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Self-(in)compatibility almond genotypes: A review

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Summary

To compile self-(in)compatibility almond genotypes, a review of 133 commercial cultivars of wide geographical origin was made. The information gathered from own and mainly published work will be useful for both grower's cultivar choice when planting and for breeder's cross design when planning. The almond *S* genotypes compiled were identified using five different methods: biological (pollination tests in the field and in the laboratory) and molecular (RNases, PCR and sequencing). In most cases, genotypes were assigned after combining more than one technique. Cultivars were classified into three categories: self-incompatible (99), self-compatible (16) and doubtful self-incompatible (18). The database is divided in 9 fields (name, origin, parentage, obtention year (crossing, selection or release), *S* genotype, technique used, reference, consensus genotype, and cross incompatibility group). A study of the 27 *S* alleles already identified and their geographical distribution within the cultivated almond is also presented. The study was divided into cultivars of known and unknown parentage and the distribution of *S* alleles frequencies was uneven among the 133 cultivars. *S* allele frequencies are related to geographical origin. Some alleles (S_1, S_5, S_7 and S_8) are more frequently observed than the others among cultivars of both known and unknown parentage. In the cultivated almond, the S_f allele is only found in the Puglia region, Italy. The S_f frequency is three times higher in cultivars released from breeding programmes than in cultivars selected by growers. From the 351 resulting possible genotypes by combination of the 27 *S* alleles identified only 20 CIG (0-XIX) have been established, which represents a small fraction of the whole genetic diversity of this polymorphic gene in almond.

Introduction

The almond [*Prunus amygdalus* Batsch or *Prunus dulcis* Miller (D.A. Webb)] is a diploid species belonging to the *Rosaceous* family. Close to the cultivated almond, there are a number of wild relatives interfertile species (*P. fenzliana* (Fritsch) Lipsky, *P. kuramica* Korsh, *P. bucharica* Korsh, *P. orientalis* Duhamel, *P. spinosissima* Bunge, *P. webbi* Spach) growing in Europe, Central Asia and the Middle East, which could have contributed through domestication to form the gene pool of the cultivated almond (Browicz & Zohary, 1996; Grasselly & Duval, 1997; Zohary & Hopf, 2000). Almond is a Mediterranean crop and is traditionally cultivated in the Mediterranean basin, Southwest and Middle Asia. More recently, almond cultivation was also introduced into areas with climatic Mediterranean type. Almond is one of the oldest cultivated nut trees in the world. It is of large economic importance, its nuts being consumed directly after toasting or used for transformation into marzipans, sweets and cakes. Its breeding has mainly relied on selection through the ages of naturally occurring types or strains, issued from spontaneous crosses selected by growers and obtained from controlled crosses by classical breeding during the last century.

Almond cultivars are largely self-incompatible, although self-compatible cultivars exist. Self-incompatibility is gametophytic and controlled by a single *S* gene with multiple codominant alleles. Twenty six *S* alleles of incompatibility (from S_1 to S_{25} and S_{7A}) a part from the self-compatible dominant allele S_f have been identified so far in the cultivated almond. Eighteen cross-incompatibility groups (CIG), formed by cultivars having the same self-incompatibility genotypes, are reported (Groups I to XVII and Group O of cultivars with unique genotypes) (Kester & Gradziel, 1996a; Boskovic et al., 2003; López et al., 2004). Self-incompatibility is expressed in the styles of the flowers as *S*-RNase glycoproteins which are responsible for stopping the self-pollen growth (Tao et al., 1997; Boskovic et al., 1997). Since self-compatible almond cultivars were reported in Puglia region in Italy (Godini, 1975; Grasselly & Olivier, 1976), self-compatibility has become one of the main aims when breeding new almond cultivars in Europe and the United States.

Two methods have been mainly used to determine the *S* genotype of almond cultivars: controlled pollinations (in the field or in the laboratory) and RNase analysis (in the laboratory) although some other have been also used. The first *S* genotypes and cross-incompatibility groups were detected through cross pollination tests in the field (Crossa-Raynaud & Grasselly, 1985; Kester & Asay, 1975; Kester et al., 1994) or in the laboratory (Herrero et al., 1977; Socías i Company & Felipe, 1977). More recently, molecular methods have been developed. Some *S* alleles were determined by using zymograms to detect the presence of particular stylar ribonucleases, which are known to correlate with *S* alleles (Batlle et al., 1997; Boskovic et al., 1997, 1999, 2003; Tao et al., 1997; Duval et al., 1998; Certal et al., 2002; Mnejja et al., 2002; Ortega & Dicenta, 2003; López et al., 2004). The molecular identification of *S* alleles by PCR based analysis using conserved or specific primers has been successfully introduced (Tamura et al., 2000; Ma & Oliveira, 2001; Channuntapipat et al., 2001, 2003; Martínez-Gómez et al., 2003; Ortega & Dicenta, 2003; Alonso, 2004; López et al., 2004, 2005a,b). Lately, identification of multiple *S* alleles in almond cultivars using specific primers through multiplex PCR in a single reaction has also been achieved (Sánchez-Pérez et al., 2004).

The information provided by the almond cultivar genotypes of self-incompatibility is useful for commercial orchard design (compatible cultivar choice is essential for production) and for planning crosses when breeding new cultivars (cross design and crossing side can be benefited from the information provided by the *S* genotypes of the genitors). Thus, crosses originating only self-compatible seedlings can be designed.

The available information regarding the *S* alleles of self-incompatibility and self-compatibility in almond cultivars has not been yet compiled, since it is comprised in a variety of publications, many having a limited readership. In addition, the determination of the alleles through stylar ribonucleases analysis is occasionally contradictory due to the electrophoresis technique used (isoelectric focusing IEF or non-equilibrium pH gradient NEpHGE), gel length and thickness, gel composition and migrating conditions and possible missnames in plant material. Recently, the self-incompatible genotypes of six cultivars were re-evaluated (López et al., 2004, 2005b).

The aim of this work was to provide a compilation of the information available on self-(in)compatibility almond genotypes based on a review of the bibliography, which refers to the determination of the *S* alleles using different methods.

Materials and methods

To compile the existing cultivar *S* genotypes, the following data were recorded: (i) cultivar identification, and (ii) *S* genotype assignation. The cultivars inclosed in this review are classified into three different categories: self-incompatible, self-compatible and doubtful self-compatibility.

Cultivar identification

The items included for cultivar identification were: (i) name (native name and synonime when existing), (ii) origin (place or breeding programme and country), (iii) parentage (original cross or mother plant if known), and (iv) obtention year reported (crossing, selection or release).

S genotype assignation

The references used were those searched in the literature published until 2004. Self-compatible cultivars are those having the S_f allele. In contrast, in self-incompatible cultivars this allele is lacking. The information related to *S* genotypes assignation was divided into the following items: (i) *S* genotype (assigned for each cultivar), (ii) techniques (applied to identify each *S* genotype), (iii) references (authors cited as reference for each *S* genotype assignation), (iv) consensus *S* genotype (assigned as the most commonly observed between different techniques), and (v) cross-incompatibility group (only for self-incompatible cultivars).

Five different techniques for genotype identification were rewiewed: (i) controlled (self)-pollinations by bagging flowers in the field (F), (ii) controlled (self)-pollinations and microscopy in the laboratory (L), (iii) stylar ribonucleases electrophoresis (R), (iv) DNA isolation and *S* allele specific PCR (P), and (v) nucleotides sequencing (S). All the methods were described in López et al. (2004).

Results and discussion

The *S* genotype of 133 commercial almond cultivars of different origins are reviewed. Cultivars are organized into three different tables according to their *S* genotype: (i) 99 self-incompatible cultivars (not having the S_f allele) (Table 1); (ii) 16 self-compatible cultivars (having the S_f allele) (Table 2); and (iii) 18 cultivars of doubtful genotype (needing further clarification) (Table 3). Thus, 115 cultivars have been completely genotyped until now. The self-compatible cultivars represent a 86.1% from the 115 completely genotyped cultivars and thus the self-incompatibles represent the 13.9%.

The American nomenclature to name *S* alleles based on letters (Kester et al., 1994) corresponds to the European numbering system (Boskovic et al., 1997). In 1996, Kester and Gradziel unified both terminologies to allow a better classification of *S* alleles and CIG, but they included some mistakes or inconsistencies. Thus, the S_a, S_b, S_c and S_d alleles were equated to the S_5, S_1, S_7 and S_8 alleles respectively. For instance, cross-incompatibility groups II and IV corresponded to S_5S_6 and S_5S_8 genotypes respectively in Kester and Gradziel (1996a), and later they were changed to S_1S_5 and S_1S_7 genotypes in Boskovic et al. (2003).

Self-incompatible cultivars (Table 1)

Table 1 compiles the genotypes of 99 self-incompatible almond cultivars. A 61% of these cultivars has an unknown origin, and the other 39% was obtained from planned crosses in different breeding programmes. Native self-incompatible cultivars have a wide geographic origin in the Mediterranean basin but not in California (USA) and Australia, where almond cultivars were introduced mainly by early Europeans setlers.

A high agreement between the different techniques applied to identify *S* genotypes of self-incompatible cultivars was observed. Since the recent introduction of molecular techniques (RNases, PCR and sequencing) some genotypes previously assigned by pollination tests have been confirmed. However, biological techniques (self-pollination or crossing tests in the field or in the laboratory) are still useful to confirm genetic incompatibilities. Cultivar reassignation of *S* alleles has been parallel to the evolution of the techniques used for their determination. From the existing 27 *S* alleles, oligonucleotide primers have been developed to amplify only 9 *S* alleles yet. Once all the primers for the known *S* alleles will be designed, the assignation of *S* genotypes would be possible for any new cultivar or selection.

Table 1 includes the recent re-assignation of five *S* genotypes using biological and molecular techniques: 'Achaak' (S_2S_{25}), 'Ardechoise' (S_1S_{25}), 'Desmayo Largueta' (S_1S_{25}), 'Ferrastar' (S_2S_{25}) and 'Gabaix' ($S_{10}S_{25}$) (López et al., 2004). A parallel work by Sánchez-Pérez et al. (2004) has confirmed seven almond genotypes using single PCR (with AS1II/AmyC5R primer) and multiplex PCR (with a combination of primers AS1II/AmyC5R and CEBASf) (Tables 1 and 2), but for 'Ardechoise' the S_1S_{10} previously assigned genotype was maintained. This conflictive S_{25} allele from 'Ardechoise' could be sequenced and compared to the S_{10} and S_{25} sequences reported for other cultivars.

The doubtful origin of four American cultivars have been confirmed after genotyping by test crosses and stylar RNases (Boskovic et al., 2003): (i) 'Jubilee' (S_8S_{15}) and 'Yosemite' (S_8S_{10}) could not derive from the cross between 'Nonpareil' (S_7S_8) and 'Mission' (S_1S_5); (ii) 'Ruby' (S_6S_{16}) could not be obtained from the cross 'Nonpareil' (S_7S_8) × 'Mission' (S_1S_5), and neither 'Wawona' (S_8S_{19}) from the cross 'Ruby' (S_6S_{16}) × 'Mission' (S_1S_5).

In this work, 16 self-incompatible cultivars had been assigned to cross incompatibility group of unique genotypes (CIG O), and the Portuguese cultivar 'Mourisca' belongs to CIG VIII (S_1S_3 genotype). In addition, two new CIG could be established as a result of this *S* genotype revision in almond: CIG XVIII (S_1S_4 genotype) and XIX (S_7S_{13} genotype). Thus, in total 20 CIG have been identified for almond.

Self-compatible cultivars (Table 2)

Table 2 shows the 16 self-compatible cultivars analysed. Only four of these cultivars ('Falsa Barese', 'Filippo Ceo', 'Genco' and 'Tuono') are native from Puglia, Italy, and the other twelve derive from different

Table 1. *S* genotypes of 99 self-incompatible almond cultivars

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
'Achaak'	Tunisia	Unknown	~1940	*S2S10*	R	Ortega (2002)	*S2S25*	XVII
				S2S25	F, R, S	López et al. (2004)		
'Aï'	Bouches-du-Rhone	Unknown	–	*S3S4*	F	Crossa-Raynaud and Grasselly (1985)	*S3S4*	O
	(France)			*S3S4*	R	Boskovic et al. (1997)		
				S3	R	López (2004)		
'Aldrich'	California (USA)	Unknown	1973	*S7S17*	R	Boskovic et al. (2003)	*S7S17*	O
'Alnem88'	Israel			*S2S10*	P	Channuntapipat et al. (2003)	*S2S10*	O*
'Anxaneta'	IRTA-Mas Bové (Reus,	'Primorskiy' × 'Cristomorto'	1977	*S2S9*	R	Boskovic et al. (2003) and López (2004)	*S2S9*	XV
	Spain)			*S2S9*	P	Channuntapipat et al. (2003)		
'Ardechoise'	France	Unknown	–	*S1S10*	R	Boskovic et al. (2003)	*S1S25*	XVI
				S1S25	F, R	López et al. (2004)		
				S1S10	P	Sánchez-Pérez et al. (2004)		
'Atocha'	Murcia (Spain)	Unknown	~1933	*S13S22*	R	Boskovic et al. (2003)	*S13S22*	O
				S13	P	Sánchez-Pérez et al. (2004)		
'Ballico'	Ballico,	Unknown	1947	*SaSb*	F	Kester et al. (1994)	*S1S5*	II
	California (USA)			*S1S5*	R	Boskovic et al. (2003)		
'Bartre' (syn.	France or Spain	Unknown	–	*S3S5*	R	Boutard (1999)	*S3S5*	O*
'Rufina Gruesa')				*S3*	R	López (2004)		
'Baxendale'	Australia	Unknown	–	*S5S7*	P	Channuntapipat et al. (2003)	*S5S7*	III
'Bertina'	Zaragoza	Unknown	–	*S6S11*	R	Boskovic et al. (2003) and	*S6S11*	O
	(Spain)					López (2004)		
'Bigelow'	California (USA)	Unknown	–	*S8S16*	R	Boskovic et al. (2003)	*S8S16*	XII
'Boa Casta'	Portugal	Unknown	–	*S8S21*	R	Certal et al. (2002)	*S8S21*	O*
'Bonita'	Portugal	Unknown	–	*S1S21*	R	Certal et al. (2002)	*S1S21*	O*
'Bonita de S. Brás'	Portugal	Unknown	–	*S8S22*	R	Certal et al. (2002)	*S8S22*	O*
'Butte'	Le Grand, California	'Nonpareil' × 'Mission'	~1953	*S1S6*	F	Kester and Gradziel (1996), Asai et al. (1996) and Gradziel (1997)	*S1S8*	VI
	(USA)			*S1S8*	R	Boskovic et al. (2003)		

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Table 1. (*Continued*)

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
‘Carmel’	Le Grand,	‘Nonpareil’	1966	*SaSd*	F	Kester et al. (1994)	*S5S8*	V
	California	× ‘Mission’ (?)		*S5S8*	R	Boskovic et al. (2003)		
	(USA)			*S5S8*	P	Martínez-Gómez et al. (2003) and		
						López et al. (2004)		
‘Carrion’	Arbuckle,	‘Nonpareil’ ×	1965	*SaSd*	F	Kester et al. (1994)	*S5S8*	V
	California (USA)	‘Mission’ (?)		*S5S8*	R	Boskovic et al. (2003)		
‘Casanova’	Portugal	Unknown	–	*S1S20*	R	Certal et al. (2002)	*S1S20*	O*
‘CEBAS 1’	CEBAS (Murcia, Spain)	‘Garrigues’ OP	1980’s	*S13S20*	R	Boskovic et al. (2003)	*S13S20*	O
‘Coelhinha’	Portugal	Unknown	–	*S1S4*	R	Certal et al. (2002)	*S1S4*	XVIII**
‘Colossal’	Portugal	Unknown	–	*S1S11*	R	Certal et al. (2002)	*S1S11*	O*
‘Cristomorto’	Puglia (Italy)	Unknown	–	*S1S2*	F	Crossa-Raynaud and Grasselly (1985)	*S1S2*	O
				S1S2	R	Boskovic et al. (1997) and López (2004)		
				S1S2	P	Channuntapipat et al. (2003)		
‘Chellaston’	Australia	Unknown	–	*S7S13*	P	Channuntapipat et al. (2003)	*S7S13*	XIX**
‘Del Cid’	Murcia (Spain)	Unknown	–	*S1S12*	R	Ortega (2002)	*S1S12*	O*
‘Desmayo Largueta’	Tarragona (Spain)	Unknown	~1820	*S1S5*	R	Boskovic et al. (1997)	*S1S25*	XVI
				S1S25	F, R, P, S	López et al. (2004)		
‘Dottie Won’	California (USA)	Unknown	–	*S8S16*	R	Boskovic et al. (2003)	*S8S16*	XII
‘Drake’	California (USA)	Unknown	~1878	*S6S8*	R	Boskovic et al. (2003)	*S6S8*	XIII
‘Duro Amarelo’	Portugal	Unknown	–	*S1S8*	R	Certal et al. (2002)	*S1S8*	VI
‘Eureka’	California (USA)	Unknown	–	*S8S13*	R	Boskovic et al. (2003)	*S8S13*	VII
‘Ferraduel’	INRA-Bordeaux (France)	‘Cristomorto’ × ‘Aï’	1960	*S1S4*	F	Crossa-Raynaud and Grasselly (1985)	*S1S4*	XVIII**
				S1S4	R	Boskovic et al. (1997)		
				S1	P	Channuntapipat et al. (2003)		
‘Ferragnès’	INRA-Bordeaux (France)	‘Cristomorto’ × ‘Aï’	1960	*S1S3*	F	Crossa-Raynaud and Grasselly (1985)	*S1S3*	VIII
				S1S3	R	Boskovic et al. (1997) and López (2004)		
				S1	P	Channuntapipat et al. (2003)		
				S1S3	R, P	Alonso (2004)		
				S1S3	P	Sánchez-Pérez et al. (2004)		
‘Ferralise’	INRA-Bordeaux (France)	‘Ferraduel’ × ‘Ferragnès’	1967	*S1S3*	F	Crossa-Raynaud and Grasselly (1985)	*S1S3*	VIII
				S1S3	R	Boskovic et al. (1997)		
				S1	P	Channuntapipat et al. (2003)		
				S1S3	R, P	Alonso (2004)		

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Table 1. (*Continued*)

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
'Ferrastar'	INRA-Bordeaux (France)	'Cristomorto' × 'Ardechoise'	1960	*S2S10*	R	Boskovic et al. (1999)	*S2S25*	XVII
				S2S10	P	Channuntapipat et al. (2003)		
				S2S25	R	López et al. (2004)		
'Fritz'	Manteca, California (USA)	'Mission' × 'Drake' (?)	1969	*S1S6*	F	Asai et al. (1996)	*S1S6*	XIV
				S1S6	R	Boskovic et al. (2003)		
				S1	P	Channuntapipat et al. (2003)		
'Fura Saco'	Portugal	Unknown	–	*S20S23*	R	Certal et al. (2002)	*S20S23*	O*
'Gabaix'	Tarragona (Spain)	Unknown	–	*S5S10*	R	Boskovic et al. (2003)	*S10S25*	O
				S5S10	P	Channuntapipat et al. (2003)		
				S10S25	F, L, R, P, S	López et al. (2004)		
'Garbí'	IRTA-Mas Bové (Reus, Spain)	'Cristomorto' OP	1973	*S1S5*	R	Boskovic et al. (2003)	*S1S5*	II
				S1S5	F, L, R, P	López et al. (2004)		
'Garrigues'	Murcia (Spain)	Unknown	–	*S7S13*	R	Ortega (2002)	*S7S13*	XIX**
'Glorieta'	IRTA-Mas Bové (Reus, Spain)	'Primorskiy' × 'Cristomorto'	1975	*S1S5*	R	Boskovic et al. (1997)	*S1S5*	II
				S1S5	P	Channuntapipat et al. (2003)		
				S1S5	F, L, R, P, S	López et al. (2004)		
'Golden State'	USA	Unknown	–	*S7S8*	P	Channuntapipat et al. (2003)	*S7S8*	I
'Grace'	California (USA)	Unknown	–	*S6S8*	F	Kester and Gradziel (1996)	*S1S8*	VI
				S1S8	R	Boskovic et al. (2003)		
'Granada'	California (USA)	'Mission' × 'Nonpareil'	–	*SaSc*	F	Kester et al. (1994)	*S5S7*	III
				S5S7	F	Grasselly (1972)		
				S5S7	R	Boskovic et al. (1997)		
'Harpareil'	Davis, California (USA)	'Nonpareil' × 'Harricott'	1926	*S7S14*	R	Boskovic et al. (2003)	*S7S14*	X
'Harvey'	Yuba City, California (USA)	'Mission' × 'Nonpareil'	1956	*SaSc*	F	Kester et al. (1994)	*S5S7*	III
				S5S7	F	Grasselly (1972)		
				S5S7	R	Boskovic et al. (1997)		
'IXL'	California (USA)	Unknown	–	*ScSd*	F	Kester et al. (1994)	*S7S8*	I
				S7S8	R	Boskovic et al. (1997)		
'Jeffries'	California (USA)	'Nonpareil' bud mutation	–	*S7AS8*	R	Boskovic et al. (2003)	*S7AS8*	IX
'Jordanolo'	Davis, California (USA)	'Nonpareil' × 'Harricott'	1926	*S7S14*	F	Gradziel (1997)	*S7S14*	X
				S7S14	R	Boskovic et al. (2003)		

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Table 1. (*Continued*)

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
'Jubilee'	Templeton, California (USA)	'Nonpareil' × 'Mission' (?)	1929	*S8S15*	F	Grasselly (1972)	*S8S15*	XI
				S8S15	R	Boskovic et al. (2003)		
'Kapareil'	Davis, California (USA)	complex hybrid of 'Nonpareil' and 'Eureka'	1951	*S8S13*	F	Gradziel (1997)	*S8S13*	VII
				S8S13	R	Boskovic et al. (2003)		
'Kutsch'	California (USA)	Unknown	–	*S8S16*	R	Boskovic et al. (2003)	*S8S16*	XII
'Languedoc'	Bouches-du-Rhone (France)	Unknown	–	*SaSb*	F	Kester et al. (1994)	*S1S5*	II
				S1S5	R	Boskovic et al. (1997)		
				S1S5	P	Martínez-Gómez et al. (2003) and López et al. (2004)		
'Livingston'	California (USA)	Unknown	1976	*SaSd*	F	Kester et al. (1994)	*S5S8*	V
				S5S8	R	Boskovic et al. (1997)		
'Long IXL'	California (USA)	Unknown	–	*S7S8*	F	Kester and Gradziel (1996) and Kester et al. (1994)	*S7S8*	I
'Marcona'	Alicante (Spain)	Unknown	–	*S11S12*	R	Boskovic et al. (1998), López (2004)	*S11S12*	O
				S11S12	P	Sánchez-Pérez et al. (2004)		
'Masbovera'	IRTA-Mas Bové (Reus, Spain)	'Primorskiy' × 'Cristomorto'	1975	*S1S9*	R	Boskovic et al. (1997), López (2004)	*S1S9*	O
				S1S9	P	Channuntapipat et al. (2003)		
'Mckinlay's Magnificent'	Australia	Unknown	–	*S7S8*	P	Channuntapipat et al. (2003)	*S7S8*	I
'Merced'	Ballico, California (USA)	'Mission' × 'Nonpareil' (?)	1948	*SbSc*	F	Kester et al. (1994)	*S1S7*	IV
				S1S7	R	Boskovic et al. (1997)		
'Mission' (syn. 'Texas')	Texas (USA)	'Languedoc OP (?)	~1891	*SaSb*	F	Kester et al. (1994)	*S1S5*	II
				S1S5	R	Boskovic et al. (1997) and Tamura et al. (2000)		
				S1S5	P	Channuntapipat et al. (2003) and Martínez-Gómez et al. (2003)		
				S1S5	F, L, R, P, S	López et al. (2004)		
'Monarch'	Modesto, California (USA)	Unknown	1982	*SaSd*	F	Kester et al. (1994)	*S5S8*	V
				S5S8	R	Boskovic et al. (1997)		
'Mono'	Le Grand, California (USA)	Unknown	1966	*SaSc*	F	Kester et al. (1994)	*S5S7*	III
				S5S7	R	Boskovic et al. (1997)		
'Monterey'	Merced, California (USA)	'Nonpareil' × 'Mission'	1962	*SbSd*	F	Kester et al. (1994)	*S1S8*	VI
				S1S8	R	Boskovic et al. (1997)		
'Mourisca'	Portugal	Unknown	–	*S1S3*	R	Certal et al. (2002)	*S1S3*	VIII*

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Table 1. (*Continued*)

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
'Ne Plus Ultra'	California (USA)	'Languedoc' OP (?)	1879	*SbSc*	F	Kester et al. (1994)	*S1S7*	IV
				S1S7	R	Boskovic et al. (1997)		
				S1S7	P	Channuntapipat et al. (2003)		
'Nonpareil'	Suisum, California (USA)	'Languedoc' OP (?)	1879	*ScSd*	F	Kester et al. (1994)	*S7S8*	I
				ScSd	R	Tamura et al. (2000)		
				S7S8	R	Boskovic et al. (1997)		
				S7S8	P	Martínez-Gómez et al. (2003) and Channuntapipat et al. (2003)		
				S7	P	Sánchez-Pérez et al. (2004)		
'Norman'	Le Grand, California (USA)	'Nonpareil' OP	1958	*S1S7*	F	Grasselly (1972)	*S1S7*	IV
				S5S8	F	Kester and Gradziel (1996)		
				S1S7	R	Boskovic et al. (2003)		
'Northland'	Ogden, Utah (USA)	'IXL' OP	1935	*S6S8*	F	Kester and Gradziel (1996)	*S1S8*	VI
				S1S8	F	Gradziel (1997)		
				S1S8	R	Boskovic et al. (2003)		
'Padre'	Davis, California (USA)	'Mission' × 'Swanson'	1946	*S1S18*	F	Asai et al. (1996) and Gradziel (1997)	*S1S18*	O
				S1S18	R	Boskovic et al. (2003)		
'Parada'	Portugal	Unknown	–	*S11S20*	R	Certal et al. (2002)	*S11S20*	O*
'Pearl'	California (USA)	Unknown	–	*S7S16*	R	Boskovic et al. (2003)	*S7S16*	O
'Peerless'	California (USA)	Unknown	<1900	*S1S6*	R	Boskovic et al. (2003)	*S1S6*	XIV
				S1	P	Channuntapipat et al. (2003)		
'Pestañeta'	Portugal	Unknown	–	*S12S23*	R	Certal et al. (2002)	*S12S23*	O*
'Pierce'	Australia	Unknown	–	*S8S23*	P	Channuntapipat et al. (2003)	*S8S23*	O*
'Price'	California (USA)	'Nonpareil' × 'Mission' (?)	1953	*S1S7*	F	Grasselly (1972)	*S1S7*	IV
				SbSc	F	Kester et al. (1994)		
				S1S7	R	Boskovic et al. (1997)		
				S1S7	P	Channuntapipat et al. (2003)		
'Primorskiy' (syn. 'Morskoy')	Yalta (Ucraine)	'Princesse 2077' × 'Nikitskiy 53'	1935	*S5S9*	R	Boskovic et al. (1997 and 2003)	*S5S9*	O
				S5S9	P	Channuntapipat et al. (2003) and López et al. (2005a)		
				S5S9	R, P	López et al. (2004)		
				S5S9	P	Sánchez-Pérez et al. (2004)		

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Table 1. (*Continued*)

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
'Ramillete'	Murcia (Spain)	Unknown	–	*S6S23*	R	Certal et al. (2002), Boskovic et al. (2003) and López (2004)	*S6S23*	O
				S23	P	Channuntapipat et al. (2003)		
'Reams'	California (USA)	Unknown	–	*S1S3*	R	Boutard (1999)	*S8S15*	XI
				S8S15	R	Boskovic et al. (2003)		
'Retsou'	Greece	Unknown	–	*S2S3*	R	Boutard (1999)	*S2S3*	O*
				S3	R	López (2004)		
'Riedenhoure'	California (USA)	Unknown	–	*S7S8*	R	Boskovic et al. (2003)	*S7S8*	I
'Ripon'	Le Grand, California (USA)	'Nonpareil' OP	1958	*SbSc*	F	Kester et al. (1994)	*S1S7*	IV
				S1S7	R	Boskovic et al. (1997)		
'Rivers Nonpareil'	California (USA)	Unknown	–	*S8S16*	R	Boskovic et al. (2003)	*S8S16*	XII
'Robson'	Durham, California (USA)	Unknown	1964	*S5S7*	F	Kester and Gradziel (1996)	*S5S7*	III
'Ruby'	Le Grand, California (USA)	'Nonpareil' × 'Mission' (?)	1946	*S6S16*	F	Asai et al. (1996) and Gradziel (1997)	*S6S16*	O*
				S6S16	R	Boskovic et al. (2003)		
'Rumbeta'	Alicante (Spain)	Unknown	–	*S11S21*	R	Boskovic et al. (2003)	*S11S21*	O
				S11	R	López (2004)		
'Sauret1'	San Luis Obispo, California (USA)	Unknown	1952	*S5S8*	R	Boskovic et al. (2003)	*S5S8*	V
'Sauret2'	San Luis Obispo, California (USA)	Unknown	1950	*SaSc*	F	Kester et al. (1994)	*S5S7*	III
				S5S7	R	Boskovic et al. (1997)		
'Smith XL'	California (USA)	Unknown	–	*S6S8*	R	Boskovic et al. (2003)	*S6S8*	XIII
'Solano'	Davis, California (USA)	complex hybrid of 'Nonpareil' and 'Eureka'	1946	*S6Sx*	F	Kester and Gradziel (1996)	*S8S13*	VII
				S8S13	F	Gradziel (1997)		
				S8S13	R	Boskovic et al. (2003)		
'Somerton'	Australia	Unknown	–	*S1S23*	P	Channuntapipat et al. (2003)	*S1S23*	O*
'Sonora'	California (USA)	complex hybrid of 'Nonpareil' and 'Eureka'	1946	*S6Sx*	F	Kester and Gradziel (1996)	*S8S13*	VII
				S8S13	F	Gradziel (1997)		
				S8S13	R	Boskovic et al. (2003)		
'Sultane'	France	Unknown	–	*S8S16*	R	Boskovic et al. (2003)	*S8S16*	XII
'Tardy Nonpareil'	Escalon, California (USA)	'Nonpareil' mutation	1942	*S7S8*	F	Crossa-Raynaud and Grasselly (1985)	*S7S8*	I
				ScSd	F	Kester et al. (1994)		
				S7S8	R	Boskovic et al. (1997)		
				S7S8	P	Channuntapipat et al. (2003)		

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Table 1. (*Continued*)

Cultivar	Origin[a]	Parentage[b]	Obtention year[c]	*S* Genotype	Technique[d]	References	Consensus *S* genotype[e]	CIG[f]
'Tarragonès'	IRTA-Mas Bové (Reus, Spain)	'Cristomorto' × 'Primorskiy'	1975	*S2S9*	R	Boskovic et al. (1997) and López (2004)	*S2S9*	XV
'Thompson'	Clovis, California (USA)	'Nonpareil' × 'Mission' (?)	1946	*SaSc*	F	Kester et al. (1994)	*S5S7*	III
				S5S7	R	Boskovic et al. (1997)		
				S5S7	P	Channuntapipat et al. (2003)		
'Tokyo'	Le Grand, California (USA)	Unknown	1965	*S6S7*	R	Boskovic et al. (1997)	*S6S7*	O
'Verdeal'	Portugal	Unknown	–	*S13S20*	R	Certal et al. (2002)	*S13S20*	O*
'Wawona'	Le Grand, California (USA)	'Ruby' × 'Mission'	1965	*S8S19*	F	Gradziel (1997)	*S8S19*	O
				S8S19	R	Boskovic et al. (2003)		
'Wood colony'	Modesto, California (USA)	Unknown	1985	*S5S7*	F	Kester and Gradziel (1996)	*S5S7*	III
'Yosemite'	Le Grand, California (USA)	'Mission' × 'Nonpareil' (?)	1957	*S8S10*	F	Gradziel (1997)	*S8S10*	O
				S8S10	R	Boskovic et al. (2003)		

[a]Origin, information reported by: Egea et al. (1985), Gradziel (1997), Grasselly and Crossa-Raynaud (1980), Kester and Gradziel (1996b), Salom (1923) and Vargas (1975).
[b]Parentage: OP = open pollinated.
[c]Obtention year (crossing, selection or release).
[d]Self-pollinations and crosses in the field (F) or in the laboratory (L), stylar ribonucleases electrophoresis (R), DNA isolation and *S* allele specific PCR (P), and nucleotides sequencing (S).
[e]Consensus *S* genotype (assigned as the most commonly observed between different techniques).
[f]CIG: cross-incompatibility group: CIG not assigned before (*), CIG established in this work (**).

Table 2. *S* genotypes of 16 self-compatible almond cultivars

Cultivar	Origin	Parentage[a]	Obtention year[b]	*S* genotype[c]	Technique[d]	References	Consensus *S* genotype[e]
'Almenara'	CEBAS (Murcia, Spain)	'Tuono' × 'Ferragnès'	1985	*S3Sf**	F	García et al. (1996)	*S3Sf*
'Antoñeta'	CEBAS (Murcia, Spain)	'Tuono' × 'Ferragnès'	1985	*S3Sf**	F	García et al. (1996)	*S3Sf*
'Aylés'	CITA (Zaragoza, Spain)	'Tuono' OP	1974	*S9Sf*	R	Boutard (1999)	*S9Sf*
'Falsa Barese'	Puglia (Italy)	Unknown	–	*S1Sf*	R	Boskovic et al. (1997)	*S1Sf*
				S1Sf	P	Channuntapipat et al. (2003)	
				S1Sf	R, P	López et al. (2005a)	
'Filippo Ceo'	Puglia (Italy)	Unknown	–	*S1Sf*	R	Boskovic et al. (1997)	*S1Sf*
'Francolí'	IRTA-Mas Bové	'Cristomorto' × 'Tuono'	1976	*S1S5*	P	Martínez-Gómez et al. (2003)	*S1Sf*
	(Reus, Spain)			*S1Sf*	F, L, R, P	López et al. (2005b)	
'Genco'	Puglia (Italy)	Unknown	∼1910	*S1Sf*	R	Boskovic et al. (1997)	*S1Sf*
				S1Sf	P	Channuntapipat et al. (2003)	
				S1Sf	R, P	López (2004)	
'Guara'	CITA (Zaragoza, Spain)	clonal selection	1974	*S10Sf*	R	Boutard (1999)	*S1Sf*
				S1Sf	R	Ortega (2002)	
'Lauranne'	INRA-Avignon (France)	'Ferragnès' × 'Tuono'	1978	*S3Sf*	R	Boskovic et al. (1997)	*S3Sf*
				Sf	P	Channuntapipat et al. (2003)	
				S3Sf	R, P	López et al. (2005a)	
				S3Sf	P	Sánchez-Pérez et al. (2004)	
'Mandaline'	INRA-Avignon (France)	'Ferralise' × 'Tuono'	1979	*S1Sf**	F	Duval (1999)	*S1Sf*
'Marita'	CEBAS (Murcia, Spain)	'Genco' × 'Ferragnès'	1985	*S3Sf**	F	García et al. (1998)	*S3Sf**
'Marta'	CEBAS (Murcia, Spain)	'Ferragnès' × 'Tuono'	1985	*S1/3Sf**	F	García et al. (1996)	*Sf*
'Steliette'	INRA-Avignon (France)	'Ferragnès' × 'Tuono'	1978	*S3Sf*	R	Boskovic et al. (1997) and López (2004)	*S3Sf*
				Sf	P	Channuntapipat et al. (2003)	
'Supernova'	ISF-Roma (Italy)	'Fascionello' mutation	1970	*S1Sf*	R	Certal et al. (2002)	*S1Sf*
'Teresa'	CEBAS (Murcia, Spain)	'Tuono' × 'Ferragnès'	1985	*S3Sf**		García et al. (1998)	*S3Sf*
'Tuono'	Puglia (Italy)	Unknown	∼1830	*S1Sf*	F	Crossa-Raynaud and Grasselly (1985)	*S1Sf*
(syn. 'Truoito')				*S1Sf*	R	Boskovic et al. (1997)	
				S1Sf	P	Channuntapipat et al. (2003)	
				S1Sf	L, R, P	Alonso (2004) and López (2004)	
				S1Sf	P	Sánchez-Pérez et al. (2004)	

[a]Parentage: OP = open pollinated.
[b]Obtention year (crossing, selection or release).
[c]*S* genotype: * deduced genotype by crossing origin.
[d]Self-pollinations and crosses in the field (F) or in the laboratory (L), stylar ribonucleases electrophoresis (R), DNA isolation and *S* allele specific PCR (P) and nucleotides sequencing (S).
[e]Consensus *S* genotype (assigned as the most commonly observed between different techniques).

Table 3. *S* genotypes of 18 doubtful self-incompatible almond cultivars

Cultivar	Origin	Parentage[a]	Obtention year[b]	*S* genotype[c]	Technique[d]	References	Consensus *S* genotype[e]
Self-compatible[f]							
'All in one'	California (USA)	almond × peach	1978	*S7S8*	R	Boutard (1999)	*S1S7*
				S1S7	P	Channuntapipat et al. (2003)	
'Le Grand'	Le Grand, California (USA)	almond × peach	1966	*S1S8*	P	Channuntapipat et al. (2003)	*S1S8*
'Moncayo'	CITA (Zaragoza, Spain)	'Tardive de la Verdière' × 'Tuono'	1974	*Sf*	F, M	Felipe and Socías i Company (1987)	*S1S9*
				S1S2	R	Boutard (1999)	
				S1S9	F, R	López (2004)	
One *S* allele identified							
'Bico de Papagaio'	Portugal	Unknown	–	*S6Sx*	R	Certal et al. (2002)	*S6Sx*
'Cacela-manta rota'	Portugal	Unknown	–	*S1Sx*	R	Certal et al. (2002)	*S1Sx*
'Duro de Estrada'	Portugal	Unknown	–	*S1S2/4*	R	Certal et al. (2002)	*S1S2/4*
'Johnston's Prolific'	Australia	Unknown	–	*S23*	P	Channuntapipat et al. (2002 and 2003)	*S23*
'Marcelina Grada'	Portugal	Unknown	–	*S11*	R	Certal et al. (2002)	*S11*
'Molar'	Portugal	Unknown	–	*S6Sx*	R	Certal et al. (2002)	*S6Sx*
'Molar de Fuzeta'	Portugal	Unknown	–	*S3/20Sx*	R	Certal et al. (2002)	*S3/20Sx*
'Molar Passarinho'	Portugal	Unknown	–	*S2Sx*	R	Certal et al. (2002)	*S2Sx*
'Pegarinhos'	Portugal	Unknown		*S12*	R	Certal et al. (2002)	*S12*
'Titan'	Fresno, California (USA)	'Tardy Nonpareil' OP	1971	*S8Sx*	R	Ballester (1998)	*S8Sx*
S genotype to verify							
'Belle d'Aurons'	Aurons (France)	'Aï' (?) OP	∼1950's	*S1S3*	R	Boutard (1999)	*S3S10*
				S3S10	R	López (2004)	
'Milow'	California (USA)	Unknown	–	*S7S19*	R	Boskovic et al. (2003)	*S1S8* / *S7S19*
				S1S8	P	Channuntapipat et al. (2003)	
'Tardive de la Verdière'	La Verdière (France)	Unknown	–	*S2S3*	R	Boutard (1999)	*S3S9*
				S3S9	R	López (2004)	
'Verd'	Spain	Unknown	–	*S11S12*	R	López (2004)	*S11S12*
'Vesta'	Ripon, California (USA)	complex hybrid of 'Nonpareil', 'Jordan', 'Jordanolo' and 'Eureka'	1956	*S6Sx*	F	Kester and Gradziel (1996)	*S10Sx*
				S8S13	F	Gradziel (1997)	
				S8S13	R	Boskovic et al. (2003)	
				S10Sx	R	López (2004)	

[a]Parentage: OP = open pollinated.
[b]Obtention year (crossing, selection or release).
[c]*Sx*: new *S* allele visualized in some Portuguese cultivars but not identified.
[d]Self-pollinations and crosses in the field (F) or in the laboratory (L), stylar ribonucleases electrophoresis (R), DNA isolation and *S* allele specific PCR (P), and nucleotides sequencing (S).
[e]Consensus *S* genotype (assigned as the most commonly observed between different techniques).
[f]Self-compatible cultivars considered although not shown in the field.

almond breeding programmes. The Spanish and French self-compatible cultivars were bred using Italian cultivars as self-compatibility donors. Nine of the 12 self-compatible cultivars released (75%) derived from 'Tuono' since this Italian cultivar has been largely used as source of self-compatibility in several breeding programmes.

Considering the self-compatible cultivars bred and included in this work: (i) Five of them were released by CEBAS-CSIC (Murcia, Spain), although only 'Antoñeta' and 'Marta' are commercially grown; (ii) Two derived from CITA (Zaragoza, Spain), being 'Guara' widely spread in Spain; (iii) 'Francolí' was commercially released by IRTA as self-incompatible but it has been recently re-classified as self-compatible (López et al., 2005b); (iv) Two cultivars obtained by INRA (Avignon, France), 'Lauranne' and 'Stelliete', being 'Lauranne' largely planted world wide; and (v) 'Supernova', which was obtained after irradiation of 'Fascinello' at ISF (Rome, Italy), is not commercially grown.

Cultivars of doubtful genotype (Table 3)

Eighteen almond cultivars were classified as doubtful, requiring futher assessment of their *S* genotypes. These cultivars have been grouped in three categories: (i) Three cultivars reported self-compatible by pollination tests in the field ('All in one', 'Le Grand' and 'Moncayo') but showing a self-incompatible genotype; (ii) Ten self-incompatible cultivars with only one *S* allele identified, being nine of them tested by the RNase analysis and the other genotyped by PCR; and (iii) Five self-incompatible cultivars with different proposed genotypes in different works or uncertain genotypes.

Regarding the first group, the two American cultivars derived from peach were unable to reach commercial fruit set after cross-pollination (Weinbaum, 1985; Gradziel and Kester, 1998; Zaiger, 1978), confirming their genetic self-incompatibility attributed after RNase or PCR analysis. The cultivar 'Moncayo', considered self-compatible and derived from the cross 'Tardive de la Verdière' × 'Tuono' (Felipe and Socías i Company 1987), was unexpectedly identified as S_1S_9 at IRTA-Mas Bové and it did not set nuts after selfing 263 flowers in the field in 2004 (López, 2004). This cultivar generally shows low fruit set levels in the field (M. Romero, personal communication), confirming its supposed genetic self-incompatibility. Felipe (2000) also affirmed that 'Moncayo' is self-compatible in the laboratory but not in the field. If 'Moncayo' was S_1S_9, a new cross-incompatibility group (CIG XX) should be established jointly with the cultivar of the same genotype 'Masbovera' (Table 1). If test crosses between these two cultivars set no fruit, 'Moncayo' *S* genotype could be clarified. In addition, the S_1S_9 genotype of 'Moncayo' would be in agreement with the S_3S_9 genotype proposed for 'Tardive de la Verdière' by López (2004), or would question the reported origin.

Recently, Certal et al. (2002) identified the *S* genotypes of several self-incompatible Portuguese almond cultivars by RNase analysis; however, eight genotypes were not fully identified and they have been included in the second group. In other two almond cultivars ('Johnston's Prolific' and 'Titan') only one *S* allele is known.

With respect to the third category, different *S* genotypes have been proposed for four cultivars after their analysis by different techniques. The PCR technique using specific primers is recommended to verify these doubtful genotypes, as PCR is more convenient than the RNases technique for the identification of new *S* alelles. If 'Verd' was $S_{11}S_{12}$, a new cross-incompatibility group (CIG XXI) should be created jointly with the cultivar of the same genotype 'Marcona' (Table 1), from which it seems to have originated as sport.

Frequency and geographic distribution of S alleles (Figure 1)

In the 133 almond genotypes analysed and documented, a total of 27 different RNases (including the S_f-RNase for self-compatibility) has been identified, showing the high polymorphism of the *S locus*. Segregation regarding only 12 of these 27 alleles (S_1, S_3, S_4, S_5, S_7, S_8, S_9, S_{10}, S_{11}, S_{12}, S_{25} and S_f) has been studied by test crosses between cultivars (Boskovic et al., 1998, 1999; Ortega & Dicenta 2003; López et al., 2004). The wide almond genetic diversity is probably due to its high degree of heterozygosis, as a result of the mainly obliged cross-pollination of this species. In the gametophytic incompatibility of *Solanaceous* species, Ioerger et al. (1990) affirmed that the frequency of *S* alleles is similar. However, large differences in the allelic frequencies are observed in the almond cultivars reviewed, probably as a consequence of domestication. The uneven *S* allele frequencies could be also due to the unrandom population studied. Cultivars of unknown parentage are considered apart from cultivars of known parentage to avoid the effect of breeders.

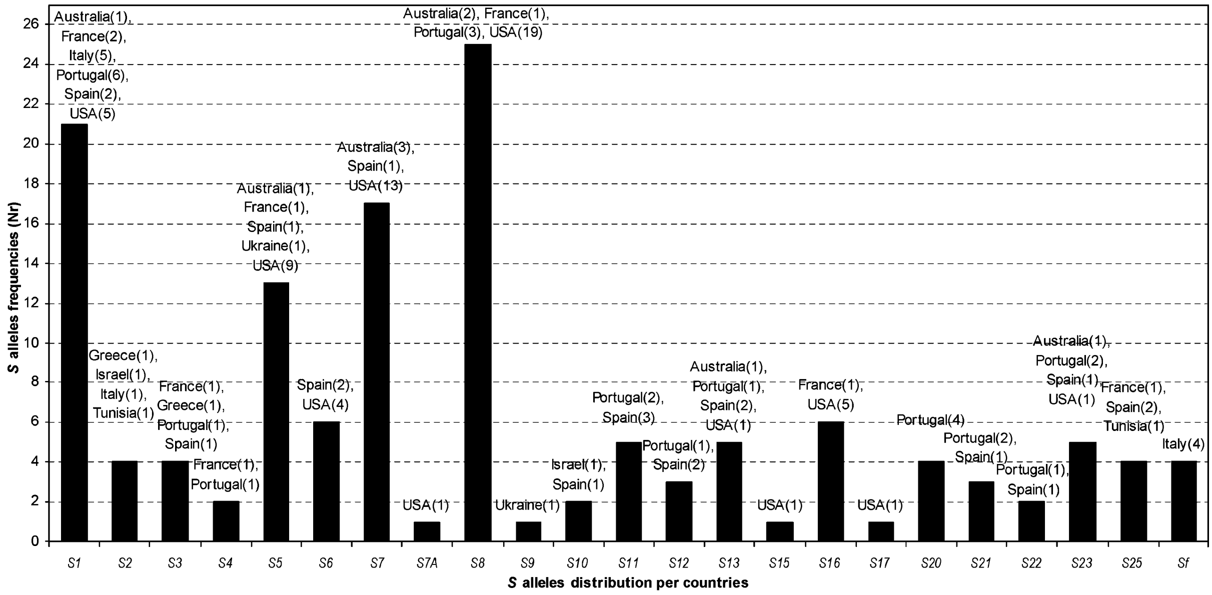

Figure 1. S alleles distribution per countries for cultivars of unknown parentage. The S_{14}, S_{18}, S_{19} and S_{24} alleles have not been observed yet in native cultivars.

Portugal (24), Spain (20) and the USA (60) are the countries with a large number of native genotyped cultivars reported, showing the effort made in their characterization (Boskovic et al., 2003; Certal et al., 2002; Channuntapipat et al., 2003). There is a large number of cultivars released from controlled crosses in American and Spanish breeding programmes. The most common S alleles in recently breed cultivars are S_1 (21.3%), S_8 (12.3%), S_7 (11.2%), S_5 (7.8%) and S_3 (7.8%). As a result of breeding for self-compatibility in the three Spanish breeding programmes, the S_f allele is more common among the Spanish releases.

The combination of the 27 S alleles identified in almond gives a total of 351 possible genotypes. However, only 20 CIG have been established so far. The most frequent genotypes derive from the combination of the four most common alleles observed (S_1, S_5, S_7 and S_8), correspond to 30.4% of the 115 cultivars fully genotyped. Cultivars S_fS_f homozygous for self-compatibility have not yet been detected. Almond S_fS_f genotypes have only been obtained at two Spanish breeding programmes (IRTA-Mas Bové and CEBAS-CSIC). The first seven seedlings were observed in a progeny derived from 'Lauranne' and probably are selfs (Boskovic et al., 1997), and the second set was observed after selfing self-compatible selections derived from 'Genco' or 'Tuono' (Ortega and Dicenta 2003).

The genotype information compiled in the almond DataBase presented in this review can be used for cross design to obtain 100% self-compatible offsprings, thus avoiding the selection for this useful character. This information will be very useful for the *Prunus* European Database which is in development (Gass et al., 1996). The discrepancies observed as a result of this revision in some cultivar S genotype assignations between different authors indicates that further genotype correction is needed, verifying the trueness to type of the plant material. Sequencing analysis should be also applied to solve S genotype inconsistencies. Once cultivar S genotype inconsistencies are solved, their genotypes should be confirmed by test crossing in the field.

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