3 Cherry

E. Dirlewanger[1], J. Claverie[1], A. Wünsch[2], and A. F. Iezzoni[3]

[1] Institut National de la Recherche Agronomique, Centre de Bordeaux, Unité de Recherches sur les Espèces Fruitières et la Vigne, BP 81, 33883, Villenave d'Ornon, Cedex. France
e-mail: dirlewanger@Bordeaux.inra.fr
[2] Unidad de Fruticultura, CITA de Aragon, Apdo. 727, 50080 Zaragoza, Spain
[3] Department of Horticulture, Michigan State University, East Lansing, Michigan 48824 1325, USA

3.1 Introduction

The cherry is one of the most popular temperate fruit crops despite of its relatively high price. The fruits are attractive in appearance, because of their bright, shiny skin color, and their subtle flavor and sweetness are appreciated by most consumers. Compared to other temperate fruits, such as apple and peach, breeding improvements for cherries have been slow. The long generation time and the large plant size of cherry trees severely limit classical breeding. Thus, the integration of molecular markers in breeding programs should be a powerful tool. Only a few genetic linkage maps are available for sweet or sour cherry and quantitative trait loci (QTLs) were reported only for sour cherry. Until now, most of the efforts were concentrated on the use of molecular markers in order to (i) identify the *S*-alleles controlling gametophytic self-incompatibility, (ii) characterize cultivars, and (iii) assess genetic diversity.

3.1.1 Brief History of the Crop

Prunus avium L. includes sweet cherry trees cultivated for human consumption and wild cherry trees used for their wood, also called mazzards (Webster 1996). The sweet cherry is indigenous to parts of Asia, especially northern Iran, Ukraine, and countries south of the Caucasus mountains. In Europe, the Romanian and Georgian wild cherry trees appeared to be very differentiated from those of central and western Europe (Tavaud 2002). The Georgian wild cherry trees were the most genetically diverse suggesting that this area could have been a main glacial refuge. The ancestors of the modern cultivated sweet cherries are believed to have originated around the Caspian and Black Seas, from where they have slowly spread. This phenomenon was driven initially by birds. Sweet cherries are now cultivated commercially in more than 40 countries around the world, in temperate, Mediterranean, and even subtropical regions. Its natural range covers the temperate regions of Europe, from the North part of Spain to the Southeastern part of Russia (Hedrick et al. 1915). They prefer regions with warm and dry summers, but require adequate rainfall or irrigation during the growing season for production of fruit with appropriate size for marketing. Rainfall at harvest time may reduce the commercial potential of the production by inducing fruit cracking.

Fruit of *Prunus cerasus* L., the sour cherry tree, are mainly used for processed products such as pies jam or liquor. Sour cherry originated from an area very similar to that of sweet cherry, around the Caspian Sea and close to Istanbul. While sour cherry is less widely cultivated than sweet cherry, large quantities of sour cherries are produced in many European countries and in the USA. Most of these are used in processing and processed cherry products are sold worldwide.

Prunus fruticosa Pall., the ground cherry tree, is sometimes used as rootstocks for other *Prunus* species. This species is widespread over the major part of central Europe, Siberia and Northern Asia (Hedrick et al. 1915).

The duke cherries, which result from crosses between *P. avium* and *P. cerasus*, are cultivated at a much smaller scale. Different names have been given to this species like *Prunus acida* Dum, *Cerasus regalis*, *Prunus avium* ssp. *regalis*, but the name used today is *P. x gondouinii* Rehd. (Faust and Suranyi 1997; Saunier and Claverie 2001). Duke cherry trees are intermediate for their tree and fruit characteristics compared to their progenitors.

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3.1.2 Botanical Descriptions

All cherry species belong to the *Cerasus* subgenus of the *Prunus* genus, part of the *Rosaceae* family. The majority of cultivated cherry trees belong to *Prunus avium* L. and *Prunus cerasus* L. species. Together with *Prunus fruticosa* Pall., these species and their interspecific hybrids constitute the *Eucerasus* section of the *Cerasus* subgenus, based on morphological criteria (Rehder 1947; Krussmann 1978). This classification and the monophyletic origin of the *Eucerasus* clade have been confirmed by chloroplast DNA variation analysis (Badenes and Parfitt 1995).

A large amount of morphological polymorphism is observed among *P. avium*, *P. fruticosa* and *P. cerasus* species. Multivariate analysis on sour cherry revealed continuous variation between the *P. avium* and *P. fruticosa* traits throughout the geographic distribution of the species. In Western Europe, *P. cerasus* trees look like *P. avium* whereas in Eastern Europe, *P. cerasus* is closer to *P. fruticosa* (Hillig and Iezzoni 1988; Krahl et al. 1991). This continuum of morphological characteristics makes the species assignation difficult when considering only phenotypic traits. The sweet cherry is a deciduous tree of large stature, occasionally reaching almost 20 meters in height, with attractive peeling bark. The sour cherry is a small tree, or more often a deciduous bush, which suckers profusely from the base. It has smaller leaves and flowers than the sweet cherry. Concerning the fruits, sweet cherries fruits are usually split into three groups: Mazzards, often wild types with small inferior fruits of various shapes and colors: Guignes, Hearts or Geans, with soft-fleshed fruits and the Bigarreaux with hard-fleshed, heart-shaped, light-colored fruits. Sour cherries cultivars are generally classified as Amarelles (or Kentishand) and as Griottes (or Morellos). Amarelles have pale red fruits flattened at the ends and uncolored juice. Griottes have, in contrast, dark spherical fruits and dark-colored juice. A third group of sour cherry cultivars, called Marasca, are characterized by small, very black-red colored and bitter fruit whose juice is of the best quality for making maraschino liquor. Marasca cultivars are sufficiently distinct to have been classified by early botanists as a subspecies of *P. cerasus* (*Prunus cerasus* Marásca (Reichb.) Schneid, Redhder 1947).

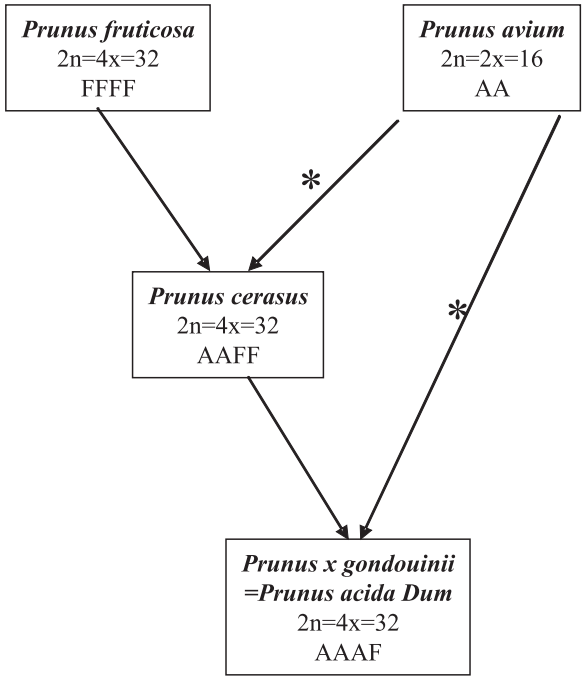

Fig. 1. Relationships and genome constitution among the species of the Eucerasus section. * *P. avium* is thought to produce diploid gametes. A and F are haploid genomes coming from *P. avium* and *P. fructicosa* respectively

3.1.3 Genome Contents

Prunus avium has a diploid genome (AA, $2n = 2x = 16$) and small haploid genome size (338 Mb) (Arumuganathan and Earle 1991) bigger than the genome of peach (290 Mb) which is the smallest *Prunus* genome evaluated to date.

Prunus fruticosa, the ground cherry tree, is a tetraploid wild species ($2n = 4x = 32$) believed to be (FFFF). The genome size is still unknown.

Prunus cerasus is an allotetraploid species (AAFF, $2n = 4x = 32$), with a genome size of 599 Mb, supposed to result from natural hybridization between *P. avium* (producing unreduced gametes) and *P. fruticosa* (Fig. 1). This origin was first suggested by Olden and Nybom (1968) who observed that artificial hybrids between tetraploid *P. avium* and *P. fruticosa* were very similar to *P. cerasus*. Isozyme analysis, genomic in situ hybridization and karyotype analysis further confirmed the hybrid origin of *P. cerasus* (Hancock and Iezzoni 1988; Santi and Lemoine 1990; Schuster and Schreiber 2000). The patterns of inheritance of seven isozymes in different crosses of sour cherry indicated that *P. cerasus* might be a segmental allopolyploid (Beaver and Iezzoni 1993; Beaver et al. 1995).

Studies based on cpDNA markers detected two distinct chlorotypes in *P. cerasus* which strongly suggest that crosses between *P. avium* and *P. fruticosa* have occurred at least twice to produce sour cherry (Badenes and Parfitt 1995; Iezzoni and Hancock 1996; Brettin et al. 2000). Moreover, these works showed that, most of the time, *P. fruticosa* was the female progenitor of *P. cerasus,* but in few cases, *P. avium* was the female parent due to the formation of unreduced ovules. Tavaud et al. (2004) demonstrated that specific alleles in *P. cerasus* were not present in the A genome of *P. avium* and probably came from the F genome of *P. cerasus*. Recent analysis with cpDNA and microsatellite markers show that some *P. cerasus* share the same chloroplastic haplotype as some *P. fructicosa*, and that some microsatellite markers are shared by both species (A. Horvath, personal communication). Triploid hybrids through the fusion of normal gametes of *P. avium* and *P. fruticosa* occur naturally but remain sterile. Due to this sterility and many unfavorable *P. fruticosa* traits, these triploids are not clonally propagated by humans (Olden and Nybom 1968).

P. x gondouinii Rehd is an allotetraploid (AAAF, $2n = 4x = 32$) species stemming from the pollinization of sour cherry by unreduced gametes of sweet cherry (Iezzoni et al. 1990). These hybrids are often sterile, due to disturbances during meiosis, but they are clonally propagated by human.

3.1.4 Economic Importance

Worldwide, 375,000 Ha of sweet cherry and 248,000 Ha of sour cherry are cultivated giving a total production of 1,896,000 Mt and 1,035,000 Mt respectively (FAO 2005). The main production areas in the world for sweet and sour cherries are located in Europe (953,000 Mt and 711,000 Mt), Asia (653,000 Mt and 208,000 Mt) and North America (228,000 Mt for sweet cherry and 115,000 Mt for sour cherry) (FAO 2005). However, a huge increase in sweet cherry hectares in production occurred 10 years ago in the Southern hemisphere especially in Chile and Argentina. In Chile, the cultivated area increased by four times in two years and nearly all the production is exported to the USA and Europe. In the Northern hemisphere, sweet cherry production is mainly located in Europe but major shifts are occurring in European production. France which was one of the main producers in Europe (100 to 120,000 tons) reduced its production by two in 2003 and 2004 (57,000 tons), and at the same time Spain doubled its production, especially with early maturing varieties. In the next following years, Turkey may become the leading world producer of sweet cherries.

3.1.5 Breeding Objectives

The main breeding objectives for sweet cherry are:

- large, attractive and good-flavored fruits,
- short juvenile phase,
- large and constant yields,
- reduced susceptibility to fruit cracking,
- self-compatibility,
- improved resistance or tolerance to diseases, especially bacterial canker induced by *Pseudomonas* mors pv. *prunorum* and *P. syringae*.

Regular yields and superior fruit quality are the two main objectives of sour cherry breeding programs. Breeding for disease resistance in sour cherry is concentrated on resistance to cherry leaf spot caused by *Blumeriella japii.*

Yields per hectare vary by the country of production, the commercial use (for fresh market or for industry) and the training system. The average yield ranges from 8 to 10 t/ha in classical orchards but can reach 30 to 40 t/ha for an intensive industrial orchard. The highest limitation to the development of the cherry culture is the high cost required to manually pick the fruit as manual picking can account for 70% of the production price. The yield of the pick up can be 6 to 8 Kg/ha and by person in a traditional orchard and can be 30 Kg/ha in intensive orchards. Several breeding programs led to the selection of new varieties that can be harvested partially with machines, such as 'Sweetheart' and 'Van' cultivars that can be harvested without the stem. In the same time, a better knowledge of the architecture of the tree led to new ways of orchards training.

Thanks to classical breeding programs, a large number of cultivars are now available. Within the last 10 years, 20 new varieties are gaining wide interest internationally such as 'Earlise' (early season), 'Summit' (middle season) and 'Sweetheart' (late season). Each of them should be widely cultivated in the next 15 to 20 years.

Classical breeding programs are time consuming, especially for cherry that requires a minimum of 3–5 years of growth before flowering and fruit pro-

duction. Prior knowledge of linkage relationships between marker loci and important flower and fruit characteristics will facilitate and shorten the selection of promising individuals. Consequently, marker-assisted selection would be especially beneficial for sweet and sour cherry breeding.

3.2 Construction of Genetic Maps

The construction of genetic maps is useful for localisation of important genes controlling both qualitative and quantitative traits in numerous plant species and, then, for improving and shortening breeding selection (Tanksley et al. 1989). In *Prunus*, many mapping studies were done on peach (Belthoff et al. 1993; Chaparro et al. 1994; Rajapakse et al. 1995; Dirlewanger et al. 1998; Lu et al. 1998; Dettori et al. 2001; Yamamoto et al. 2001) or on interspecific crosses between peach and other *Prunus* species (Foolad et al. 1995; Joobeur et al. 1998; Jauregui et al. 2001; Bliss et al. 2002; Dirlewanger et al. 2004a; Quilot et al. 2004). An highly saturated linkage map including 562 markers, based on segregation analyses of an almond (cv. 'Texas') × peach cv. ('Earlygold') F_2 population serves as a reference map for the *Prunus* scientific community (Dirlewanger et al. 2004b). Several genetic linkage maps were also obtained for other *Prunus* such as almond (Viruel et al. 1995; Joobeur et al. 2000) and apricot (Hurtado et al. 2002; Lambert et al. 2004). Despite the potential usefulness of genetic linkage maps for sweet or sour cherry, saturated cherry linkage maps have not yet been constructed.

In the subgenus *Cerasus*, several maps have been published using five segregating populations (Table 1). Until now, only partial maps for sweet or sour cherry are available. The earliest of them was constructed in a sweet cherry using random amplified polymorphic DNA (RAPD) and allozyme analysis of 56 microspore-derived callus culture individuals of the cv. 'Emperor Francis' (Stockinger et al. 1996). Two allozymes and 89 RAPD markers were mapped to 10 linkage groups totalling 503 cM. Interestingly, another map integrating isozyme genes exclusively, was obtained using data from two interspecific F_1 cherry progenies: *P. avium* 'Emperor Francis' × *P. incisa* E621 and *P. avium* 'Emperor Francis' × *P. nipponica* F1292 (Bošković and Tobutt 1998). This map, one of the most exhaustive ever made with isozyme markers in the Plant Kingdom, included a total of 47 segregating isozyme genes, from which 34 were aligned into seven linkage groups.

Another genetic linkage map is in progress in the INRA of Bordeaux (France) for sweet cherry using an intraspecific F_1 progeny including 133 individuals from a cross between cultivars 'Regina' and 'Lapins'. These cultivars were chosen as parents for their distinct agronomic characters and especially because they differ for resistance to fruit cracking which is a limiting factor in sweet cherry production. 'Regina' is resistant and 'Lapins' is susceptible to fruit cracking. 'Lapins' is a self-compatible cultivar as opposed to 'Regina'. Moreover, they differ for several other characters: blooming and maturity dates, peduncle length, and fruit color, weight, firmness, titratable acidity and refractive index. Preliminary maps of each parent and their comparison with the referenced *Prunus* map 'Texas' × 'Earlygold' (T×E) is described by Dirlewanger et al. (2004b). These maps include microsatellite markers, 30 of which are located in the 'Régina' map are anchors marker with T×E map, 28 located in the 'Lapins' map are anchors with T×E map. Only one non-collinear marker was detected but for all other markers the location in the maps were in the homologous linkage group. These results are in agreement with the high level of synteny among the *Prunus* genus (Arús et al. 2005). The two sweet cherry maps will be used for detection of QTLs involved in fruit quality as soon as the progeny produces fruits, in 2006.

A sweet cherry genetic linkage map is also in progress at Michigan State University (US) from a F_1 progeny from a cross between a wild forest cherry with small (~2 g) highly acidic dark-red colored fruit (NY54) and a domesticated variety with large (~6 g), yellow/pink, sub-acid fruit 'Emperor Francis' (EF). The F_1 population is composed of approximately 700 individuals, 200 of them will be used for map construction and initial QTL analysis. The remaining progeny will be used for fine mapping major QTL identified. The objective of the study is to identify QTLs that control fruit quality traits that have been improved during domestication. In addition, this cross is fully compatible and progeny segregation for the *S*-locus fits the expected 1:1:1:1 ratio (Ikeda et al. 2005). This population will be used to fine map the *S*-locus region due to the large family size and the absence of skewed segregation that exists in many of the *Prunus* mapping populations.

Table 1. Cerasus linkage maps

Population	Type (nb. of individuals)	Nb. of markers in the map	Marker type	Linkage groups	Total distance (cM)	Longest gap (cM)	Unlinked markers	References
P. avium 'Emperor Francis'	Microspore-derived calli	89	RAPD (90), isozyme (2)	10	503	27	3	Stockinger et al. 1996
P. avium 'Napoleon' × ***P. incisa*** E621	F1 (63)	34	Isozymes	7	174 r.u.[1]	24 r.u.	13	Bošković and Tobutt 1998
P. avium 'Napoleon' × ***P. nipponica*** F1292	F1 (47)							
P. avium 'Régina' (R) × 'Lapins' (L)	F1 (133)	R: 68 L: 54	SSRs	11 9	639 495	26 30	1 10	Dirlewanger et al. 2004b
P. avium NY54 × 'Emperor Francis'	F1 (200)	in progress						Iezzoni 2004
P. cerasus 'Rheinische Schattenmorelle' ('RS') × 'Erdi Botermo' ('EB')	F1(86)	RS: 126 EB: 95 Consensus: 160	RFLPs RFLPs RFLPs (144) SSRs (16)	19 16 19	461 279 442	19 20 17	17 23	Wang et al. 1998 Canli 2004a

[1] Distance is measured in recombination units (r.u.)

In sour cherry, linkage maps were constructed at Michigan State University (US) from 86 individuals from the cross of two cultivars; 'Rheinische Schattenmorelle' (RS) and 'Erdi Botermo' (EB). Since sour cherry is a tetraploid, informative restriction fragment length polymorphisms (RFLPs) were scored as single-dose restriction fragments (SDRF) according to Wu et al. (1992). A genetic linkage map was constructed for RS that consists of 126 SDRF markers assigned to 19 linkage groups covering 461 cM (Wang et al. 1998). The EB linkage map had 95 SDRF markers assigned to 16 linkage groups covering 279 cM (Wang et al. 1998). Due to the limited number of shared markers between the RS × EB map compared to other *Prunus* maps, putative homologous linkage groups could only be identified in for the *Prunus* LGs 2, 4, 6, and 7. The other linkage groups were arbitrarily numbered from the longest to shortest and therefore the sour cherry linkage groups numbers have not been rigorously aligned with that of the *Prunus* consensus map. The RS × EB population was subsequently scored using 10 *Prunus* microsatellite primer pairs (Canli 2004a) and a consensus map of 442 cM, less than the previously reported RS map of 461 cM, was constructed. A total of 16 microsatellite markers were added to 10 of the 19 linkage groups; however, the linkage groups were not re-numbered to reflect these markers. In addition, four of the microsatellite primer pairs identified duplicate linked markers. This "double mapping" of a marker is due to the inclusion of progeny individuals exhibiting tetrasomic inheritance for that linkage group. If this correction had been done by Canli (2004a), it is likely that the number of microsatellite markers added to the map would be reduced to twelve.

The difficulty of identifying SDRFs and eliminating progeny that resulted from non-homologous pairing for the linkage group under study, illustrate the complexity of linkage mapping in a segmental allopolyploid. Therefore, future work at Michigan State University will concentrate on linkage map construction in the diploid sweet cherry.

3.3 Gene Mapping and QTLs Detected

In sour or sweet cherries most of the agronomically important traits have complex inheritance. Only self-incompatibility (SI) is controlled by a single locus (*S*) with multiple alleles, and fertilization only takes

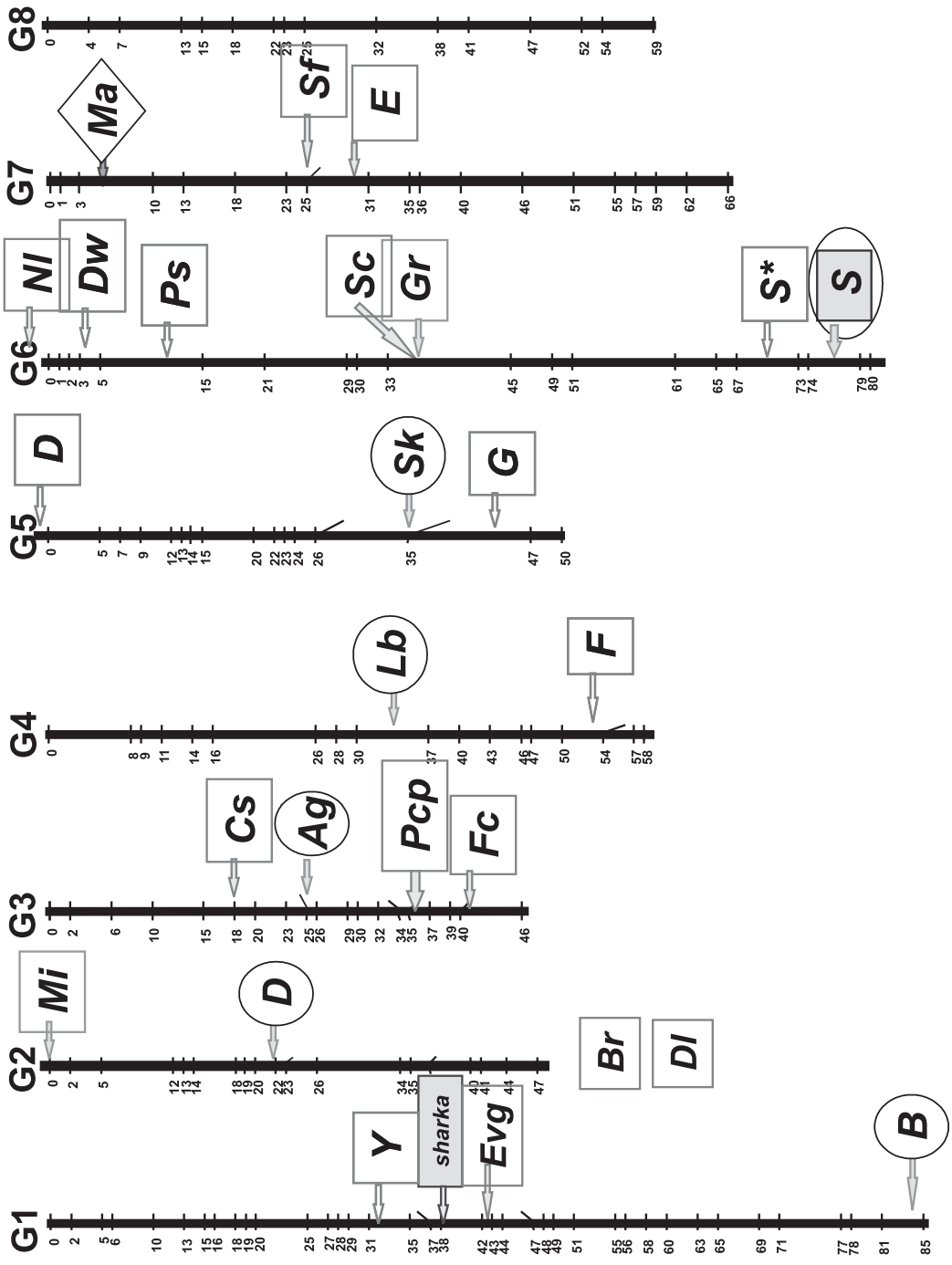

Fig. 2. Approximate position of 28 major genes mapped in different populations of apricot (gray background), peach (square), almond or almond × peach (ring), and Myrobalan plum (rhombus) on the framework of the *Prunus* reference map (Dirlewanger et al. 2004b). Gene abbreviations correspond to: *Y*, peach flesh color; *B*, almond/peach petal color; *sharka*, plum pox virus resistance; *B*, flower color in almond × peach; *Mi*, nematode resistance from peach; *D*, almond shell hardness; *Br*, broomy plant habit; *Dl*, double flower; *Cs*, flesh color around the stone; *Ag*, anther color; *Pcp*, polycarpel; *Fc*, flower color; *Lb*, blooming date; *F*, flesh adherence to stone; *D*, non-acid fruit in peach, *Sk*, bitter kernel; *G*, fruit skin pubescence; *Nl*, leaf shape; *Dw*, dwarf plant; *Ps*, male sterility; *Sc*, fruit skin color; *Gr*, leaf color; *S**, fruit shape; *S*, self-incompatibility (almond and apricot); *Ma*, nematode resistance from Myrobalan plum; *E*, leaf gland shape; *Sf*, resistance to powdery mildew. Genes *Dl* and *Br* are located on an unknown position of G2

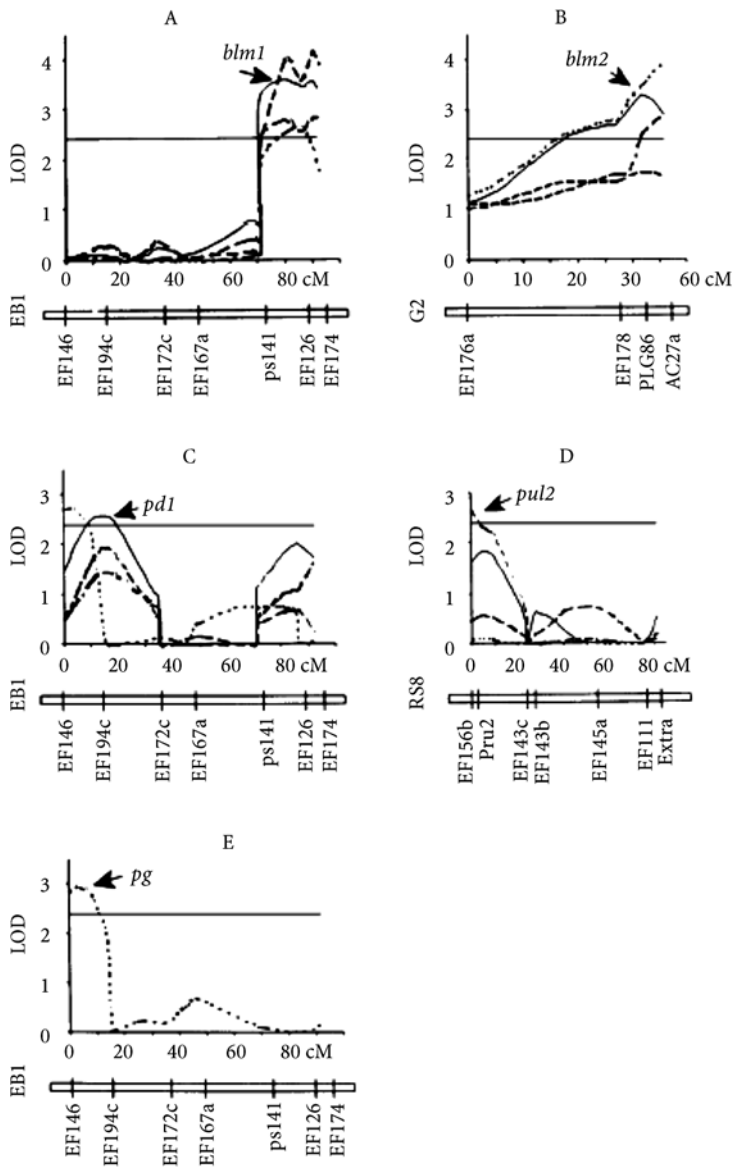

Fig. 3. QTLs detected for flower and fruit traits in sour cherry (Wang et al. 2000). LOD scores for bloom date on linkage groups EB 1 (*blm*1) (**A**) and Group 2 (*blm*2) (**B**); pistil death (*pd*) on linkage groups EB 1 (**C**) and RS 8 (**D**); pollen germination percentage (*pg*) on linkage group EB 1 (**E**). Peak LOD scores for each trait are indicated by *arrows*. Linkage groups are shown below the *x-axes*. The *horizontal line* indicates the level of significance at LOD = 2.4. *Curves* represents results from individual years of 1995 (· · ·), 1996 (- - -), 1997 (– –) and over years (—)

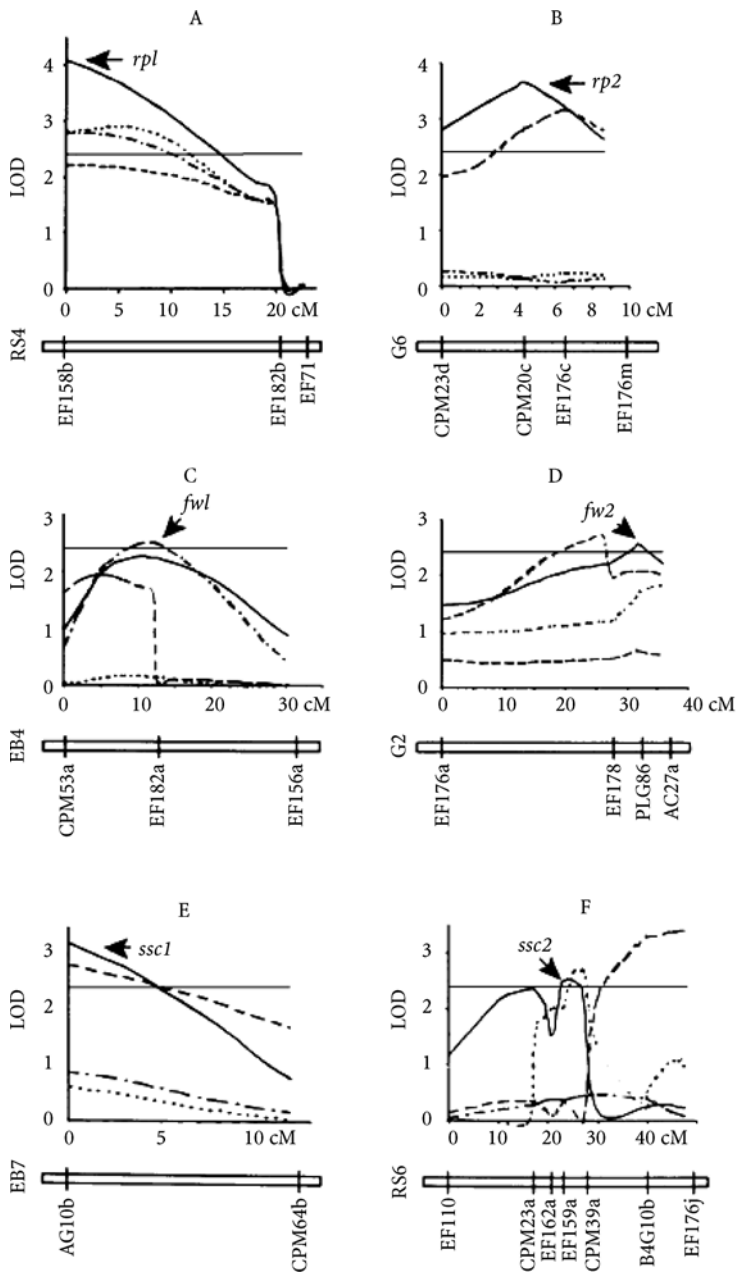

Fig. 3. (continued) LOD scores for ripening date on linkage groups RS 4 (*rp1*) (**A**) and Group 6 (*rp2*) (**B**); fruit weight on linkage groups EB 4 (*fw1*) (**C**) and Group 2 (*fw2*) (**D**); soluble solids concentration on linkage groups EB 7 (*ssc1*) (**E**) and RS 6 (*ssc2*) (**F**)

place when the *S* allele in the haploid genome of the pollen is different from the two *S* alleles in the diploid tissue of the style. In contrast, blooming and ripening time, flower bud and pistil death and characters controlling fruit quality are quantitative traits. The self-incompatibility locus is located in the distal part of the linkage group 6 in almond (Ballester et al. 1998; Bliss et al. 2002) and in apricot (Vilanova et al. 2003) on the same area (Fig. 2; Dirlewanger et al. 2004b). According to the high level of synteny within *Prunus* (Arús et al. 2005), the gene S may be located on the same place in cherry.

Linkage relationships between molecular markers and agronomically important quantitative traits have been extensively studied in many tree fruit crops. In peach many QTLs involved in fruit quality (Dirlewanger et al. 1999; Etienne et al. 2002; Quilot et al. 2004) and diseases resistance (Quarta et al. 1998; Viruel et al. 1998; Foulongne et al. 2003) have been reported. However, the only QTL study published to date in cherry is a QTL analysis of flower and fruit traits using the sour cherry RS × EB linkage mapping population (Wang et al. 1998). Eleven QTLs (LOD > 2.4) were identified for six traits (bloom time, ripening time, % pistil death, % pollen germination, fruit weight, and soluble solids concentration) (Wang et al. 2000, Fig. 3). The percentage of phenotypic variation explained by a single QTL ranged from 12.9% to 25.9% (Wang et al. 2000). Subsequently, three microsatellite markers were identified that mapped within the putative location of the previously described QTLs (Wang et al. 2000) for bloom time (*blm2*), pistil death (*pd1*) and fruit weight (*fw2*), respectively (Canli 2004a). Unfortunately these three microsatellite markers were not used in QTL analyses to determine their location relative to the previously published QTLs.

The identification of bloom time QTL is of particular interest for cherry breeding as the development of new cultivars with late bloom would significantly reduce the probability of spring freeze damage to the pistils (Iezzoni 1996). Sour cherry exhibits extreme diversity for bloom time with many cultivars blooming exceedingly late in the spring (Iezzoni and Hamilton 1985; Iezzoni and Mulinix 1992). This late bloom character in sour cherry is likely due to the hybridization and continued introgression with the very late blooming ground cherry, *P. fruticosa*.

Bloom time in cherry is a quantitative trait; however its high broad sense heritability (0.91) led to the identification of two bloom time QTL, *blm*1 and *blm*2, in the RS × EB population (Wang et al. 2000). Unfortunately the genetic effects of these two QTL alleles from EB were to induce early bloom. To identify QTL with alleles conferring late bloom time, a second mapping population between the mid-season blooming 'Balaton®' and late blooming 'Surefire' was developed at Michigan State University (US). The population exhibited transgressive segregation for bloom time permitting a bulked segregant approach to identify markers linked to bloom time QTL (Bond 2004). To date, a third QTL for late bloom, named *blm*3, was identified using AFLP markers that is significantly associated with late bloom using Single Marker QTL analysis (Bond 2004). This QTL allele is present in Surefire and confers late bloom time. We are in the process of determining the linkage map location of this QTL. Using this same mapping population, two AFLP markers were identified that differed between the early and late bulks (Canli 2004b). However these markers were never scored on the 'Balaton' × 'Surefire' progeny population and the marker results described could not be repeated.

3.4 Marker-Assisted Breeding for Self-Incompatibility and Molecular Cloning

3.4.1 Self-Incompatibility

Sweet cherry, like in other Rosaceae species, operates a strict self-incompatibility system that has been naturally selected to promote out-breeding (De Nettancourt 2001). This mechanism avoids the fertilization of flowers of one genotype by its own pollen. As a consequence, commercial fruit set in this species depends upon the presence of other compatible pollinating genotypes or on the introduction of self-compatible cultivars. In sour cherry, self-incompatible as well as self-compatible genotypes have been identified (Lansari and Iezzoni 1990; Yamane et al. 2001; Hauck et al. 2002). Sour cherry is a tetraploid hybrid of diploid sweet cherry and tetraploid ground cherry, and thus the self-incompatibility mechanism seems to be conserved only in some genotypes.

The type of self-incompatibility operating in the Rosaceae is called gametophytic self-incompatibility (GSI) (De Nettancourt 2001), and it is shared by

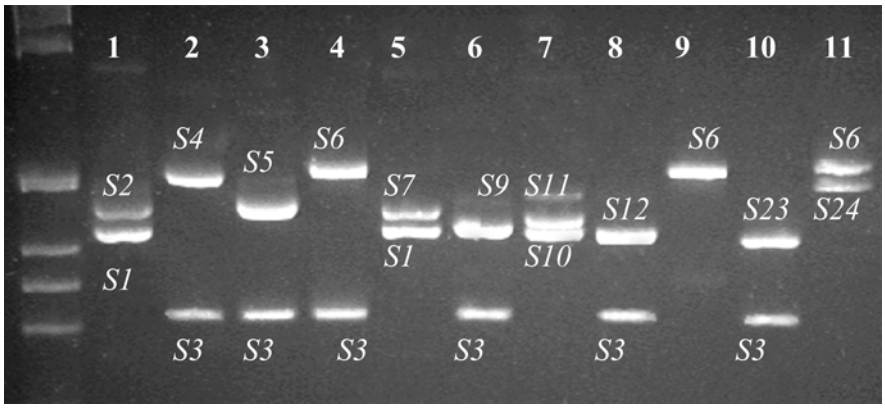

Fig. 4. PCR amplification with primers PruT2-SI32, of cultivars: *1*: Summit (S_1S_2); *2*: Bing (S_3S_4); *3*: Hedelfingen (S_3S_5); *4*: Hartland (S_3S_6); *5*: Charger (S_1S_7); *6*: Burlat (S_3S_9); *7*: Orleans 171 ($S_{10}S_{11}$); *8*: Schneiders (S_3S_{12}); *9*: Noble (S_6S_{13}); *10*: Vittoria (S_3S_{23}); *11*: Pico Colorado (S_6S_{24})

other plant families like the Solanaceae and Scrophuliaraceae. Self-incompatibility has been extensively studied at the molecular level (Kao and Tsukamoto 2004). It is now known that GSI is controlled by different genes of one polymorphic locus (S) that determine the incompatibility response of the pollen and the style (McCubbin and Kao 2000). The incompatibility phenotype of the style in sweet and sour cherry is determined by a ribonuclease called *S*-RNase (Boskovic and Tobutt 1996; Tao et al. 1999c; Yamane et al. 2001) and the specificity of the pollen is now believed to be determined by the product of the recently identified F-box gene *SFB* (Yamane et al. 2003; Ikeda et al. 2004a; Ushijima et al. 2004). These two factors would interact in an allele specific manner to give rise to the self-incompatibility reaction. The mechanism of this reaction is such that the growth of the pollen tube is inhibited in the style when the *S*-allele of the pollen factor matches either of the two *S*-alleles of the *S*-RNases expressed in the diploid style tissue. Several models have been proposed to explain in which manner these factors mediate to produce the incompatibility reaction (Luu et al. 2001; Kao and Tsukamoto 2004; Ushijima et al. 2004). In sour cherry there is evidence that a similar mechanism takes place to inhibit the growth of pollen tubes, but self-compatibility seems to be caused by different mutations in each genotype, either in the *S*-RNase, in SFB or in additional factors involved in the reaction (Hauck et al. 2002). The progress made in the knowledge of the genetic and molecular basis of the self-incompatibility reaction has allowed the application of molecular techniques in two main aspects of sweet cherry breeding, the identification of cross-compatible combinations of different varieties by the identification their S-alleles and the selection of self-compatibility.

3.4.2 S-Allele Typing

Self-incompatibility in sweet cherry prevents inbreeding but the same mechanism also prevents cross-pollination among varieties with the same *S*-alleles. This situation makes it necessary to know the *S*-haplotypes of each variety to be able to establish which cultivar combinations are compatible and, thus, to select which varieties can be inter-planted. Varieties with the same incompatibility alleles and, therefore, cross-incompatible, form an incompatibility group. Until the molecular basis of self-incompatibility were known, *S*-allele typing and incompatibility group assignment was carried out by controlled pollinations followed by the recording fruit set (Crane and Brown 1937; Matthews and Dow 1969) or by the observance of pollen tube growth in the style by fluorescent microscopy. Since the style *S*-factor in GSI was known to be a ribonuclease in Solanaceae (McClure et al. 1989), it was possible to identify *S*-alleles in sweet cherry by correlating known *S*-alleles with bands obtained from stylar proteins separated by isoelectric focusing and stained for ribonuclease activity (Boskovic and Tobutt 1996). Subsequently different bands were correlated to new incompatibility alleles (Boskovic et al. 1997).

The cloning and sequence characterization of the *S-RNases* of sweet cherry (Tao et al. 1999a, b) allowed the development of PCR and RFLP based methods to type the sweet cherry *S*-alleles. Tao et al. (1999c) developed an *S*-allele typing method based in the utilization of two pairs of PCR primers, designed in the conserved regions of the sweet cherry *S-RNase* sequences. These *S-RNase* sequences have two introns varying in length for each different allele and, consequently, PCR amplification with those primers allows to distinguish the different *S*-alleles according to the

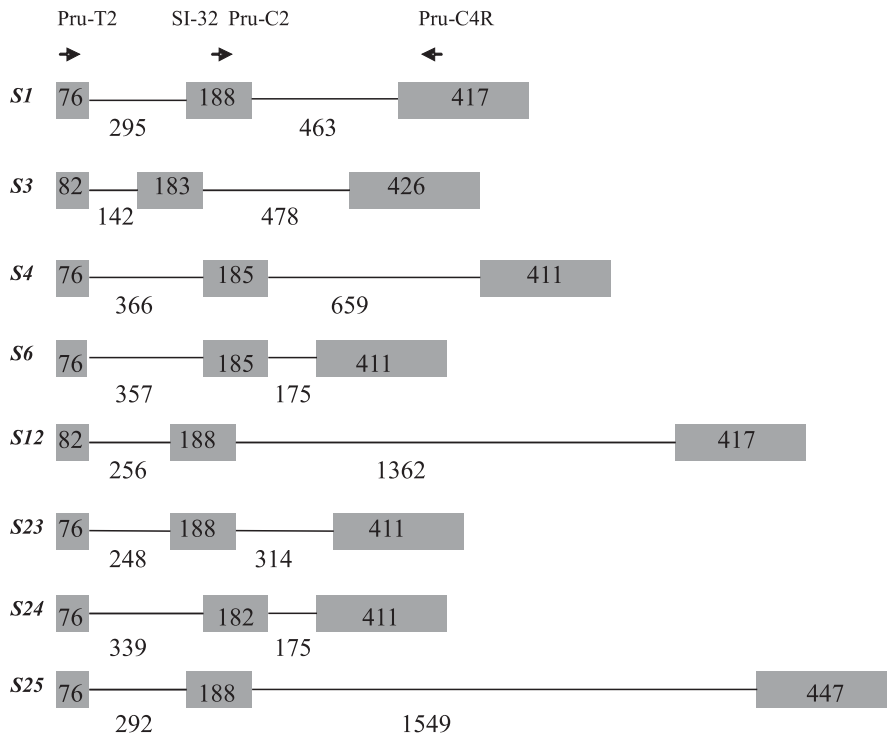

Fig. 5. Schematic representation of genomic DNA of 8 sweet cherry *S*-RNases. *Boxes* represent exons, *lines* represent introns and *arrows* represent PCR primers. PCR primers shown Pru-T2, Pru-C2 and Pru-C4R from Tao et al. (1999c), SI-32 from Wiersma et al. (2001)

size of the amplified fragments (Figs. 4 and 5). Subsequently, other sweet cherry *S*-RNases were cloned and other PCR methods based in conserved sequence primers (Wiersma et al. 2001), allele specific primers (Sonneveld et al. 2001; Sonneveld et al. 2003), and PCR followed by restriction fragment analysis (Yamane et al. 2000b) have been developed. Simultaneously RFLP profiles have also been used to assign self-incompatibility alleles to different sweet cherry genotypes (Hauck et al. 2001). The introduction of molecular methods in sweet cherry *S*-allele typing has allowed a rapid confirmation of the *S*-alleles and incompatibility groups of different cultivars reported previously, the identification of the *S*-genotype of new varieties and the identification of putative new *S* alleles by their correlation with new PCR products (Table 2; Tao et al. 1999; Yamane et al. 2000a, b; Hauck et al. 2001; Sonneveld et al. 2001; Wiersma et al. 2001; Choi et al. 2002; Zhou et al. 2002; Sonneveld et al. 2003; Wunsch and Hormaza 2004a, c, d; De Cuyper et al. 2005; Iezzoni et al. 2005).

3.4.3 Self-Compatibility

The use of self-compatible varieties in sweet cherry orchards can avoid some of the problems derived from self-incompatibility, such as the cost derived from the need to use pollinator varieties and a more erratic production (Teherani and Brown 1992). As a consequence, obtaining and introducing self-compatible varieties has been one of the main objectives of sweet cherry breeding (Brown et al. 1996). Self-compatibility was induced in sweet cherry by X-radiation, giving rise to several self-compatible seedlings (Lewis 1949). The variety 'Stella' (Lapins 1970), descendent of one of these seedlings (JI2420), is self-compatible and has been widely used as a progenitor in self-compatible sweet cherry breeding. Most of the self-compatible varieties currently used derive from 'Stella'. Self-compatibility in these genotypes is caused by a pollen function mutation in the *S4′* allele (*S4′* standing for mutated *S*4 allele), (Boskovic et al. 2000). To carry on selection of self-compatible seedlings derived from these genotypes it is necessary to differentiate the genotypes that inherited the *S4′* allele. However, since the *S4-RNase* in these genotypes is intact, it was not possible to differentiate genotypes that presented the *S4′* mutant allele from genotypes with a 'normal' *S*4 allele, by using *S*-allele typing methods based on S-RNase sequence allele diversity. It was not until the recent finding of the pollen determinant of GSI in *Prunus* (Yamane et al. 2003; Ushijima et al.

Table 2. Incompatibility groups and *S*-allele genotype of some of the most widely used sweet cherry cultivars. Nomenclature according to Tobutt et al. (2001). For extensive reviews in sweet cherry *S*-allele genotypes see Iezzoni et al. (in press) and Tobutt et al. (2001 and 2004)

Inocomp. Group	*S*-Genotype	Cultivar
I	S_1S_2	Black Tartarian, Early Rivers, Sparkle, Starking Hardy Giant, Summit
II	S_1S_3	Cristalina, Gil Peck, Lamida, Regina, Samba, Sumele, Van, Venus
III	S_3S_4	Bing, Emperor Francis, Kristin, Lambert, Napoleon, Sommerset, Star, Ulster
IV	S_2S_3	Merton Premier, Sue, Vega, Velvet, Victor, Viva, Vogue
V	S_4S_5	Late Black Bigarreau
VI	S_3S_6	Elton Heart, Governor Wood, Hartland, Satonishiki, Ambrunesa, Duroni 3
VII	S_3S_5	Hedelfingen
VIII	S_2S_5	Vista
IX	S_1S_4	Black Republican, Chinook, Merton Late, Rainier, Sylvia, Garnet, Viscount*
X	S_6S_9	Early Lyons, Black Tartarian, Ramon Oliva*
XII	S_6S_{13}	Noble*
XIII	S_2S_4	Corum, Deacon, Merchant*, Peggy Rivers, Royalton, Sam, Schmidt, Vic
XIV	S_1S_5	Valera
XV	S_5S_6	Colney
XVI	S_3S_9	Burlat, Moreau, Chelan, Tieton
XVII	S_4S_6	Elton Heart, Merton Glory, Larian
XVIII	S_1S_9	Brooks, Marvin, Earlise
XIX	S_3S_{13}	Reverchon
XXI	S_4S_9	Inge
XXII	S_3S_{12}	Princess, Schneiders
XXV	S_2S_6	Arcina
SC/O	$S_3S'_4$	Newstar, Sonata, Stella, Sunburst, Staccato, Sweetheart
SC/O	$S_1S'_4$	Celeste, Lapins, Santina, Skeena

SC: Self-compatible cultivar. O: Universal donor. *: Cultivars also reported with another *S*-allele genotype

2004;) that has been possible to establish a method that allows to determine genotypes carrying the mutated *S4′* allele (Ikeda et al. 2004b). This method is based in the identification of a 4 bp deletion in the *SFB* sequence of the *S4′* allele when compared with the normal *S4* allele. This deletion has been used to design molecular markers that identify the *S4′* allele by PCR followed by polyacrylamide gel electrophoresis or restriction digestion (Ikeda et al. 2004b). Additional sources of self compatibility, that can broaden the genetic base of cultivated germplasm and that can also be highly useful to understand the mechanism of GSI, are also being studied (Wunsch and Hormaza 2004b; Sonneveld et al. 2005).

3.5 Conclusion and Future Scope of Works

3.5.1 Genome Mapping and QTL Detection

Genetic mapping and QTL detection efforts will be continued especially in sweet cherry. Since sweet cherry is diploid, it is much easier to develop a linkage map as it avoids the difficulties associated with tetraploidy in sour cherry, e.g. partial disomic inheritance, with occasional intergenomic pairing and pre- or post-zygotic selection. According to the high level of synteny already demonstrated within the *Prunus*, results obtained in sweet cherry will be useful for sour cherry. For the same reason, we can expect that cherry will benefit from knowledge generated for a multitude of Rosaceae genera. A Rosaceae database (www.genome.clemson.edu/gdr) has recently been created with the objective of assembling all this

information and making it available worldwide to researchers working in this group of species. An international consortium led by Albert Abbott at Clemson University (Clemson, SC) has developed tools for the characterization of the *Prunus* genome. The enormous progress made during the last decade on genetic knowledge of the cultivated species of the Rosaceae, and particularly of peach as its more logical model, can be exploited for cherry.

3.5.2 Self-(in)compatibility: Molecular Cloning and MAS

The identification and characterization in the late 90s of the *S-RNase* gene in sweet cherry has accelerated *S*-allele genotyping and incompatibility group assignment, as this information can now be obtained using molecular tools like PCR. Since then, the incompatibility group of a great number of varieties has been confirmed, and the S-genotype of the most widely used cultivars has been identified. Additionally the screening of more exotic germplasm has allowed the rapid identification of new *S*-alleles. On the other side, the more recent finding of the *SFB* gene has led to the design of PCR markers for the early screening of self-compatible seedlings carrying *S4′*.

In sweet cherry self-compatibility is a priority in commercial varieties and thus the investigation of new sources of self-compatibility will allow the development of molecular markers that permit a more rapid introduction of this character in elite germplasm. This is of special importance in this species, where breeding for self-compatibility has been mostly done from the same source, with the consequent narrowing of the genetic base. Additionally, the study of self-compatibility in sweet cherry and the knowledge of how the mechanism is operating in tetraploid sour cherry, will help to understand the gametophytic self-incompatibility reaction, a mechanism, which molecular and biochemical basis are still not fully understood.

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