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REVIEW

Quantitative Trait Loci (QTL) and Mendelian Trait Loci (MTL) Analysis in *Prunus*: a Breeding Perspective and Beyond

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Abstract Trait loci analysis, a classic procedure in quantitative (quantitative trait loci, QTL) and qualitative (Mendelian trait loci, MTL) genetics, continues to be the most important approach in studies of gene labeling in *Prunus* species from the Rosaceae family. Since 2011, the number of published *Prunus* QTLs and MTLs has doubled. With increased genomic resources, such as whole genome sequences and high-density genotyping platforms, trait loci analysis can be more readily converted to markers that can be directly utilized in marker-assisted breeding. To provide this important resource to the community and to integrate it with other genomic, genetic, and breeding data, a global review of the QTLs and MTLs linked to agronomic traits in *Prunus* has been performed and the data made available in the Genome Database for Rosaceae. We describe detailed information on 760 main QTLs and MTLs linked to a total of 110 agronomic traits related to tree development, pest and disease resistance, flowering, ripening, and fruit and seed quality. Access to these trait loci enables the application of this information in the post-genomic era, characterized by the availability of a high-quality peach reference genome and new high-throughput DNA and RNA analysis technologies.

Keywords *Prunus* · Breeding · Phenotype · Quantitative trait loci · QTL · Mendelian trait loci · MTL · eQTL · Marker-assisted breeding

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Introduction

The *Prunus* genus (family Rosaceae, order Rosales) comprises about 230 species, many of which produce edible drupes (with fruits and seeds of economic interest depending on species) and are widely grown around the world (Potter 2012). The annual worldwide production of *Prunus* species cultivated for edible fruits and seeds were around 41 million metric tons in 2011, including 21.52 million tons of peach and nectarine fruits [*Prunus persica* (L.) Batsch] ($2n=2x=16$); 11.35 million tons of prune (*Prunus domestica* L.) ($2n=6x=$

48), plum (*Prunus salicina* Lindl) ($2n=2x=16$), sloe (*Prunus spinosa* L.) ($2n=4x=32$), and cherry plum fruits (*Prunus cerasifera* Ehrh.) ($2n=2x=16$); 3.84 million tons of apricot fruits (*Prunus armeniaca* L.) ($2n=2x=16$); 2.24 million tons of sweet (*Prunus avium* L.) ($2n=2x=16$), sour (*Prunus cerasus* L.) ($2n=4x=32$), and ground (*Prunus fruticosa* Pall.) ($2n=4x=32$) cherry fruits; and 2.01 million tons of almond kernels [*Prunus amygdalus* (Batsch) syn. *Prunus dulcis* (Miller) Webb] ($2n=2x=16$) (http://faostat.fao.org).

Prunus breeding must address challenges arising from the specifics of the species physiology, including growth duration resulting from an extended juvenile period (between 3 and 10 years depending on the species) and a complex physiology due to multi-annual mechanisms of dormancy. The physiology is also significantly influenced by environmental conditions. For this reason, developing new *Prunus* cultivars is an expensive and time-consuming process involving generation of large populations of seedlings from which the best genotypes are selected (Gradziel and Martínez-Gómez 2013). In this context, the development of efficient marker-assisted selection strategies is particularly useful in *Prunus* (Arús et al. 2005). The first approach to gene labeling and development of molecular markers for marker-assisted selection (MAS) used segregating progenies (mapping populations) for molecular characterization and establishment of the relationship with agronomic traits by genetic linkage maps and trait loci analysis including quantitative (quantitative trait loci, QTL) and qualitative (Mendelian trait loci, MTL) traits.

A QTL can be described as a genomic region hypothetically responsible for quantitative genetic variation of a trait where the allelic variation of a locus is associated with the variation of the trait (polygenic traits) (Asins 2002; Collard et al. 2005). In addition, a MTL can be described as a genomic region linked for a unique gene responsible for a trait (monogenic traits) (Lionneton et al. 2004). However, in the case of *Prunus* studies, in the original manuscripts, most of MTLs were named as QTLs. In the absence of information about specific genes, loci trait analysis can be performed using model parameters considered as quantitative or qualitative traits, and then for each mapping population, the values of genotypic parameters can be predicted based on the allelic composition of the molecular markers flanking the QTLs or MTLs (Bertin et al. 2010). A well-established procedure in quantitative genetics, trait loci analysis, continues to be the most important approach in the preliminary studies of gene identification of *Prunus* breeding traits. The recent sequencing of the complete genome of peach (Verde et al. 2013), together with the availability of new technologies for high-throughput genome and transcriptome analysis, offers new possibilities for QTL and MTL application and candidate gene identification in what has been described as the post-genomic era (Martínez-Gómez et al. 2012). However, even with a complete reference sequence available for *Prunus* species, molecular genetic linkage maps will continue to be a major tool in genetics, genomics, and breeding.

As important as QTL and MTL identification has been in *Prunus*, their use in breeding has been limited due to several factors. These include dispersion of the information in many publications, the specifics of the assayed population, and the lack of standardization in nomenclature and methodology. The development of a *Prunus* QTL and MTL database would be very useful for data comparison, data mining, and meta-analysis of the huge range of information disseminated in many publications (Hu et al. 2012). Trait loci data are usually stored in clade-oriented databases that integrate genomic and genetic data for closely related organisms. These databases offer more integrated and complete data for the organisms than general nucleotide sequence databases, such as Genbank, DDJB, and EMBL (Arús et al. 2012; Wergzyn et al. 2012). The Genome Database for Rosaceae (GDR, www.rosaceae.org; Jung et al. 2008) is the community database for Rosaceae, which integrates genetic, genomic, and breeding data. ESTree database (www.itb.cnr.it/estree/) specializes in functional genomics data for *Prunus*. At the inception of this work, GDR contained 885 QTLs and MTLs linked to agronomic traits in different species from the Rosaceae family and 228 in *Prunus* (peach and sour cherry). Associated data includes the name of the studied population, the significance of the QTL or MTL (log of odds (LOD) and R^2), the effect, and the name and symbol of the QTL or MTL.

The purposes of this study were (1) to complete the curation of the information available for the *Prunus* QTLs and MTLs from literature and to integrate the data in GDR, and (2) to provide a comprehensive review of the QTLs and MTLs including a discussion of the main implications of this information for the development of MAS strategies.

Methodology

To compare information about the identification of QTLs and MTLs linked to polygenic and monogenic agronomic traits in the different *Prunus* species, the following criteria were recorded: mapping population assayed, genetic linkage analysis performed, and trait loci analysis applied.

Mapping Populations

The following information about the studied populations was recorded: "species" (including interspecific hybrids and related species), "population pedigree," "population name" (using the most recent publications as a main reference), "country," "population type," and "population size."

Genetic Linkage

In the genetic linkage analysis, the following information was collected: "type of markers assayed," "number of markers mapped," "linkage map size" (in centimorgan), "total number of linkage groups," and "mean distance" of mapped marker (in centimorgan/marker).

QTL and MTL Identification

We integrated various types of QTL and MTL information from peer-reviewed publications. The information incorporated into this database includes the "agronomic trait name," using as main reference the most cited name and the different synonyms referenced; the "symbol" or "alias" of the trait using the most referenced symbol as main reference; "loci" QTL or MTL; the "nearest marker" closest to the QTL or MTL; "marker type"; "linkage group"; "analysis method"; "analysis software"; the "nearest marker position in centimorgan"; "peak position"; and the "significance of the QTL or MTL" expressed as "LOD score," "*p* value," or "Kruskal–Wallis (KW) score".

Results and Discussion

Supplemental Table 1 contains the information listed by species and date of release, developed from multiple bibliography sources, with the QTLs and MTLs linked to agronomic traits described in the different *Prunus* studies (including peach and related interspecific hybrids, apricot, almond, sour and sweet cherry, and plum-related interspecific hybrids). To date, 760 main QTLs (670) and MTLs (90) have been described, mainly in peach and related interspecific hybrids (498 QTLs), and also in apricot (142), almond (90), sour and sweet cherry (21), and plum and related interspecific hybrids (9). These QTLs and MTLs were linked to a total of 110 agronomic traits related to tree development, pest and disease resistance, flowering, ripening, and fruit and seed quality.

In total, ~760 QTLs and MTLs were reviewed in this database (Supplemental Table 1). These data greatly extend the *Prunus* GDR database. Tables 1, 2, 3, 4, and 5 summarize the collected information.

Mapping Populations

Genetic mapping is based on recombination frequency calculations for the DNA markers (or genes) available in a mapping population. Peach has been the most studied species in *Prunus* in terms of genetic linkage analysis, followed by apricot, almond, cherry, and plum (Tables 1 and 2). With its relatively small genome size, short juvenile period of 2–3 years, and a self-compatible mating system, peach is considered one of the best genetically characterized species in the Rosaceae and the model species for the genus *Prunus* (Baird et al. 1994; Arús et al. 2012).

In plants, the construction of a linkage map and the subsequent analysis of QTLs require a segregating population derived from sexual crosses between parents differing in as many agronomic traits of interest as possible. In the case of *Prunus*, most QTL studies have been based on intraspecific crosses with the exception of peach, where some studies have been performed with interspecific crosses (Tables 1 and 2). Cultivated peaches are characterized by a genetic origin with a limited genetic diversity and low variability (Byrne 1990). For this reason, parents that provide higher polymorphism also combining adequate phenotype differences are selected in different related species to construct interspecific populations such as almond, *Prunus davidiana* (Carrière) Franch or *Prunus ferganensis* (Kostov and Rjabov) Kovalev and Kostov (Table 1). However, we have to note that *P. ferganensis* has been recently classified as *Prunus persica* (Yoon et al. 2006; Verde et al. 2013). Arús et al. (2012) indicated that one of the main limitations for map construction in peach is its low level of genetic variability, which results in a high proportion of monomorphic molecular markers in a particular intraspecific progeny. On the other hand, plum and almond are the most polymorphic species with the highest heterozygosity and variability, whereas intermediate genetic variability has been observed in apricot and sour and sweet cherry (Byrne 1990; Sánchez-Pérez et al. 2006).

The level of genetic heterozygosity and linkage disequilibrium (LD) in *Prunus* is significantly linked to mating system differences (Byrne 1990; Sorkheh et al. 2008; Aranzana et al. 2010). Peaches are self-compatible (lower heterozygosity and greater LD), and apricots are self-compatible in many cases. On the other hand, sweet and sour cherry are mostly self-incompatible, and plum and almond are typically self-incompatible and thus outcrossed (higher heterozygosity and lower LD). This high genetic heterozygosity is the reason why the majority of the mapping populations in almond, apricot, plum, and cherry have been obtained through intraspecific crosses (Table 2).

The highest number of mapping studies in *Prunus* has been performed in the USA, followed by France, Spain, and Italy. Additionally, a few studies in peach have been performed in Japan and the Czech Republic and Switzerland for apricot (Tables 1 and 2). In the case of almond, most studies have been performed in Spain.

Regarding the genetic structure of *Prunus* mapping populations, the typically assayed populations were of type F_1, F_2, or BC_1, according to the genetic diversity and levels of LD to different *Prunus* species (Tables 1 and 2). These different population types utilized for mapping have advantages and disadvantages. In the case of the peach, the species that is the least polymorphic and has the greatest LD values, most

Table 1 Mapping populations assayed in the analysis of QTLs and MTLs linked to agronomic traits in peach and related interspecific hybrids

Population pedigree	Country	Population type	Population size	Type of marker assayed	Markers mapped[a]	Map size (cM)[a]	Mean distance[a]	References
NC174RL×Pillar	USA	F_2	96	Isoenzyme, RAPD	85	396	4.80	Chaparro et al. (1994)
(1161×2678)×Early Sungrand	France	F_2	270	RAPD	38	350	9.21	Dirlewanger and Bodo (1994)
N. Jersey Pillar×KV77119	USA	F_2	71	RAPD, RFLP	65	332	5.10	Rajapakse et al. (1995)
Summergrand×P1908 (*P. davidiana*)	France	F_1	77	Isoenzyme, RAPD	71	160.3	2.25	Dirlewanger et al. (1996)
Padre (almond)×54P455	USA	F_2	64	RAPD	51	349.5	6.85	Warburton et al. (1996)
B8-23-16×A104-115	USA	F_1	112	RAPD	21	136.6	6.50	Warburton et al. (1996)
N. Jersey Pillar×KV77119	USA	F_2	48	AFLP, RAPD, RFLP, SSR	75	540	7.00	Abbott et al. (1998)
Suncrest×Bailey	USA	F_2	48	AFLP, RAPD, RFLP, SSR	145	850-900	5.90	Abbott et al. (1998)
Lovel×Nemared	USA	F_2	55	AFLP, RAPD, RFLP, SSR	157	1,300	9.13	Abbott et al. (1998)
Ferjalou Jalousia×Fantasia	France	F_2	63	AFLP, RAPD, RFLP	249	712	4.50	Dirlewanger et al. (1998)
Summergrand×P1908 (*P. davidiana*)	France	F_1	77	RAPD, RFLP	97	471	4.85	Viruel et al. (1998)
Ferjalou Jalousia×Fantasia	France	F_2	63	AFLP, RAPD, RFLP	127	nd	Nd	Dirlewanger et al. (1999)
IF7310×(IF7310×*P. ferganensis*)	Italy	BC_1	75	RAPD, RFLP	55	414	7.25	Quarta et al. (2000)
IF7310×(IF7310×*P. ferganensis*)	Italy	BC_1	75	RAPD, RFLP, SSR	109	525	4.80	Dettori et al. (2001)
Akame×Juseitou	Japan	F_2	126	AFLP, RAPD, SSR	92	1,020	11.10	Yamamoto et al. (2001)
Padre (almond)×54P455 (peach)	USA	F_2	64	CG, RFLP, SCAR, SSR	161	1,144	6.80	Bliss et al. (2002)
Ferjalou Jalousia×Fantasia	France	F_2	63	CG, RFLP, SSR	50	nd	Nd	Etienne et al. (2002)
IF7310. × (IF7310×*P. ferganensis*)	Italy	BC_1	70	RAPD, RFLP, SSR	109	509	10.19	Verde et al. (2002)
Summergrand×P1908 (*P. davidiana*)	France	F_1	77	AFLP, SSR	133	678	5.10	Foulongne et al. (2003)
Summergrand×P1908F2 (*P. davidiana*)	France	BC_2	99	AFLP, SSR	153	874	5.71	Foulongne et al. (2003)
(SD40×Summergrand) (*P. davidiana*)×Zephir	France	BC_2	269	AFLP, SSR	41	385	9.41	Foulongne et al. (2003)
Summergrand×P1908 (*P. davidiana*)	France	F_1	139	AFLP, RFLP, SSR	85	590	6.94	Quilot et al. (2004)
Summergrand×P1908 (*P. davidiana*)	France	F_1	77	CG, SSR	106	468	4.41	Decroocq et al. (2005)
GDR (peach physical map)	USA	nd	nd	CG, SSR	288	499	1.73	Lalli et al. (2005)
Texas (almond)×Early Gold	Spain	F_2	75	CG, EST	248	491	1.97	Silva et al. (2005)
Ferjalou Jalousia×Fantasia	France	F_2	207	AFLP, SSR	184	621	3.37	Dirlewanger et al. (2006)
3-17-7×Nemaguard (*P. davidiana*)	USA	F_2	100	AFLP, SSR	172	737	4.70	Blenda et al. (2007)
Ferjalou Jalousia×Fantasia	France	F_2	207	SSR	155	nd	Nd	Dirlewanger et al. (2009)
Summergrand×P1908F2 (*P. davidiana*)	France	BC_2	99	CG, SSR	113	487.2	4.30	Marandel et al. (2009a)
Dr. Davis×Georgia Belle	USA	F_1	152	CG, EST, SRAP, SSR	211	818.2	3.87	Ogundiwin et al. (2009)
Venus×Big Top	USA	F_1	75	SSR	27 (4)	54.6 (4)	2.02 (4)	Cantin et al. (2010)
Contender×Fla.92-2C	USA	F_2	378	AFLP, SSR	124	534.1	4.30	Fan et al. (2010)
Rubira×P1908 (*P. davidiana*)	France	F_1	171	SSR	84	454.2	5.40	Rubio et al. (2010)
Bolero×Oro A	Italy	F_1	169	CAP, SSR	31	263	8.62	Eduardo et al. (2011)
Contenter×Ambra	Italy	F_2	129	CAP, SSR	26	255.4	9.82	Eduardo et al. (2011)

Table 1 (continued)

Population pedigree	Country	Population type	Population size	Type of marker assayed	Markers mapped[a]	Map size (cM)[a]	Mean distance[a]	References
Texas (almond)×Earlygold (bin.)	Spain	F_2	6	CG, SSR	127	nd	Nd	Illa et al. (2011)
Summergrand×P1908 (*P. davidiana*)	France	F_1	18	RAPD, SSR	120	497.8	4.10	Lambert and Pascal (2011)
Dr. Davis×Georgia Belle	USA	F_1	55	SNP, SSR	44	152	5.45	Dhanapal et al. (2012)
KV930278 (F_2)	USA	F_2	92	AFLP, SSR	37 (2)	92.9	2.49	Sajer et al. (2012)
Summergrand×P1908 (*P. davidiana*)	France	F_1	77	RAPD, SSR	124	468.9	3.78	Sauge et al. (2012)
Flordaguard×Late Arkansas	USA	F_2	50	SSR	30	390.4	13.01	Blaker et al. (2013)
SL0736×PI091459	USA	F_2	50	SSR	25	293	11.72	Blaker et al. (2013)
Bolero×Oro A	Italy	F_1	126	SNP, SSR	123	199.6	1.62	Eduardo et al. (2013)
Dr. Davis×Georgia Belle	USA	F_1	55	SNP, SSR	738	369	0.81	Martínez-Garcia et al. (2013a)
Dr. Davis×F81-24	USA	F_1	69	SNP, SSR	1,037	422	0.81	Martínez-Garcia et al. (2013a)
O'Henry×Clayton	USA	F_2	63	SNP	1,167	421.4	1.60	Yang et al. (2013)

P. ferganensis has been recently classified as *P. persica* (Yoon et al. 2006; Verde et al. 2013)

nd no data

[a] The linkage group analyzed is between parentheses

populations are F_2. The shortest generation time and its self-compatibility make peach a good candidate for the creation of F_1 hybrids and F_2 populations (Aranzana et al. 2010; Arús et al. 2012). F_2 populations, though more difficult to develop, should be more informative in the genetic dissection of quantitative traits mainly in the case of low heterozygosity genotypes because genetic effects are additive and dominant, while epistatic effects can be estimated and should be more informative in the case of low heterozygosity genotypes (Zhang 2012).

F_2 populations are also common in interspecific crosses in the case of peach and related species. In the case of other *Prunus* species, the use of F_1 populations is more extensive because these populations are easier to develop in species with a longer period of juvenile growth. In addition, in many cases, these species present gametophytic self-incompatibility that makes it impossible to produce F_2 type populations. Higher polymorphism and lower LD make F_1 populations more suitable for the rest of *Prunus* species in comparison with peach (Aranzana et al. 2010). Finally, backcrosses (BC_1 and BC_2) have been used to map different traits in interspecific crosses in peach and intraspecific crosses in apricot (Tables 1 and 2).

Overall, the generation of large populations is desirable for an increased mapping resolution. However, in *Prunus* species, the generation of large populations is limited because of orchard management costs and the multi-annual nature of the trees. The size of mapping populations in the *Prunus* assay ranged from 48 descendants (Abbott et al. 1998) to 270 (Dirlewanger and Bodo 1994) in peach progenies (Tables 1 and 2). This range agrees with the size of populations typically used for genetic mapping studies in plants and with the range of 50 and 250 recommended by Collard et al. (2005). At the same time, these authors also noted that the larger populations result in higher resolution maps, allowing for detection of QTLs with smaller effects. The reduced progeny size has been described as the main reason for the limited resolution of the QTLs identified in *Prunus* species. Using larger populations in *Prunus* would thus generate high-resolution maps, allowing for more accurate QTL detection and positional cloning studies (Dirlewanger et al. 2012).

Genetic Linkage Analysis

Genetic linkage maps indicate the relative position and the relative genetic distance between DNA markers in the genome of an organism. In *Prunus*, the first genetic linkage studies were performed in 1994 in peach (Chaparro et al. 1994; Dirlewanger and Bodo 1994) (Tables 1 and 2). The first step in the construction of a linkage map is the identification of molecular markers that reveal differences between parents and then between descendants. In *Prunus,* the first studies were carried out using isozyme biochemical markers and random amplified polymorphic DNAs (RAPDs) (Chaparro et al.

Table 2 Mapping populations assayed in the analysis of QTLs and MTLs in almond, apricot, sour and sweet cherry, plum, and related interspecific hybrids

Specie	Population pedigree	Country	Population type	Population size	Type of marker	Markers mapped[a]	Map size (cM)[a]	Mean distance[a]	References
Almond	Ferragnes×Tuono	Spain	F_1	134	RFLP	7 (6)	52 (6)	7.42 (6)	Ballester et al. (1998)
	D.3.5×Bertina	Spain	F_1	134	RAPD, RFLP	14 (4)	58 (4)	6.81 (4)	Ballesteret al. (2001)
	R1000×Desmayo	Spain	F_1	167	SSR	53	400.6	7.56	Sánchez-Pérez et al. (2007)
	R1000×Desmayo	Spain	F_1	167	SSR	12 (5)	58.1 (5)	4.84 (5)	Sánchez-Pérez et al. (2010)
	Texas×Earlygold. (bin.)	Spain	F_2	6	CG, SSR	nd	nd	Nd	Sánchez-Pérez et al. (2010)
	Vivot×Blanquerna	Spain	F_1	77	SSR	43	377.1	8.76	Fernández. i Martí et al. (2011)
	Vivot×Blanquerna	Spain	F_1	77	SSR	56	462	8.25	Font i Forcada et al. (2012)
	R1000×Desmayo	Spain	F_1	167	SSR	60	440.8	7.35	Sánchez-Pérez et al. (2012)
	Vivot×Blanquerna	Spain	F_1	77	SSR	57	462	8.10	Fernández i Martí et al. (2013)
Apricot	Goldrich×Currot	Spain	F_1	81	AFLP, RAPD, RFLP, SSR	132	511	3.90	Hurtado et al. 2002
	Lito×Lito	Spain	F_2	76	AFLP, CG, SSR	211	504	2.38	Vilanova et al. (2003)
	Lito×Lito	Spain	F_2	76	AFLP, CG, SSR	11 (1)	99 (1)	9.00 (1)	Soriano et al. (2005)
	Polonais×SEO	France	F_1	220	SSR	56 (1,3,5)	311 (1, 3, 5)	5.5 (1, 3, 5)	Lambert et al. (2007)
	LE-3246×Vestar	Czech R.	BC_1	67	AFLP, SSR	357	523.0	1.46	Lalli et al. (2008)
	Goldrich×Currot	Spain	F_1	81	AFLP, RAPD, SSR	17 (1)	86.8 (1)	5.10 (1)	Sicard et al. (2008)
	Lito×Lito	France	F_2	76	AFLP, CG, SSR	25 (1)	107.2 (1)	4.20 (1)	Sicard et al. (2008)
	Polonais×SEO	France	F_1	220	SSR	34 (1)	137.1 (1)	4.15 (1)	Sicard et al. (2008)
	Goldrich×Currot	Spain	F_1	81	SSR	148	519	3.50	Soriano et al. (2008)
	Lito×Lito	Spain	F_2	76	SSR	204	527	2.58	Soriano et al. (2008)
	Harlayne×Marlen	France	F_1	147	CG, SSR	120	144.2	1.20	Marandel et al. (2009b)
	Perfection×A1740	USA	F_1	100	AFLP, SSR	655	550.6	0.84	Olukolu et al. (2009)
	Harlayne×Vestar	Czech R.	F_1	65	SSR	31 (1,5)	199.5 (1,5)	6.43	Pilarová et al. (2010)
	Goldrich×Moniquí	France	F_1	120	SSR	148	555	6.53	Ruiz et al. (2010)
	Lito×BO8160431	Italy	F_1	120	SSR	118	430.2	3.65	Ruiz et al. (2010)
	Z5067×Currot	Spain	BC_1	73	SSR	6 (5)	25 (5)	4.16	Campoy et al. (2011)
	Harcot×Reale Imola	Italy	F_1	98	SSR	20 (1)	143 (1)	7.15 (1)	Dondini et al. (2011)
	Lito×BO8160431	Italy	F_1	350	SSR	27 (1)	91.1 (1)	3.37 (1)	Dondini et al. (2011)
	Goldrich×Currot	Spain	F_1	81	SSR	47 (1)	97 (1)	1.50 (1)	Vera-Ruiz et al. (2011)
	Lito×Lito	Spain	F_2	76	SSR	63 (1)	70.7 (1)	1.53 (1)	Vera-Ruiz et al. (2011)
	Lito×BO8160431	Italy	F_1	118	CG, SSR	101 (1,2,6,7)	347 (1,2,6,7)	3.4 (1,2,6,7)	Cervellati et al. (2012)
	Harostar×Rouge de Mauves	Switzerland	F_1	102	AFLP, SSR	63-53	684	4.9-6.9	Socquet-Juglard et al. (2013a)
	Harostar×Rouge de Mauves	Switzerland	F_1	102	AFLP, SSR	63-53	684	4.9-6.9	Socquet-Juglard et al. (2013b)
	Z701-1×Palsteyn	Spain	F_1	160	SSR	41	369.3	9.00	Salazar et al. (2013)
Plum	P2175×P2646	France	F_1	288	SCAR, SSR	5 (7)	11.8 (7)	2.36 (7)	Claverie et al. (2004)

Table 2 (continued)

Specie	Population pedigree	Country	Population type	Population size	Type of marker	Markers mapped[a]	Map size (cM)[a]	Mean distance[a]	References
Plum/Alm./Peach	P2175×GN22	France	F_1	101	SCAR, SSR	12 (2)	16.0 (2)	1.33 (2)	Claverie et al. (2004)
	P2175×GN22	France	F_1	101	SCAR, SSR	169	763.3	4.51	Dirlewanger et al. (2004a)
	P2175×Alneml	France	BC_1	29	SCAR, SSR	6 (7)	16.6 (7)	2.76 (7)	Van Ghelder et al. (2010)
Sour cherry	Rhein. × Er. Botermo	USA	F_1	86	RFLP	55	272.2	4.00	Wang et al. (2000)
Sweet cherry	Emperor F. × N. York	USA	F_1	190	AFLP, CAP, EST, SSR	90 (3,6,8)	293 (3,6,8)	3.2 (3, 6, 8)	Sooriyapathirana et al. (2010)
	Emperor F. × N. York	USA	F_1	190	AFLP, CAP, EST, SSR	32 (2,6)	171.0 (2,6)	5.30 (2,6)	Zhang et al. (2010)

[a] The linkage group analyzed is between parentheses

1994). Isoenzyme markers were soon superseded by the more informative and polymorphic DNA markers, such as restriction fragment-length polymorphisms (RFLPs) (Rapajapse et al. 1995), considered the first generation of DNA markers, and RAPDs. RFLPs were more efficient because of their codominant nature and unlimited number of markers, although their application has been limited due to the complexity and time-consuming nature of RFLP analysis.

The utilization of PCR-based markers, which are less laborious and time consuming, greatly increases the possibilities of genome characterization and mapping. RAPDs were the first PCR markers assayed (second DNA marker generation) (Dirlewanger and Bodo 1994), although their dominant nature and low reproducibility drastically limited their utilization (Martínez-Gómez et al. 2007). Other markers based on PCR were the cleaved amplified polymorphic sequences, candidate genes (CGs), and sequence characterized amplified regions (SCARs). Simple sequence repeats (SSRs) have become the PCR markers of choice in genetic mapping because of their high polymorphism, abundance, codominance, and transportability across species (Gupta et al. 1996; Campoy et al. 2010) (Tables 1 and 2, and Supplemental Table 1). The most recent genetic linkage maps developed in *Prunus* are either based solely on these markers (Illa et al. 2009; Rubio et al. 2010; Campoy et al. 2011; Dondini et al. 2011; Font i Forcada et al. 2012; Sánchez-Pérez et al. 2012) or combined with recently developed molecular markers from DNA sequencing (third DNA marker generation) to compensate for their lack of abundance in the genome. SSRs continue to be the markers of choice for anchoring to genetic maps. Sequence-based DNA markers developed in *Prunus* include expressed sequence tags (ESTs) and single nucleotide polymorphisms (SNPs) (Tavassolian et al. 2010; Ahmad et al. 2011). Currently, the high capacity of sequencing offered by the new high-throughput technologies has made the development of high-density SNP markers possible. Eduardo et al. (2013) and Martínez-García et al. (2013a, b) have identified the first QTLs linked to SNPs in a highly saturated linkage map of peach using only SNPs, albeit with previous reference maps developed using SSRs.

There is no absolute number of DNA markers required for a genetic linkage map, since the number of markers varies with the number and length of chromosomes, and the size of the genome of the organism. For detection of QTLs, preliminary genetic mapping studies generally report between 100 and 200 markers. However, as the genome size of a species increases, more markers are required for fine mapping (Collard et al. 2005). Using fluorescent techniques, the genome size (number of nucleotide bases) of *Prunus* was initially estimated to be 300 Mbp (Baird et al. 1994). However, recent sequencing of the peach genome indicates a size of 227 Mbp for this species (Verde et al. 2013). The size of this genome is relatively small compared to that of other plants;

Table 3 QTLs and MTLs linked to agronomic traits related to tree and flower identified in *Prunus*

Agronomic trait	Symbol	Loci[a]	Species	Linkage group
Tree development				
Evergrowing	*Ev*	MTL	Peach	G1
Internode length	*Il*	QTL	Peach	G1
Leaf color (red/yellow)	*Gr*	MTL	Peach, plum	G6
Leaf gland (globose/glandular)	*E*	MTL	Peach	G7
Leaf shape (narrow/wide)	*Nl*	MTL	Peach	G6
Leafing date	*Lf*	QTL	Almond	G4, G5
Peach tree short life	*PTSL*	QTL	Peach	G2, G2, G4, G5, G6
Pillar growth type	*Br*	MTL	Peach	G1, G2
Plant height (normal/dwarf)	*Dw*	MTL	Peach	G6
Total branch number	*TB*	QTL	Apricot	G1, G6
Tree shape	*TSh*	QTL	Apricot	G1, G5
Trunk diameter	*TD*	QTL	Apricot	G1, G2
Weeping shape	*Pl*	QTL	Peach	G2
Flowering and ripening				
Anther color (yellow/anthoc.)	*Ag*	MTL	Peach	G3
Blooming date (flowering time)	*Bd*	QTL	Almond, apricot, cherry, peach	G1, G2, G4, G5, G6, G7, G8
Chilling requirement	*CR*	QTL	Almond, apricot, peach	G1, G2, G3, G4, G5, G6, G7, G8
Double flower	*Dl*	MTL	Peach	G1, G2
Flower color	*Fc*	QTL	Peach	G3
Flower morphology	*Sh*	MTL	Peach	G8
Fruit abortion	*Af*	MTL	Peach	G6
Fruit development period	*fdp*	QTL	Apricot, peach	G4
Heat requirement	*HR*	QTL	Almond, peach	G1, G2, G7, G8
Late blooming	*Lb*	MTL	Almond	G4
Male sterility	*Ps*	MTL	Peach	G6
Polycarpel	*Pcp*	MTL	Peach	G3
Productivity	*P*	QTL	Almond, peach	G4, G6
Ripening (maturity, harvesting)	*Rp*	QTL	Almond, apricot, cherry, peach	G1, G2, G3, G4, G5, G6, G7, G8
Self-incompatibility	*S*	MTL	Almond, apricot, peach	G6, G8
Time of reproductive bud break	*IRB*	QTL	Apricot	G1, G4, G7
Pest and disease resistance				
Aphid resistance	*MP*	QTL	Peach	G1, G2, G3, G4, G6, G8
Leaf curl resistance	*Lc*	QTL	Peach	G3
Nematode resistance	*Ma*, *Mi*, *Mja*	MTL	Almond, peach, plum	G2, G7
Powdery mildew resistance	*PM*	MTL, QTL	Peach	G1, G2, G4, G5, G6, G7, G8
PPV (D, M) resistance	*PPV*	MTL, QTL	Apricot, peach	G1, G2, G3, G4, G5, G6, G7
Xanthomonas resistance	*XR*	QTL	Apricot, peach	G1, G2, G3, G4, G5, G6, G8

[a] Quantitative (QTL) or Mendelian (MTL). In the original manuscripts most of MTLs were named as QTLs

one of the smallest is *Arabidopsis thaliana* L. Heynh with 125 Mbp together with *Genlisea margaretae* Hutch with 63 Mbp and one of the largest is lily (*Lilium longiflorum* Duch) (Bennett and Leitch 2011) with 35,817 Mbp. In *Prunus* mapping assays, given the relatively small genome size, the number of markers mapped in the whole genome ranges from 25 in a peach population (Blacker et al. 2013) to 655 in an apricot (Olukolu et al. 2009) and 1,167 in a peach (Yang et al. 2013) population (Tables 1 and 2).

The size of the whole linkage map (in centimorgan) and total number of linkage groups are dependent on the technology available at the time the genetic maps were generated. In general, the first maps were smaller. For example, the estimated genome size for peach was 160.3 cM (Dirlewanger et al. 1996) or 173.0 cM (Warburton et al. 1996), whereas in more recent research, the linkage maps are 879 cM in peach (Decroocq et al. 2005), 555 cM in apricot (Ruiz et al. 2010), and 763 cM in plum (Dirlewanger et al. 2004a) (Tables 1 and 2

Table 4 QTLs and MTLs linked to agronomic traits related to fruit quality identified in *Prunus*

Agronomic trait	Symbol	Loci[a]	*Prunus* species	Linkage group
Acidity (titrable acidity)	*Ac*	QTL	Apricot, peach	G4, G6, G8
Chavicol	*Chavicol*	QTL	Peach	G3
Citric acid	*cit*	QTL	Peach	G1, G3, G4, G5, G7
E-3-nonen-2-one	*E-3-nonen-2-one*	QTL	Peach	G4, G6
E-β-damascenone	*E-β-damascenon.*	QTL	Peach	G4, G7
Eugenol	*Eugenol*	QTL	Peach	G5
Firmness	*Fr*	QTL	Peach	G1, G4, G5, G7, G8
Flesh adhesion (cling/freestone)	*F*	MTL	Peach	G4
Flesh color (white/yellow)	*Y*	MTL	Peach	G1
Flesh color (around the stone)	*Cs*	QTL	Apricot, cherry, peach	G1, G2, G3, G6, G8
Flesh bleeding	*FBL*	QTL	Peach	G4
Flesh browning	*FBr*	QTL	Peach	G5
Fructose	*fru*	QTL	Peach	G1, G2, G4, G6, G7, G8
Fruit shape (flat/round)	*S**	MTL	Peach	G6
Fruit shape (fruit form)	*Fsh*	MTL, QTL	Apricot	G1, G3, G5
Fruit skin color (ground color)	*Sc*	QTL	Apricot, cherry, peach	G2, G3, G5, G6, G7, G8
Fruit diameter (fruit size)	*Fd*	QTL	Peach	G3, G4
Fruit weight	*Fw*	QTL	Apricot, cherry, peach	G1, G2, G3, G4, G5, G6, G8
Glucose	*glu*	QTL	Peach	G2, G3, G4, G5, G6, G7, G8
Graininess	*gra*	QTL	Peach	G4
Leatheriness	*L*	QTL	Peach	G4
Linalool	*Linalool*	QTL	Peach	G4
Malic acid (malate)	*mal*	QTL	Apricot, peach	G2, G3, G4, G5, G6
Mealiness	*M*	QTL	Peach	G1, G4
Nonanal	*Nonanal*	QTL	Peach	G4
Non-acid fruit (subacid)	*D*	MTL, QTL	Apricot, peach	G2, G3, G5
p-Menth-1-en-9-al	*p-Menth-1-en-9*	QTL	Peach	G4
pH	*pH*	QTL	Apricot, peach	G2, G3, G4, G5
Phenylacetaldehyde	*Phenylacetal.*	QTL	Peach	G6, G7
Quinase	*qui*	QTL	Peach	G8
Skin hairiness (nectarine/peach)	*G*	MTL	Peach	G5
Soluble solid contents	*SSC*	QTL	Apricot, cherry, peach	G1, G2, G3, G4, G5, G6, G7
Sorbitol	*sor*	QTL	Peach	G4, G6
Squalene	*Squalene*	QTL	Peach	G6
Sucrose	*suc*	QTL	Peach	G3, G5, G6, G7
γ-Octalactone	*γ-Octalactone*	QTL	Peach	G3, G4
γ-Decalactone	*γ-Decalactone*	QTL	Peach	G4, G6
γ-Dodecalactone	*γ-Dodecalactone*	QTL	Peach	G3, G6
δ-Decalactone	*δ -Decalactone*	QTL	Peach	G6, G7
6-Pentyl-α-pyrone	*6-Pentyl-α-pyr.*	QTL	Peach	G2, G6
3-Methylbutanoic acid	*3-Methylb. acid*	QTL	Peach	G6

[a] Quantitative (QTL) or Mendelian (MTL). In the original manuscripts most of MTLs were named as QTLs

and Supplemental Table 1). The current tendency is to generate new maps that are smaller in size using a high number of markers to increase the quality of the maps (Rubio et al. 2010; Martínez-García et al. 2013a; Sauge et al. 2012). Regarding the total number of linkage groups, although the first maps described up to 12 or 13 groups (Chaparro et al. 1994; Abbott et al. 1998), it is currently established that the total number of linkage groups is eight (Supplemental Table 1),

Table 5 QTLs and MTLs linked to agronomic traits related to nut and seed (kernel) identified in *Prunus*

Agronomic trait	Symbol	Loci[a]	*Prunus* species	Linkage group
Nut morphology				
Double kernels	*Dk*	MTL	Almond	G4
Geometric diameter	*GDn*	QTL	Almond	G2, G6
Length	*Ln*	QTL	Almond	G1, G5, G6, G7
Length/width (LW)	*Ln/Wn*	QTL	Almond	G7
Shell hardness	*D*	MTL	Almond	G2
Size	*Sz*	QTL	Almond	G2, G7
Spherical index	*Sin*	QTL	Almond	G2, G3, G7
Thickness	*Tn*	QTL	Almond	G2, G3
Thickness/length	*Tn/Ln*	QTL	Almond	G1, G5, G7
Weight	*Wgn*	QTL	Almond, apricot	G1, G2, G7
Width	*Wn*	QTL	Almond	G2, G3
Seed morphology				
Geometric diameter	*GDn*	QTL	Almond	G1, G7
Length	*Ln*	QTL	Almond	G1, G5, G6, G7
Length/width (LW)	*Ln/Wn*	QTL	Almond	G2, G3, G6
Spherical index	*Sin*	QTL	Almond	G7
Size	*Sz*	QTL	Almond	G7
Thickness	*Tn*	QTL	Almond	G6, G7
Thickness/length	*Tn/Ln*	QTL	Almond	G1, G2
Weight	*Wgn*	QTL	Almond	G1, G7
Width	*Wn*	QTL	Almond	G3, G5
Seed quality				
Amygdalin hydrolase	*AH*	QTL	Almond, apricot	G1, G7
Glucosyl transferase	*GT*	QTL	Almond	G3, G8
Kernel taste (bitterness/sweet)	*Sk*	MTL	Almond, peach	G5
Linoleic acid	*Linoleic*	QTL	Almond	G2, G7
Mandelonitrile lyase	*MDL*	QTL	Apricot	G1
Palmitic acid	*Palmitic*	QTL	Almond	G3, G7
Palmitoleic acid	*Palmitoleic*	QTL	Almond	G3, G5, G7
Oil seed content	*Oil*	QTL	Almond	G6
Oleic acid	*Oleic*	QTL	Almond	G2, G7
Prunasin hydrolase	*PH*	QTL	Almond, apricot	G1, G2, G6
Stearic acid	*Stearic*	QTL	Almond	G1, G5, G6, G7
Tocopherol homologes	*T-*	QTL	Almond	G1, G4, G7
Total seed protein	*Protein*	QTL	Almond	G6, G7
Seed dormancy				
Abnormal growth	*AG*	QTL	Peach	G6, G8
Germination date	*GD*	QTL	Peach	G1, G4, G6, G7, G8
Stratification requirements	*SR*	QTL	Peach	G7

[a] Quantitative (QTL) or Mendelian (MTL). In the original manuscripts most of MTLs were named as QTLs

corresponding to the basic number of chromosomes of diploid *Prunus* ($2n = 2x = 16$).

In previous studies, the mean distance between markers ranged from 13.01 cM per marker on average in a peach progeny (Blacker et al. 2013) to 0.84 cM per marker in apricot (Olukolu et al. 2009). Currently, however, with the use of SNP markers, the level of map saturation is increasing. Martínez-García et al. (2013a) constructed a map using SNP markers with a mean distance of 0.50 markers per cM (Tables 1 and 2). Smaller distances between markers typically produce more accurate QTLs. Darvasi et al. (1993) reported that the power of detecting a QTL was virtually the same for a marker spacing of 10 cM as for an infinite number of markers, and only slightly decreased with a marker spacing of 20 cM.

Currently, all of the constructed linkage maps contain a framework of markers common with the reference map 'Texas'×'Earlygold' (T×E), which allows for identification of the linkage groups and ensures good coverage and marker spacing of the genome (Aranzana et al. 2003; Arús et al. 2012). In addition, the selective or bin mapping approach offers an alternative strategy for locating new markers and QTLs in an established genetic linkage map (Howad et al. 2005). This technique allowed the first mapping attempt using only a subset of six individual plants from the reference population of 65 individuals of T×E. The advantage of this strategy is that mapping takes less time, is more cost effective, and is adequate for simplifying the construction of high-density maps. The reference map has been divided into 67 bins or regions (from 8 to 25 cM) in which to locate current and future markers. Using this technique, 151 microsatellite (SSRs) markers have been incorporated into the *Prunus* reference map using only those six individuals. This relatively fast approach has been successfully used to map QTLs linked to agronomic traits in peach (Eduardo et al. 2011; Illa et al. 2011) and almond (Sánchez-Pérez et al. 2010).

Finally, regarding the location of a QTL, the critical point in QTL analysis and MAS development is how closely a QTL is mapped with respects to the markers. Boopathi (2013) recommended that initial genotyping in an experimental cross be performed with markers at 10–20 cM spacing. This is also suggested that for markers spaced at 10 cM or closer, there is really little point in increasing marker density when the goal is simple detection of a linked QTL. Generally, QTLs have been located to intervals of 15–20 cM. This is probably sufficient for QTL location but this level of precision is nowhere near satisfactory for map-based cloning strategies. Developing additional markers in the region of an inferred QTL may improve the resolution of its localization. Informative markers that flank a QTL within 5 cM seem adequate (Xu and Crouch 2008).

QTL and MTL Identification

QTLs and MTLs are based on the association of a particular phenotypic trait with a DNA region (genotype). In *Prunus*, as

well as in other crops, many agricultural traits are controlled by many genes and are characterized as quantitative, polygenic, multifactorial, or complex traits (Arús et al. 2005; Bertin et al. 2010). To date, 760 different loci have been described in *Prunus* linked to a total of 110 agronomic traits (86 of these traits characterized as quantitative and 24 as Mendelian) related to tree development, pest and disease resistance, flowering, ripening, and fruit and seed quality (Tables 3, 4, and 5 and Supplemental Table 1). These loci were in most cases quantitative (QTLs) (670 loci) with several markers involved in the expression of the trait. In addition, in some cases (90 loci), these loci were Mendelian (MTLs) mainly in the case of tree and flower agronomic traits. These QTLs and MTLs have sufficient phenotypic effects to be detected according to the LOD values described by the different authors.

Regarding the species studied, peach is still the most important; 498 of the identified trait loci were described in peach and related interspecific hybrids, 142 in apricot, 90 in almond, 21 in sour and sweet cherry, and 9 in plum and related interspecific hybrids. These loci have been studied mainly in agronomic traits linked to fruit quality (41 traits), nut and seed morphology (18), flowering and ripening (15 traits), seed quality (14), tree development (13), pest and disease resistance (6), and seed dormancy (3).

The QTL and MTL analysis methods used to map genomic regions controlling the agronomical traits include the KW test, composite interval mapping, multiple interval mapping, multiple QTL mapping, and simple interval mapping (Supplemental Table 1). These are the usual methods used in plants (Asins 2002). These methods vary in the amount of statistical power to detect QTLs and MTL and their interactions, as well as in their ability to define the confidence interval and to estimate genetic effects. The softwares used are also listed in Supplemental Table 1. These softwares are the most commonly used in plant assays. Software like MAPMAKER/QTL or MAPMAKER based on the maximum likelihood is best suited for data with a normal distribution (Lander et al. 1987), while those based on a multiple regression such as QTL CARTOGRPHER and PlabQTL are more robust for data with non-normal distribution (Basten et al. 1997). Other software used includes Join Map and FlexQTL (Van Ooijen 2006; Bink et al. 2008).

The significance of the *Prunus* QTLs and MTLs has been expressed as LOD score, p value, or KW score. In general, these values are related to the nature of the traits and the presence of a few major or several minor genes involved in their expression. An LOD score above 3 is generally used as a critical value. An LOD score of ≥ 3 implies that the null hypothesis ($r = 0.5$) is rejected. This value implies a ratio of likelihoods of 1,000 to 1 (i.e., among the 1,000 analysis, there is a chance of 1 error type of detecting something when in fact there is nothing). In practice, an LOD threshold of 2.5–3 is often used to declare significance to minimize the frequency of errors (Würschum 2012). However, due to the statistical analyses involved in trait loci detection (nature of the statistical analysis, variability in the statistical analysis, lack of standardization, etc.), a large part of the QTLs identified to date are inconsistent for use in *Prunus* breeding. This inconsistency was highlighted by Lambert et al. (2007), who detected different QTLs for plum pox virus (PPV) resistance in apricot using different statistical analysis programs (Kruskal–Wallis, multiple regression, interval mapping, composite interval mapping). As a result, these authors suggested that QTLs detectable by only one statistical analysis method could be possible artifacts.

It is also important to consider that environmental effects may have a profound influence on the expression of quantitative traits. As a result, although the replication of *Prunus* QTL and MTL experiments at different sites is a common practice due to the long generation time for trees, the evaluation of traits and loci analysis for different years has also been largely applied in most *Prunus* studies in order to improve the identification of loci linked to these traits. Accordingly, Collard et al. (2005) recommended replication of experiments across sites and over time in different seasons and years. Similarly, Asins (2002) proposed three possible causes for the lack of QTL and MTL stability: the power of the statistical test used, the low contribution to the genetic variation of the trait, and differential gene expression of the trait dependent on the year. This lack of stability affected by environment has been described in various *Prunus* species (Foulongne et al. 2003; Quilot et al. 2004; Decroocq et al. 2005; Sánchez-Pérez et al. 2012), although the validity of the identified QTLs and MTLs is maintained by authors. In all these studies, at least 2 years are the accepted recommendation for the study of the mapping populations in order to stabilize the preliminary loci linked to the different agronomic traits.

QTLs and MTLs should be validated by testing their effectiveness in determining the target phenotype in different genotypes through the allelic association of the DNA marker and the phenotype. This indicates whether a marker could be used in routine screening for MAS (Collard et al. 2005). In the case of *Prunus*, such validation has been performed with QTLs associated with several agronomic traits including bitterness in almond (Sánchez-Pérez et al. 2010), PPV resistance in apricot (Soriano et al. 2012), and maturity date in peach (Song et al. 2012). In these studies, SSRs have been the markers of choice.

Regarding location of QTL and MTL (Tables 3, 4, and 5), we can show that many agronomic traits in *Prunus*, including fruit quality, fruit production, and pest and disease resistance, are polygenic (Martínez-Gómez et al. 2007), with complex inheritance and several regions of the genome involved in their expression (Bertin et al. 2010). In many cases, each of these loci explains small portions of total phenotype variance

of the trait. The location of QTLs and MTLs also indicates a clustering of these loci in relation to several traits. For example, various studies in *Prunus* (Silva et al. 2005; Sánchez-Pérez et al. 2007, 2012; Olukolu et al. 2009; Fan et al. 2010) showed that endodormancy breaking and flowering QTLs are clustered in two important regions in G4 and G1. QTL clustering has also been described in G4 in almond in relation to other traits, such as flowering time, productivity, double kernel, or kernel weight (Sánchez-Pérez et al. 2007). In peach, QTL clustering was also observed in traits related to fruit quality (Etienne et al. 2002; Eduardo et al. 2011), revealing the particular interest of some regions of the genome involved in interconnected metabolic process. Overlapping of these QTLs suggests shared biochemical pathways in different traits related to fruit quality and tree development. In this sense, an initial trait category (ontology) has been established in the GDR databases (www.rosaceae.org) to classify the different QTLs and MTLs. The first categories of these loci are related to tree development, pest and disease resistance, flowering, ripening, and fruit and seed quality include anatomy, biochemical, growth and development, quality, stature or vigor, sterility or fertility, stress, and yield.

New Molecular and Biological Challenges and Opportunities

The recent release of the complete peach genome sequence and availability of the new high-throughput technologies for genome and transcriptome analysis offer new possibilities for QTL and MTL applications and candidate gene identification in what has been described as the post-genomic era (Martínez-Gómez et al. 2012). In this respect, we are facing a revolution in the use of new high-throughput analysis techniques, which may mean a scientific paradigm shift in *Prunus* QTL and MTL identification. These challenges and opportunities are of special interest in the case of *Prunus*, where despite the large number of loci described so far, the association between genes and agronomic traits is still limited (Arús et al. 2005; Iezzoni et al. 2010; Esmenjaud and Srinivasan 2012).

The availability of the first complete *Prunus* reference genome presents one of the most interesting molecular opportunities for extending the accurate application of loci data and for the identification of candidate genes linked to agronomic traits. The International Peach Genome Initiative (Verde et al. 2013) released the complete peach genome sequence [peach genome (v1.0)] in April 2010. It is available via several sites including GDR (Jung et al. 2008). Peach v1.0 generated from DNA from the doubled haploid cultivar 'Lovell' consists of eight scaffolds representing the eight chromosomes of peach, numbered according to their corresponding linkage groups ($1n = 1x = 8$) with a size of 227 Mbp (Arús et al. 2012; Verde et al. 2013). In addition, 28,689 transcripts and 27,852 protein-coding genes have been identified in this reference *Prunus* genome. More recently, Zhang et al. (2012) assembled a 280-M genome of *Prunus mume* Siebold & Zucc. by combining 101-fold next-generation sequencing and optical mapping data. These authors anchored 83.9 % of scaffolds to eight chromosomes with genetic map constructed by restriction site-associated DNA sequencing.

The lack of consistency between phenotype and loci identification limits the utility of the collected data. One of the most important sources of experimental errors in QTL analysis studies is inaccurate phenotypic evaluation (Collard et al. 2005; Furbank and Tester 2011). The accuracy of phenotypic evaluation is extremely important for the accuracy of QTL mapping. A reliable QTL or MTL map can only be produced from reliable phenotypic data. Phenotypic variation is produced through complex interactions between the genotype and the environment. For example, we can observe a substantial number of genome regions involved in the expression of certain agronomic traits, such as aphid resistance, blooming date, chilling requirements, fruit weight, ripening time, PPV resistance, etc. (Tables 3, 4, and 5). The accuracy of phenotypic evaluation is critical for the accuracy of QTL and MTL identification and other genomic studies (Houle et al. 2010). This could be the reason for the lack of precision in the identified loci in terms of the development of suitable markers for assisted selection in breeding programs. Standardized phenotyping (Ingvarsson and Street 2011), mainly in the evaluation of very complex traits, such as productivity, stress resistance, or pest and disease resistance, is a challenging approach, requiring a well-established international network of cooperation to align the characterization of the different collections for further QTL studies (Fridman and Zamir 2012). This is one of the main objectives of the RosBREED consortium (http://www.rosbreed.org) and FruitBreedomics (www.fruitbreedomics.com) created to foster research, infrastructure establishment, training, and extension for applying efficient marker-assisted selection strategies in the Rosaceae family (Iezzoni et al. 2010).

Some examples of the problems with population phenotyping include the reduced number of evaluated seedlings (Campoy et al. 2011; Fernández i Martí et al. 2011; Font i Forcada et al. 2012), the transformation of quantitative traits into qualitative traits (Hurtado et al. 2002; Vilanova et al. 2003; Olukolu et al. 2009; Vera-Ruiz et al. 2011), and the problems associated with evaluating very complex traits including pest and disease resistance. Aphid resistance evaluation is a paradigmatic case (Lambert and Pascal 2011; Sauge et al. 2012).

Another important barrier for *Prunus* breeding and loci identification is the poor understanding of the epigenetic mechanisms in these species (Gradziel and Martínez-Gómez 2013). The DNA composition of affected cultivars remains unchanged, although the gene activity is altered in a heritable manner and the DNA sequence appears identical in differentially expressed genotypes. This phenomenon has been described in *Prunus* in noninfectious bud-failure in almond

(Gradziel and Martínez-Gómez 2013) and bud dormancy release in peach (Leida et al. 2012).

The complete reference genome will be of great interest for future molecular studies in *Prunus*, due to the easy identification of DNA markers in this genome. Furthermore, we must note the great possibilities that the reference genome offers for placing the loci of interest representative of the different QTLs identified (Salvi et al. 2005). Alternatively, de novo sequencing of new genotypes from each *Prunus* using high-throughput DNA sequencing technologies (DNA-Seq) to be used as references in each species presents another option for further re-sequencing studies. DNA-Seq technology allows for faster re-sequencing of different genotypes and species, assuming a reference-like genome exists, which is not possible with de novo assembling (Edwards and Batley 2010; Jackson et al. 2011). The first whole genome re-sequencing and de novo assembly studies in *Prunus* have been performed in prune (Dardick et al. 2011) using the reference peach genome. The development of these reference genomes will facilitate the isolation of genes via QTL map-based cloning in the different *Prunus* species following the peach model.

Fine mapping consists of the saturation of a map region to better localize the identified QTL and MTL. The more markers one map has, the smaller the average interval size and, thus the higher the map resolution. Currently, SNP markers are the most suitable markers to increase the resolution of the initial maps developed with SSRs or increase the resolution of specific regions of the map. SNP markers are the most abundant molecular marker, estimated to exist more than 1 per 1,000 bp, and widely distributed throughout the genome although their occurrence and distribution varies among species. Even degraded DNA samples can be used for SNP detection and hundreds of markers can be assayed in one chip. Furthermore, SNPs that occur in both coding and noncoding regions of genes as well as in intergenic regions may have functional consequences. SNPs can influence gene function by changing the encoded amino acid (non-synonymous SNPs). These functional effects are the biological cause for the association of SNPs with different agronomic traits in plants. In *Prunus*, Aranzana et al. (2012) found an average of one SNP every 598 bp, and this variability was higher in noncoding (one SNP every 390 noncoding bp) than in coding (one SNP by 1,850 coding bp) regions, although we have to note the difficulty of developing SNPs from noncoding regions when no reference physical map is available as the case of most *Prunus* species with the exception of peach. SNP markers are rapidly becoming the markers of choice for applications in breeding due to the huge numbers developed using next generation DNA and RNA sequencing technology (Bundock et al. 2009; Edwards and Batley 2010; Jackson et al. 2011; Martínez-Gómez et al. 2011).

Ahmad et al. (2011) described the application of DNA-Seq technologies to identify high-frequency SNPs distributed throughout the peach genome. They discovered 6,654 SNPs distributed on all the peach genome scaffolds with ~1 SNP/40,000 nucleotide bases. In addition, a set of 9,000 SNPs has recently been selected in peach using DNA-Seq for inclusion in a genotyping chip (peach 9 K SNP array) for variability studies, linkage mapping, and association mapping analysis (Verde et al. 2012). Koepke et al. (2012) also described the identification of 2,243 putative SNPs in 887 contigs after stringent filtering of RNA-seq data from cherry transcriptomes, and Peace et al. (2012) verified 1,825 polymorphic SNPs in sweet cherry and 2,058 polymorphic SNPs in sour cherry including these SNPs in the RosBREED cherry 6 K SNP array v1. The main advantage of these SNP chips for developing molecular markers is the simultaneous analysis of thousands of polymorphisms in a single experiment. In addition, SNP genotyping utilizes an array platform that is cost effective and can easily be automated.

The development of high-density maps incorporating thousands of SNPs will provide researchers with more powerful tools for loci identification in the different *Prunus* due to the high number of markers available (Eduardo et al. 2013; Martínez-García et al. 2013a). These markers are of special interest in the case of self-incompatible *Prunus* species with lower LD (Aranzana et al. 2010; Khan and Korban 2012) where the linkage of genes and DNA markers is more difficult. Klagges et al. (2013) have elaborated two maps spanning 752.9 and 639.9 cM with an average distance of 1.1 and 0.9 cM using the described cherry 6 K SNP array. These maps displayed high synteny and colinearity between each other, with the *Prunus* bin map, and with the peach genome v1.0 for all eight LGs (G1–G8). In addition, Martínez-García et al. (2013b) have recently analyzed the prediction of the effects associated with different SNPs linked to fruit quality traits in peach. A total of 2,163 effects were detected by these authors, also extending the list of genes and proteins that could be related to these traits.

One potential goal of the GDR *Prunus* database would be to directly align candidate genes from the reference genomes, transcripts, SNPs, and other mapping features to QTLs and MTLs to assist researchers in identifying candidate genes or markers linked to agronomic traits of interest. QTL and MTL map locations measured by linkage distances in centimorgan (a statistical unit) must be converted into physical distances in base pair (a physical unit) (Hu et al. 2012), integrating quantitative genetics (natural variation induced through sexual crossing) and molecular genetics (at the base pair level) data. The final goal is to convert conventional QTL into expression QTL (eQTL). The eQTLs are genetic regions identified by applying QTL localization methods to data on the abundance of transcripts in a segregating population with variable genotypes (Druka et al. 2010; Li et al. 2012). eQTLs are derived from polymorphisms in the genome that result in differential measurable transcript levels (Boopathi 2013).

Map-based cloning (MBC) and association mapping approaches to isolate genes or alleles for functional analysis

mainly from MTL map information and physical maps have been successfully applied to a reduced number of traits such as the *evergrowing* locus (*Ev*), self-compatibility genes (*S*), *Plum pox virus* (*PPV*) resistance genes, nematode resistance genes (*Ma*, *Mi*, *Mja*), and flesh color (white/yellow) in peach (*Y*) (Horn et al. 2012; Esmenjaud and Srinivasan 2012). However, often the region of the QTL spans 5–10 cM (thousands of base pair), with the likelihood of hundreds of genes being present within this region, making the identification of the gene(s) linked to the traits difficult (Khan and Korban 2012). In addition, the markers identified in preliminary genetic mapping studies are seldom suitable for MAS without further testing, validation, and additional development (Boopathi 2013). Gametophytic self-compatibility (or self-incompatibility) was the first trait selected by molecular methods in almond breeding programs (Gradziel et al. 2001), and currently, MAS is only being applied to nematode resistance in plum rootstock breeding (Claverie et al. 2004) and *Plum pox virus* resistance in apricot breeding (Soriano et al. 2012). The last example of MBC is the monogenic trait flesh color (white/yellow) in peach, where different genes (Carotenoid Cleavage Dioxygenase, *ccd4*) have been recently identified controlling this trait (Adami et al. 2013).

Furthermore, the above-mentioned synteny among *Prunus* genomes (Arús et al. 2006; Jung et al. 2009) and transcriptomes (Martínez-Gómez et al. 2011) offers additional molecular opportunities for the identification of loci linked to agronomic traits. We can consider the *Prunus* genus as a single gene pool (Jung et al. 2009). In this regard, a similar order and transferability of molecular markers has been observed in the different *Prunus* maps when compared to T×E (Aranzana et al. 2003). This synteny has also been studied in *Prunus* in relation to other genera inside the Rosaceae family (Dirlewanger et al. 2004b; Arús et al. 2006; Shulaev et al. 2008; Jung et al. 2012). In addition, syntenic linkage groups can result in similar alleles and homologous genes including orthologous genes (encoding protein with the same function) and paralogous genes (encoding protein with related but non-identical functions) (Shulaev et al. 2008).

The comparison of genomes of different species allows an evolutionary view of the genome by identification of conserved fragments followed by comparative mapping (Dirlewanger et al. 2012; Sargent et al. 2012; Jung et al. 2012). Genetic and physical maps constructed in one species can be compared by means of common markers with closely related species. These comparative maps can be used to study genome evolution and to make inferences about the organization of genes, repeat sequences, and other genomic features. Meta-analysis of QTLs is emerging as an essential tool for quantitative aggregation and synthesis of knowledge from independent studies on the same or similar trait analyses in one species or different species (Wu and Hu 2012). For example, Marandel et al. (2009b) performed a meta-analysis of QTL for PPV resistance in apricot integrating the information of different maps in a consensus map. In addition, Hu et al. (2012) indicated that QTL data from multiple experiments can be aligned and combined to describe a generalized QTL using the original QTL as metadata. Finally, Dirlewanger et al. (2012) have recently used this strategy to compare the genetic determinism of flowering date and maturity date in peach, apricot, and sweet cherry, integrating different QTL data from four different families using meta-QTL analysis.

Conclusions

To date, 670 QTLs and 90 MTLs have been described and linked to a total of 110 agronomic traits (86 of these traits characterized as quantitative and 24 as Mendelian) related to tree development, pest and disease resistance, flowering, ripening, and fruit and seed quality. However, despite the substantial number of QTLs linked to agronomic traits, the development of suitable markers for assisted selection in *Prunus* breeding programs has been very limited. In this context, application of the full range of genomics tools presents new molecular challenges and opportunities in the labeling of agronomic genes and the development of efficient marker-assisted selection strategies in *Prunus* to increase breeding outcomes. The development of a comprehensive database for QTLs linked to agronomic traits in *Prunus* integrated with other genetic, genomic, and breeding data should therefore be of great interest and utility. This GDR *Prunus* database will be useful for data comparison, data mining, and meta-analysis of the huge range of information disseminated in 70 publications. The integration of QTL with other genomic and breeding data will open the door for application of the available information in the post-genomic era, characterized by the availability of a complete genome and new high-throughput DNA and RNA analysis technologies. In this regard, we are facing a revolution in the use of new high-throughput analysis techniques, which may mean a scientific paradigm shift in *Prunus* QTL identification and application in breeding.

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