLE and ALSTON, 1996), *Pl-d* from D12 clone (VISSER and VERHAEGH, 1980) and *Pl-m* from Mildew Immune Selection (DAYTON, 1977). The existence of different physiological races of *P. leucotricha* has been demonstrated, but the putative race-specificity of powdery mildew resistance genes remain to be understood (DUNEMANN *et al*., 2007). It has been recognised that durable powdery mildew resistance can probably be most efficiently achieved by the pyramiding of different monogenic resistances. Several molecular marker approaches have been performed so far. Table 2 gives identified *Pl* genes with LG groups and the markers which can be applied for MAS.

The rosy apple aphid (*Dysaphis plantaginea*), rosy leaf curling aphid (*Dysaphis devecta*) and woolly apple aphid (*Eriosoma lanigerum*) are widespread pest insects that reduce the growth of leaves, fruits and shoots in apple. Aphid control in apple orchards generally involves insecticides, but possible alternatives such as growing resistant cultivars are needed for more sustainable integrated pest management. Five woolly apple aphid resistance genes (*Er-1*, *Er-2*, *Er-3*, *Er-m*, *Er-l*; BUS *et al*., 2008; GARDINER *et al*., 2001; GARDINER *et al*., 2007), three rosy leaf curling aphid resistance genes (*Sd-1*, *Sd-2*, *Sd-3*; *Sd-1* and *Sd-2* are tightly linked and probably allelic; CEVIK and KING, 2002) and one rosy apple aphid resistant gene (*Sm-h*, ALSTON and BRIGGS, 1970) have been identified so far. Table 2 presents major genes carrying resistance to these pests, with LG groups and markers which can be applied for MAS. The use of molecular markers closely linked to aphid resistance genes is a powerful selection tool that accelerates the breeding of new cultivars with more durable resistance, containing two or more pyramided resistance genes.

Table 2. Major genes for resistance in apple

Gene/LG	Progeny/Reference	Markers/distance from genes in cM	*Malus* source/Reference
Apple scab (*Venturia inaequalis*)			
Va/LG1	'Fortune' x PRI 1841-11 and NY 489 x PRI 1841-11 (HEMMAT *et al*., 2003)	SCAR: $P136_{700}$/n.d., 18% r.f.	'Antonovka PI172623' (HOUGH *et al*., 1970)
Vb/LG12	'Golden Delicious' x 'Hansen's baccata #2' (ERDIN *et al*., 2006)	Microsatellites: Hi02d05/8 and Hi07f01/14	'Hansen's baccata #2' (DAYTON and WILLIAMS, 1968)
Vc			'Cathay' (KORBAN and CHEN, 1992)
Vbj/LG2	A722-7 x 'Golden Delicious' (GYGAX *et al*., 2004)	SCAR: $OPZ13_{773}$/0	*Malus baccata jackii* (DAYTON and WILLIAMS, 1968)
Vd/LG10	'Durello di Forli' x 'Fiesta' (TARTARINI *et al*., 2004)	RAPD: OPAF07880bp/2.0 Microsatellite: G63Tru91a/2.0	'Durello di Forli' (TARTARINI *et al*., 2004)
Vd3/LG1	1980-015-25 x 1973-001-041 (SORIANO *et al*., 2009)	Microsatellite: CH-V$f1_{129}$/1	Resistant selection 1980-015-25 (SORIANO *et al*., 2009)
Vf/LG1	16 crosses (HUARACHA *et al*., 2004)	SCARs: ACS3/0.1; ACS7/0; ACS9/0	*Malus floribunda 821* (HOUGH *et al*., 1953)
Vfh			*Malus floribunda 821* (BÉNAOUF and PARISI, 2000)
Vg/LG12	'Prima' x 'Fiesta' (DUREL *et al*., 1999)	RFLP: MC105/3.0	'Golden Delicious' (BÉNAOUF *et al*., 1997)
Vh8/LG2	'Royal Gala' x *Malus sieversii* W193B (BUS *et al*., 2005a)	SCARs: $OPL19_{433}$/1.3; $OPB18_{628}$/4.3; OPB18799 (Vh8 SCAR)/5.1; Microsatellite: $CH3d01_{124}$/18.5	*Malus sieversii* W193B (BUS *et al*., 2005a)
Vj			'Jonsib' (KORBAN and CHEN, 1992)
Vm/LG17	'Golden Delicious' x 'Murray' (PATOCCHI *et al*., 2005)	Microsatellite: Hi07h02/0	*Malus micromalus* 245-38 (DAYTON and WILLIAMS, 1970)
Vh2/LG2	'Golden Delicious' x TSR34T15 (BUS *et al*., 2000)	SCAR: $OPL19_{433}$/n.d., 8.2% r.f.	Russian apple R12740-7A (BUS *et al*., 2005b)
Vr2/LG2	GMAL 2473 x 'Idared'	AFLPs: $EA35MA41_{262}$/0	Russian apple R12740-7A

	(PATOCCHI *et al*., 2004)		(PATOCCHI *et al*., 2004)
Vh4/LG2	'Empire' x R12740-7A (HEMMAT *et al*., 2002)	SCAR: $S22_{1300}$/n.d., 9.8% r.f.	Russian apple R12740-7A (BUS *et al*., 2005b)
Powdery mildew (*Podosphaera leucotricha*)			
Pl-1/LG12	'Idared' x Robust 5; 'Idared' x 78/18-4 (DUNEMANN *et al*., 2007)	SCAR: $AT20_{450}$	*Malus x robusta* OP3762 (KNIGHT and ALSTON, 1968)
Pl-2/LG11	'Fiesta' x 'Totem' (FERNÁNDEZ–FERNÁNDEZ *et al*., 2008)		*Malus x zumi* OP3752 (KING and ALSTON, 1968)
Pl-8			*Malus sargenti* 843 (KORBAN and DAYTON, 1983)
Pl-d/LG12	'Fiesta' x A871-14 (JAMES *et al*., 2004)	Microsatellite: CH03c02/8.0	D12 (VISSER and VERHAEGH, 1980)
Pl-m	'Fuji' x MIS O.P. 93.051 G02-054 (GARDINER *et al*., 2003)	SCAR: $OPAC20_{1800}$/0.7	Mildew Immune Selection (DAYTON, 1977)
Pl-a	M9 x 'Aotea' (GARDINER *et al*., 2004)	$OPN18_{1000}$/11.5	'Aotea 1' (Taylor, 1981)
Pl-w/LG8	'Fiesta' x ('Gloster 69' x 'White Angel') (JAMES and EVANS, 2004)	Microsatellite: CH01e12/10 and CH05a02y/13	'White Angel' (BATLLE and ALSTON, 1996)
Aphids (*Eriosoma lanigerum*, *Dysaphis devesta*, *Dysaphis plantaginea*)			
Er-1/LG8	'Sciglo' x 'Northern Spy' (BUS *et al*., 2008)	SCAR: NZsc_O05/7.9	'Northen Spy' (KNIGHT *et al*., 1962)
Er-2/LG17	M9 x 'Robusta 5' (BUS *et al*., 2008)	SSR: NZms_EB145764/5.5	*Malus x robusta* (KING *et al*., 1991)
Er-3/LG8	M9 x 'Aotea 1' (BUS *et al*., 2008)	SNP: NZsn_O05/4.1	'Aotea 1' (BUS *et al*., 2000)
Er-m	'Fuji' x MIS O.P. 93.051 G02-054 (GARDINER *et al*., 2007)	SCAR: $OPA04_{950}$/7 RAPD: $OPZ20_{1200}$/6	Seedling 93.051 G07-062
Er-l	'Prima' x Longfield O.P. 93.043 G07-062 (GARDINER *et al*., 2001)	SCAR: $OPAD01_{630}$/13	Seedling 93.043 G07-062
Sd-1/LG7	Resistant cultivars; susceptible cultivars; 6 segregating families (CEVIK and KING, 2002)	*Sd-1* located in 1.3 cM interval between $2B12a_{196}$ and SdSSRa	'Cox's Orange Pippin' (ALSTON and BRIGGS, 1968)
Sd-2/LG7	'Double Red Northern Spy' x 'Totem'	SCAR: $2B12a_{196}$/0 Microsatellite: SdSSRa/0	'Northen Spy' (ALSTON and BRIGGS,

	(CEVIK and KING, 2002)	1977)
Sd-3		*Malus x robusta* OP MAL59/9 (ALSTON and BRIGGS, 1977)
Sm-h		*Malus x robusta* OP MAL59/9 (ALSTON and BRIGGS, 1970)

Table 3. Mapping of major genes which are not involved in resistance in apple

Gene	**Progeny**	**Linkage group**	**Markers/distance from genes in cM**	**Reference**
S	'Prima' x 'Fiesta' 'Fiesta' x 'Totem'	LG17	Izoenzim: AAT-1/<1; RFLP: MC038b/1 Gene specific marker	MALIEPAARD *et al*., 1998 FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
Rs	'Rome Beauty' x 'White Angel'	LG17	RAPD: P124e/n.d.	WEEDEN *et al*., 1994
Rf	'Wijcik McIntosh' x NY75441-58	LG9	RAPD: $BC226_{1175}$/0	CONNER *et al*., 1997
Rt	'Fiesta' x 'Totem'	LG9	Gene specific marker	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
Gfc	'Fiesta' x 'Totem'	LG9	Gene specific marker	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
Ma	'Prima' x 'Fiesta'	LG16	RAPD: $OPT16_{1000}$/0	MALIEPAARD *et al*., 1998
Co	'Fiesta' x 'Totem'	LG10	SSR:CH03d11/3	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
Subfamilies I and IV *Mal d 1* (7 genes)	'Prima' x 'Fiesta' 'Jonathan' x 'Prima'	LG13	Gene specific markers	GAO *et al*., 2005b
Subfamilies II and III *Mal d 1* (9 genes)	'Prima' x 'Fiesta' 'Jonathan' x 'Prima'	LG16	Gene specific markers	GAO *et al*., 2005b
Mal d 1.05	'Prima' x 'Fiesta' 'Jonathan' x 'Prima'	LG6	Gene specific marker	GAO *et al*., 2005b
Mal d 2.01A	'Prima' x 'Fiesta'	LG9	Gene specific marker	GAO *et al*., 2005c

Mal d 3.01	'Jonathan' x 'Prima'	LG12	SNP: Mal d 3.0101a-JO/0	GAO *et al*., 2005a
Mal d 3.02	'Prima' x 'Fiesta' 'Jonathan' x 'Prima'	LG4	SNP: Mal d 3.0201c-PM/0	GAO *et al*., 2005a
Mal d 4.01	'Prima' x 'Fiesta'	LG9	Gene specific marker	GAO *et al*., 2005c
Mal d 4.2A	'Prima' x 'Fiesta'	LG2	Gene specific marker	GAO *et al*., 2005c
Mal d 4.3A	'Prima' x 'Fiesta'	LG8	Gene specific marker	GAO *et al*., 2005c
ACS1	'Fiesta' x 'Totem'	LG15	Gene specific marker	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
ACO1	'Fiesta' x 'Totem'	LG10	Gene specific marker	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
ETR1	'Fiesta' x 'Totem'	LG15	Gene specific marker	FERNÁNDEZ–FERNÁNDEZ *et al*., 2008
Sl-1	6 progenies segregating for *Vf*	LG1	± 14 cM from *Vf*	GARDINER *et al*., 2007
Sl-2	6 progenies segregating for *Vf*	LG1	1 - 8 cM from *Vf*	GARDINER *et al*., 2007

The major genes that are not involved in resistance in apple are presented in Table 3. The following genes have been identified and mapped: self-incompatibility (S.,MALIEPAARD *et al*., 1998; FERNÁNDEZ–FERNÁNDEZ *et al*., 2008), rootsuckers (*Rs*, WEEDEN *et al*., 1994), fruit skin colour (*Rf*, CONNER *et al*., 1997), red tissues (*Rt*, FERNÁNDEZ–FERNÁNDEZ *et al*., 2008), green flesh background colour (*Gfc*, FERNÁNDEZ–FERNÁNDEZ *et al*., 2008), fruit juice pH (*Ma*, MALIEPAARD *et al*., 1998), columnar habit (*Co*, FERNÁNDEZ–FERNÁNDEZ *et al*., 2008), fruit allergens (*Mal d*, GAO *et al*., 2005a,b,c), ethylene production (*ACS1*, *ACO1*, *ETR1*, MARIĆ, 2004; FERNÁNDEZ–FERNÁNDEZ *et al*., 2008; MARIĆ *et al*., 2009b) and sub-lethal genes (*Sl*, GARDINER *et al*., 2007).

Over the past few years, research has been focused on identifying functional markers, i.e. DNA sequences putatively involved in the expression of given traits. The functional marker approach became possible with the availability of DNA sequences in databases. Gene identification in other plants also helps to identify homologs in apple. For example, the genomic fragments of the genes involved in ethylene synthesis (*ACS1* and *ACO1*) and perception (*ETR1*) in apple have been amplified and allelic forms of these genes identified (SUNAKO *et al*., 1999; ORAGUZIE *et al*., 2004; COSTA *et al*., 2005; MARIĆ *et al*., 2005a,b; COLGAN *et al*., 2006; ZHU and BARRITT, 2008; MARIĆ *et al*., 2007; FERNÁNDEZ–FERNÁNDEZ *et al*., 2008; MARIĆ *et al*., 2009a). ALSTON *et al*. (2000) and BROWN (2003) summarized other traits under simple genetic control that could be investigated, such as dwarfing, pale green lethal, yellow leaf mottle, partial and full fruit russetting, double flowering and other resistances to diseases and pests that are amenable to study.

QTL identification and mapping in apple

Many important characters in apple are under polygenic control, e.g. duration of the juvenile period, cold hardiness, vigour, flowering season, ripening season, fruit size, shape and productivity, fruit colour, fruit flavour (JANICK *et al*., 1996). The ability to assess complex phenotypes at the seedling stage would greatly accelerate breeding of new apple cultivars. Genetic mapping of quantitative trait loci (QTLs) involves identifying and determining the degree of association between these traits and a set of genetic markers (GARDINER *et al*., 2007). A saturated genetic map covering the entire genome is essential for accurate QTL identification. If certain regions of the genome are not adequately covered by genetic markers, QTLs located in those regions will not be reliably mapped. The identification of QTLs linked to important traits in apple, such as disease resistance, tree growth, fruit quality, is still at an initial stage.

KING *et al*. (2000) carried out a quantitative genetic analysis of traits associated with fruit-flesh firmness using a population derived from the 'Prima' x 'Fiesta' cross. QTLs accounting for differing degrees of variation for firmness, stiffness and a number of sensory attributes were identified on seven linkage groups, with large effects on LG1, LG10 and LG16. Further work extended the range of mechanical measurements to include compression and wedge fracture tests (KING *et al*., 2001). The wedge fracture tests identified significant QTLs on LG16 and LG1. The QTL on LG16 was located in the same region as the QTL identified for certain sensory textural attributes, such as crispness and juiciness.

QTLs have been identified for apple scab resistance using recent genetic maps constructed in the following populations: 'Prima' x 'Fiesta' (DUREL *et al*., 2003), 'Fiesta' x 'Discovery' (LIEBHARD *et al*., 2003), 'Discovery' x TN10-8 (CALENGE *et al*., 2004). Four significant regions are identified on LG1, LG11, LG15 and LG17 (DUREL *et al*., 2003). Eight QTLs have been detected by LIEBHARD *et al*. (2003); six for leaf scab (LG6, LG7, LG10, LG11, LG12 and LG17) and two for fruit scab (LG15 and LG17). The strongest scab resistance QTL from 'Prima' x 'Fiesta' was identified on LG17 (DUREL *et al*., 2003), coinciding with scab resistance QTL detected by LIEBHARD *et al*. (2003). CALENGE *et al*. (2004) revealed three major QTLs on LG1, LG2 and LG17; the region identified on LG1 corresponds to the region around *Vf* which was identified by DUREL *et al*. (2003) as well.

Five QTLs for resistance to powdery mildew were identified in the F_1 progeny of the cross 'Idared' x U 211 (STANKIEWICZ-KOSYL *et al*., 2005). One of the QTL (LG12) explained 48–72% of the phenotypic variation and its effect was stable over the years. The apple powdery mildew resistance genes *Pl-1* (DUNEMANN *et al*., 2007) and *Pl-d* (JAMES *et al*., 2004), as well as apple scab resistance genes *Vb* (ERDIN *et al*., 2006) and *Vg* (DUREL *et al*., 1999) have already been mapped to LG12, suggesting the possibility of resistance QTL/gene clusters in this region.

CALENGE *et al*. (2005) identified QTLs for resistance to fire blight using two populations derived from the crosses between 'Prima' x 'Fiesta' and 'Fiesta' x 'Discovery'. One major and four minor QTLs were detected in both progenies, the QTL on LG7 explaining 34.3–46.6% of the resistance. KHAN *et al*. (2006), using a

different strain of *Erwinia amylovora* and a different 'Fiesta' x 'Discovery' progeny, confirmed the QTL for resistance on LG7 and demonstrated the stability of this QTL.

The QTL analysis to study the genetic control of growth traits in apple was performed by KENIS and KEULEMANS (2007). This was carried out on the progeny raised from a cross between 'Telamon' (columnar tree form) and 'Braeburn' (standard growth habit). A major cluster of QTLs was located in the *Co* gene region (LG10), confirming the major influence of this gene on tree architecture. These results are in agreement with CONNER *et al*. (1998).

CONCLUSION

Genetic markers can assist apple breeders to improve their breeding outcomes in several ways, from assessing genetic diversity of the germplasm, to cultivar protection. Major advantage of the use of markers in apple breeding are improving efficiency by enabling early selection for adult traits, simultaneous selection for multiple traits including resistance gene pyramiding and selection for traits that are expensive for phenotypic screening. The cost of MAS was identified as one of the main reasons why less than 50% of fruit and ornamental breeders used molecular markers in their programmes. According to published data, markers have been increasingly used for selection in apple breeding. New apple cultivars continue to be released by programmes worldwide. To increase selection efficiency and to reduce MAS cost in apple breeding, knowledge on the most useful phenotypic characters to select for is essential. Latest advances in apple genetics offer opportunities for cultivar improvements as never before.

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PRIMENA MOLEKULARNIH MARKERA U OPLEMENJIVANJU JABUKE

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I z v o d

Jabuka (*Malus x domestica* Borkh.) je ekonomski najznačajnija vrsta roda *Malus* Miller. Po proizvodnji, prometu i potrošnji zauzima prvo mesto među listopadnim voćem i treće među svim vrstama voćaka u svetu. Oplemenjivanje jabuke zauzima značajno mesto u programima više naučnih institucija širom sveta. Zahvaljujući tom radu jabuka je vrsta sa najviše opisanih monogenskih karaktera: 76 gena, koji kontrolišu morfološke osobine i otpornost prema bolestima i štetočinama, i 69 gena koji kodiraju enzime. Razvoj molekularnih markera (RFLPs, AFLPs, SCARs i SSRs) omogućio je mapiranje genoma jabuke i formiranje nekoliko saturisanih genetičkih mapa na kojima je lociran veliki broj gena koji determinišu osobine esencijalno važne u daljem unapređenju sortimenta jabuke. Markeri u blizini ovih gena igraju značajnu ulogu u izboru roditeljskih parova, selekciji sejanaca koji nose pozitivne osobine i posebno su značajni u detektovanju recesivnih karaktera kao što je, na primer, besemenost. Markeri su omogućili i predselekciju za poligenski regulisane kvantitativne osobine. Poslednjih godina značajna pažnja je posvećena proučavanju biohemijskih i fizioloških procesa uključenih u determinaciju značajnih fenotipskih osobina jabuke, npr. dozrevanje i trajašnost ploda jabuke.

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