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Review of Self-(In) compatibility in Apricot (*Prunus armeniaca* L.)

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Abstract: Apricot (*Prunus armeniaca* L.) belongs to the *Rosaceae* family where ribonuclease-mediated gametophytic self-incompatibility is a prevailing mechanism to prevent self-fertilization. From the middle of the past century, more and more self-incompatible apricot cultivars were released from breeding programs using Asian genotypes with enhanced resistance against biotic and abiotic stress factors. Presently, 17 apricot *S*-alleles are known and only 2 inter-incompatibility groups. This review depicts the historical inferences of self-incompatibility in apricot, summarizes all available data regarding the inheritance of the trait and the molecular mechanisms beyond the fertility phenotype. By collecting the results obtained from open field fruit set evaluation, histological and high throughput molecular analyses, an updated cultivar table is established describing the *S*-genotype for 23 cultivars and assigning them to 2 incompatibility (I–II) and 2 compatibility groups (0.1 and 0.2). The structure of the known incompatibility alleles or haplotypes is also presented and the transition from self-incompatibility to self-compatibility is discussed in details.

Key words: Apricot · *Prunus armeniaca* · self-incompatibility · *S*-allele · *S*-RNase

INTRODUCTION

Self-incompatibility may also be a problem in apricot?: As many flowering plants, *Prunus* species also bear the male and female organs in close proximity within the same flower. The physical structure and temporal development of the flower is such that self-fertilization would occur in the absence of specific mechanisms to prevent it. The self-incompatibility trait regulates the breeding system by ensuring a greater or lesser amount of outcrossing in a population [1]. SI has been a favourite topic for botanists and geneticists since Darwin [2] first discussed the phenomenon and suggested the idea of its central significance in the evolution of flowering plants. Within the last two decades, scientists have been able to complement Darwin's genetic observations with molecular and biochemical analyses, which have significantly contributed to the clarification of the complex series of interactions occurring at the pollen-stigma interface [3].

Species of the *Rosaceae* family show gametophytic self-incompatibility (GSI) to prevent inbreeding depression. The realization of the self-incompatibility (SI) entailed problems in case of sweet cherry or almond and the probable solutions to these problems date back to the beginning of the 20th century. On the contrary, apricot has been considered traditionally a self-compatible (SC) species [4]. In Hungary, Horn [5] evaluated most Hungarian cultivars as self-fruitful, though no data were published to support this statement. Apricots have been classified into eight different eco-geographical groups [6]. The European, North American, South African and Australian cultivars belong to the "European" group. This group is the youngest and least variable among the four most important groups. In the middle of the past century two North American cultivars ('Riland' and 'Perfection') were shown to be self-incompatible [7]. Maliga [8] described the cultivar 'Ananas', while Brózik and Nyéki [9] considered the cultivar 'Szegedi mammut' to be self-incompatible.

Egea *et al.* [10] found two and Burgos *et al.* [11] described three other SI cultivars. Among 123 main European and American cultivars or selections 42 proved self-incompatible [12]. The explanation why the number of SI cultivars seemed to increase gradually during the last decades is in connection with the fact that in contrast to the generally self-compatible European apricot cultivars, the majority of the Middle-Asian and Irano-Caucasian ones were qualified as self-sterile [4]. Lomakin [13] reported female sterility

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(the concept used by him) to be present in 24% of the European group, compared to 29% of the Irano-Caucasian group, 31% of the Central Asian and 39% of the Chinese group. These are involved in many genetic improvement programs (especially in North America, but also in many other countries) due to their valuable properties (e.g. increasing frost withstanding of cultivars with low ecological tolerance or enhance the resistance against the devastating plum pox potyvirus), but self-incompatibility may also be inherited in the offsprings.

The inheritance of the self-incompatibility trait: To determine the inheritance of self-(in)compatibility trait in apricot, progenies from 19 different crosses were evaluated (both parents self-compatible, both parents self-incompatible, one of the parents is SC and the other is SI) by Burgos *et al.* [14]. Segregating progenies were studied by determining the percentage of fruit set or following pollen tube growth with fluorescence microscopy. Results indicated that a monofactorial system with a multiallelic series appears to control the trait. Alleles for self-compatibility would allow the pollen tubes to grow in any style and reach the ovules. Alleles for self-incompatibility would stop the pollen tube growth if the same allele is present in the pollen grain and the pistil. Karyiannis and Tsaftaris [15] also tested the inheritance of SI character among hybrids obtained from the crosses and reciprocal crosses of the self-compatible Greek cultivar 'Bebecou' with two SI cultivars 'Veecot' and 'Sunglo' from North America. On the basis of the 1:1 ratio of phenotypes of seedlings, they concluded that 'Bebecou' can be heterozygous for the compatibility allele. They deduced that 'Sunglo' and 'Veecot' could not have an incompatibility allele in common with 'Bebecou'.

Audergon *et al.* [16] investigated 100 seedlings belonging to two progenies, obtained from crossing the SI 'Goldrich' as seed parent and two SC pollinizer cultivars, 'Amabile Vecchioni' and 'Icapi 34/6'. Their results showed hybrid segregation percentages that were not in agreement with the monogenic hypothesis reported earlier. However, the success of fertilization should have been influenced by other factors (e.g. alterations in the viability of pollen grains or growth rate of pollen tubes carrying different *S*-alleles). Most of the results support the model in apricot, which was previously drawn by de Nettancourt [17] for GSI, as being controlled by a single multialleleic locus, the *S*-locus. The S-gene product in styles is a ribonuclease enzyme (*S*-RNase) [18], while the recently identified pollen product is an F-box protein [19, 20].

Compatibility assessment by fruit set and pollen tube growth - The 1st generation studies: Determination of fruit set after controlled crosses and observing pollen tube growth are methods traditionally used mainly to determine fertility relations. Nyujtó *et al.* [21] by observing the cross-pollination of cultivars belonging to the Hungarian Óriás ("giant-fruited") group ('Ceglédi óriás', 'Szegedi mammut', 'Nagykõrösi óriás' and 'Ligeti óriás') found that these cultivars did not fertilize each other. Later, Szabó and Nyéki [22] described that by putting these "giant-fruited" cultivars next to each other in an orchard, they would not perform effective cross-pollination, thereby they form an inter-incompatibility group (Table 1). Molecular analysis of this cross-incompatible cultivar group was conducted nearly 20 years later, which completely confirmed all the formerly obtained open field data [23-27].

An inter-incompatibility group was defined between two Spanish cultivars: 'Moniquí Fino' and 'Moniquí Borde' by Egea *et al.* [7]. However, their names and morphological similarities indicate that they may be slightly different clones of the same cultivar; therefore they are not involved in Table 1. Burgos *et al.* [8] have not found cross-incompatibility after crossing eight SI cultivars from the same Spanish population. Many Spanish apricot cultivars originated from crosses between North African cultivars (mainly SI) and European cultivars (mainly SC) [28]. Hence, according to the authors' interpretation, a great degree of heterozygosity is supposed to be present among these cultivars; nevertheless under GSI it is not surprising. The argument must be supplemented by the fact that this kind of hybridization could extend the genetic bases and the allelic variation of the *S*-locus. Egea and Burgos [29] studied cross-compatibility between some North American cultivars by examining pollen tube growth using fluorescence microscopy and fruit set from controlled pollination in the orchard. The percentages of fruit set following self-pollination confirmed that 'Lambertin-1', 'Goldrich', 'Hargrand' and 'Harcot' are self-incompatible and the first three are cross-incompatible in all possible combinations. 'Harcot' was compatible with the three other cultivars. All cross-incompatible cultivars have 'Perfection', an old SI cultivar [4] among their ancestors. These cross-incompatible apricots would have the same genotype for the SI trait and the authors designated those two alleles as S_1 and S_2 (Table 1).

Viti *et al.* [30] studied 48 crosses over a two-year period and they confirmed that self-pollination of 'Harcot', 'Moniquí' and 'Hargrand' resulted in an

Table 1: An updated apricot cultivar table demonstrating the *S*-genotypes of 23 cultivars and assigning them to four groups according to their inter-(in)compatibility properties

Group	Cultivars	Origin	*S*-genotype	References
Group I	Goldrich			
	Hargrand			
	Lambertin-1	USA	S_1S_2	[29]
Group II	Ceglédi óriás			
	Ligeti óriás			
	Szegedi mammut			
	Nagykörösi óriás	Hungary	S_8S_9	[22]; [25]
Group 0 (universal donors)	Mauricio	Spain	S_cS_1	[36]
1. Self-compatible cultivars	Canino	Spain	S_cS_2	[36]
	Pepito	Spain	S_cS_2	[33]
	Colorao*	Spain	S_cS_5	[33]
	Rial Fino	Spain	S_cS_6	[39]
	Beliana	Morocco	S_cS_7	[36]
	Modesto	USA	S_cS_{13}	[25]
	Currot	Spain	S_cS_c	[36]
	Palau	Spain	S_cS_c	[41]
	Ginesta	Spain	S_cS_c	[41]
Group O (universal donors)	Harmat	Hungary	$S_{10}S_{11}$	[25]
2. Self-incompatible cultivars with unique genotype	Korai zamatos	Hungary	$S_{12}S_{13}$	[25]
	Moniquí	Spain	S_2S_6	[33]
	Priana	Spain	S_2S_7	[36]
	Sunglo	USA	S_2S_3	[33]
	Voski	Ukraine	$S_{11}S_{13}$	[25]

*Cultivar 'Colorao' was described as self-compatible on the basis of its *S*-genotype [41]; however, this is a male sterile cultivar and thereby cannot be considered as a 'universal donor'

incompatible combination. Andrés and Durán [31] examined some aspects of the reproduction physiology of 20 Spanish apricot clones. Self-incompatibility of these clones was determined not only in field conditions but also in the laboratory by means of pollen tube growth. They have revealed that 'Moniquí Azaraque' requires more time for the pollen tube to advance through the different areas into which the pistil was divided than any other tested cultivar and the pollen tubes after self-pollination did not pass beyond the base of the style. This lead to the hypothesis that 'Moniquí Azaraque' might be a self-incompatible clone. They have found that the clone 'Chicanos Archena' could be characterized by the lowest fertilization time from the 19 apricot clones tested. Alburquerque *et al.* [32] clarified that pollen tubes of 'Beliana' and 'Palstein', two cultivars that consistently set good yields grew faster than those of 'Guillermo' and 'Bergeron', which was characterized by low fruit production. Ovules matured earlier and in a larger number in cvs. 'Beliana' and 'Palstein'.

Monitoring fruit set or pollen tube growth through the style was not even phased out when more recent protein or DNA based molecular techniques became available for self-incompatibility studies, but remained valuable tools to check molecular information at phenotypic level.

Direct determination of *S*-allele composition by protein and DNA based molecular typing - The 2nd generation studies: Burgos *et al.* [33] analysed stylar proteins by non-equilibrium pH gradient electrofocusing (NEpHGE) to identify *S*-RNases in nine apricot cultivars. The method itself was based on the protocol elaborated by Wilson [34] and modified by Boškovic and Tobutt [35]. They presented the first report in apricot describing six *S*-RNase izozymes for self-incompatibility and one for self-compatibility, designated as S_1-S_6 and S_c, respectively, in North American and Spanish apricot genotypes. Two generations of seedlings from the cross 'Moniquí' × 'Pepito' and 'Gitano' × 'Pepito' were used to monitor the inheritance of RNase bands and the results followed the expected segregation ratios. Number of SI alleles was extended when a previously unidentified S_7-allele could have been revealed by electrofocusing [36]. By genotyping new cultivars, it was demonstrated that in all SC cultivars examined, the self-compatibility allele is

the same and is associated with an RNase izozyme with high activity. Among the established cultivars and seedlings, some individuals homozygous for S_c were also detected, which can be an appreciated *S*-genotype in any breeding program since all of their progenies will carry the S_c-allele allowing them to be self-compatible.

Nine new SI alleles (S_8-S_{16}) were described in twenty-seven apricot accessions, which were analysed for stylar ribonucleases separated using newly designed NEpHGE protocols and *S*-haplotype related PCR amplification with cherry consensus primers [24, 25]. NEpHGE revealed 12 bands correlated with distinct *S*-alleles, three of which corresponded to the previously described S_1-, S_2- and S_4-alleles. Alleles S_3, S_5, S_6 and S_7 were not used in this study, but these alleles could be later characterized as having different intron sizes than the newly detected ones. These results support that the genetic background of the East European and Central Asian cultivars is wider and more variable compared to that of the Mediterranean and American accessions [37]. The *S*-RNase isoenzyme pattern showed a good correlation with the PCR data obtained by sweet cherry consensus primers. From a theoretical point of view, these results provided further support to the hypothesis that *S*-RNase gene family within the *Prunoideae* was highly conserved in the course of evolution [38]. This was the first report combining the advantages of protein and DNA based methods in *S*-genotyping of apricot cultivars. Isoelectric points of thirteen apricot *S*-RNases were also determined by Halász *et al.* [25].

Sutherland *et al.* [39] developed a primer set (EM primers) involving three degenerate consensus primers flanking the second intron for use across the *Prunus* genus. They described correlations between apricot genotypes reported from *S*-RNase activity gels and from PCR pattern obtained by this primer set. The EM primers could successfully amplify six apricot *S*-alleles (S_1-S_6) and the self-compatibility allele, S_c, in addition they proved successful for the detection of S_8–S_{15} alleles [40].

Vilanova *et al.* [41] combining two PCRs distinguished the 8 known alleles (S_1-S_7 and S_c). Two sets of consensus primers, designed from apricot and sweet cherry sequences, were used to amplify fragments containing the first and the second introns. Sixteen apricot accessions were genotyped successfully by the applied technique.

Nine *S*-alleles were described from 6 Chinese apricot cultivars using *S*-allele-specific PCR amplification with a primer pair of PruC2 and PruC5 (designed by Tao *et al.* [42]) and confirmed by Sothern blot analysis and test pollinations [43]. Two cultivars, 'Hongfeng' and 'Xinshiji' possessed identical genotype, which means they form an incompatibility group. The results of this analysis unfortunately were not reconciled with the existing allele series of apricot [25, 33, 36], therefore its data could not be involved among the data summarized in Table 1 and all described genotypes and the establishment of a newer incompatibility group will require further investigations.

The structure of the apricot *S*-locus: A genetic linkage map of apricot was constructed based on the F_2 population derived from the self-pollination of an F_1 individual ('Lito') originated from a cross between the self-incompatible 'Stark Early Orange' and the self-compatible 'Tyrinthos' [44]. The SI trait was mapped on linkage group G6. An interesting analysis was carried out to monitor SC phenotype in the F_2 population: primers AS1 and Pru-C4R [42] were found to amplify an approximately 1.5 kb fragment in every SI cultivar but not in SC ones. A similar result was obtained by a similar primer set (Pru-C2 and Pru-C4R) in Japanese apricot except that a fragment of the same size occurred exclusively in the SC cultivars [45].

To facilitate gene discovery in apricot, a bacterial artificial chromosome (BAC) library was constructed from the cultivar 'Goldrich' [46] as an initial step towards the identification of the pollen *S*-gene in apricot. This work was accomplished by Romero *et al.* [20], who analyzed the *S*-locus structure and identified the *S*-RNase and SFB genes of apricot. For these analyses, they used the cultivars 'Goldrich' (S_1S_2) and 'Harcot' (S_1S_4). Their results show that the *S*-locus genomic structure in *Prunus armeniaca* is similar to those of other *Prunus* species reported to date [19, 47, 48]. The apricot *S*-RNases have the typical features of *Prunus* T_2-type RNases with five conserved domains (C1, C2, C3, RC4 and C5) and one hypervariable region (RHV). Motifs necessary for the RNase activity surrounding the histidine residues are present in the C2 and C3 domains. Apricot *S*-RNases like other known *Prunus S*-RNases contain two introns. The first intron is located within the junction between the signal peptide and the mature protein and the second one within the hypervariable region (RHV). The sizes of these introns vary in an *S*-haplotype specific manner. Romero *et al.* [20] determined the length of the introns within S_1-, S_2 and S_4-alleles. Splice junctions (GT/AG) are conserved in all of them and AT content of their sequences ranged from 65% to 78%. The three studied *S*-RNase alleles show an amino acid identity with a mean of 77.5%. This high sequence polymorphism supports

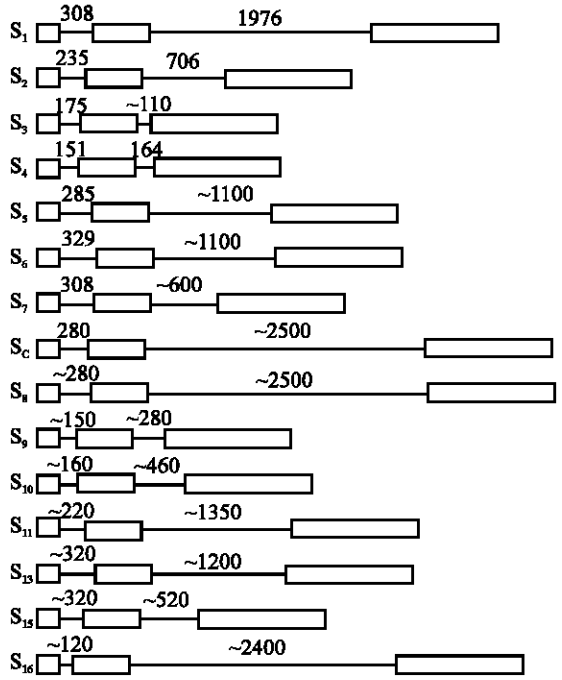

Fig. 1: Schematic structures of 15 apricot (S_1-S_{11}, S_{13}, S_{15}, S_{16} and S_c) RNase genes. S_1, S_2 and S_4 were determined from cDNA sequences [20]; S_3, S_5-S_7 and S_c [41] as well as S_8-S_{11}, S_{13}, S_{15}, S_{16} [40] were deduced from the genomic PCR amplification products

these genes as candidates for the pistil *S*-determinants. By genomic PCR analyses using consensus primers, the determination of the approximate intron lengths of the S_3, S_5, S_6, S_7 and S_c alleles [41] as well as those of S_8, S_9, S_{10}, S_{11}, S_{13}, S_{15} and S_{16} [40] was carried out (Fig. 1).

Apricot SFBs (*S*-haplotype specific F-box) are also similar to the *Prunus* SFB alleles with one F-box domain, four (hyper)variable regions (V1, V2, HVa, HVb) and with an intron upstream of the coding sequence. Three of the variable regions (V2, HVa, HVb) are located at the C-terminal region pointing out this area as responsible for the SFB specificity. These domains are not strongly hydrophobic. SFB_1, SFB_2 and SFB_4 are also highly polymorphic with a mean of 79.4% amino acid identities.

One of the most important requirements for the *S*-RNase based GSI systems is the physical linkage between *S*-RNase and SFB genes in order to suppress recombination. In the S_2-haplotype, the physical distance between SFB_2 and S_2-RNase alleles is only 2.9 kb [20]. The S_1- and S_2-haplotype regions analysed are highly divergent with many interspersed repetitive sequences such as microsatellites, direct and inverted repeats, palindromes and putative retroelements. The transcriptional orientations of the S_2-RNase and the SFB_2 genes are the same, in contrast to the inverse orientation observed in Japanese apricot, almond and cherry [19, 47, 48].

Organ-specific expression studies provided additional evidence for *S*-RNases and SFBs being the pistil and pollen components, respectively, of self-incompatibility system in apricot, revealing that *S*-RNases are expressed in style tissues but not in pollen or leaves. In contrast, SFBs are exclusively expressed in pollen and not expressed in leaves or styles.

Model for self-compatibility in apricot: In almond, a pistil-part mutation resulted in an inactive *S*-RNase molecule, while in sweet cherry and Japanese apricot self-compatible pollen-part mutants carry defective SFBs that were hypothesized to polyubiquitinate not only the non-self *S*-RNases but also cognate *S*-RNases for subsequent degradation by the 26 S proteasome pathway [49]. Considering the fact that heterozygote SC apricot genotypes show two izozyme bands of high ribonuclease activity (an integral pistil function), a pollen-part mutation within the F-box region (a failure in pollen function) could also be proposed in the SC *P. armeniaca* cultivars [33, 25]. Recently, the pollen component gene of the self-compatibility haplotype, SFB_C, was isolated and shown to carry a 358 bp insertion within the predicted open reading frame. This results in a truncated protein that lacks the hypervariable regions having crucial role in the allele-specific recognition process [50]. The loss of pollen-*S* function was further supported by the identification of the original, non-mutated form of the apricot SFB_C-allele (Halász *et al.*, unpublished results). Various putative models for the SI reaction and predictive mechanisms of self- and non-self discrimination have been discussed recently [51].

Sonneveld *et al.* [52] proposed a model of *S*-RNase and SFB interaction that suggests a role for SFB proteins to prevent self *S*-RNases from being degraded and not recruit non-self *S*-RNases for degradation as it was dictated by other models [49]. In the light of this model, self-compatibility in apricot may be attributed to the following molecular events: the S_C-RNase and the mutated F-box protein are not able to form a stable complex, so the *S*-RNases will consequently be polyubiquitinated and degraded, which will result in fruit set.

Other fruit setting problems and future perspectives: Male sterility means that no viable pollen is formed.

Shrunken, discoloured anthers are indicative of male-sterile pollen, while fertile anthers are swollen and yellow [53]. RAPD markers combined with bulk segregant analysis successfully revealed a marker linked to male fertility [54]. Lillecrapp *et al.* [53] presented the first report of a simultaneous mutation in both female and male function in apricot. Low fruit set of the cultivar 'Trevatt blue' was attributed to small multiple ovules retarded in development and to anthers with degenerated microspores and some failure in tapetal breakdown. Burgos and Egea [55] by analysing a great number of progenies provided evidence that the male-sterility trait in apricot is controlled by a single recessive gene. Male sterility is the most important reason of fruit setting problems in peach; however, in apricot the previously detailed self-incompatibility mechanism has more considerable consequences. 'Colorao' is one of the representatives of the reported male sterile apricot cultivars (Table 1) [33]. Besides genetically controlled traits, environmental factors have also impacts on flower biology and flowering dynamics of apricot, influencing the fruit set [56].

As more and more problems, e.g. plum pox virus infection [57-59] and highly desirable characters such as improved nutritional value of fruits [60] become evident in apricot growing, breeders must find newer ways to combat or reach them, respectively [61]. However, self-incompatibility, which was only recently recognized in certain apricot cultivars, shows a warning sign that several unfavourable characters may also be transmitted by the accessions intensively used in breeding programs. By *S*-genotyping of large germplasm collections and summarizing the obtained data, fertility problems should have been eliminated well before they manifest themselves in economic losses. Table 1 summarizing all presently available data that may help to design crosses in breeding programs and achieve optimal cultivar association within orchards.

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