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Inheritance of S-genotypes in Paviot × Kabaasi apricot F_1 progenies

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ABSTRACT

Self-incompatibility plays an important role in the fertilization of fruit species such as apricot. Apricot (*Prunus armeniaca* L.) shows gametophytic self-incompatibility, which is controlled by a multi-allelic S-locus. In this study, S-alleles of 77 F_1 progenies derived from Paviot, which is one of the French local cultivars, and Kabaasi, one of the most important Turkish dried apricot cultivars, parents were identified by S-RNase intron regions polymerase chain reaction (PCR) amplification and DNA sequencing. The results from the S-allele PCR analysis revealed that the Paviot female parent had an S_cS_2 genotype and the Kabaasi male parent had S_1S_9 alleles. Forty-three of the F_1 progenies showed self-compatibility allele (S_c) by having either S_cS_9 or S_cS_1 alleles. Thirty-four of the F_1 progenies were self-incompatible by having either S_2S_1 or S_2S_9 alleles. The distributions of detected alleles in F_1 progenies were determined as follows: S_cS_1 31.2%, S_1S_2 27.3%, S_cS_9 24.7% and S_2S_9 16.8%. The results from the study are relevant for the data obtained in apricot breeding programmes in the selection of crossing combinations and in the establishment of commercial orchards.

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Prunus armeniaca; Paviot; Kabaasi; F_1 progenies; self-incompatibility; S-genotypes

Introduction

Apricot is one of the most important fruit species due to its commercial importance. Turkey ranks first in the world in apricot production with approximately 676.000 metric tons annually, with the apricot production fluctuating from year to year due to spring frosts.[1] In recent years, molecular techniques are widely used to characterize fruit tree germplasm resources. DNA molecular markers are highly effective and informative in the assessment of the genetic diversity and genetic relationships of fruit trees.[2–6]

Self-incompatibility in *Prunus* species, including apricot, is controlled by a simple multi-allelic S-locus that rejects its own pollen and has a homomorphic, gametophytic self-incompatibility system.[7] Self-incompatibility alleles allow pollen tube growth in the pistil and access to the ovaries. In cases where the same allele disputes exist on haploid pollen and diploid pistil, the growth of pollen tubes is blocked and a dispute arises due to the S-allele-specific S-RNase gene ribosomal RNA degradation system.[8–11] The effects of the self-incompatibility mechanism force pollination with foreign pollens to occur; and thus the emergence of genetic diversity and an increase in heterozygosity.[12]

Many European apricot cultivars are self-compatible, whereas those in Central Asia and Iran and the Caucasus, including Turkey, are self-incompatible.[13] Prominent apricot cultivars grown in Turkey are located within the Iran–Caucasian eco-geographical group. The apricot cultivars of economic importance in Turkey are found to be, generally, self-incompatible.[2,14–16]

Self-incompatibility plays an important role in the fertilization of fruit species such as apricot. Self-incompatible apricot cultivars need suitable pollinators for fructification.[17,18] A breeding target is to breed self-compatible apricot cultivars having high fruit quality. Therefore, it is imperative to determine the S-alleles of apricot cultivars.[19]

The self-incompatibility mechanism can be determined using conventional methods such as pollination tests and pollen tube growth tests. However, these tests are labour-intensive and time-consuming, and also influenced by environmental factors.[20,21] The use of molecular techniques to reveal S-alleles in genotypes has recently become the most commonly used method that gives the best results, as it allows early selection.[18]

In this study, we report S-alleles of Paviot, which is one of the French local cultivars, and Kabaasi, one of the most important Turkish dried apricot cultivars, by S-RNase intron region polymerase chain reaction (PCR) amplification and DNA sequencing. In addition, the segregation of S-alleles in Paviot × Kabaasi F_1 populations is also reported.

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Materials and methods

Plant material

The plant materials were provided by the Apricot Research and Application Central Directorate of Agricultural Center of İnönü University. In this study, 77 F_1 progenies and their parents (Paviot and Kabaasi) were used. F_1 progenies were produced in a project supported by TUBITAK [project no: TOGTAG-3099] in the period 2003−2005. Leaf samples from each plant were stored at 4 °C after lyophilization.

DNA extraction

DNA isolation from leaf samples was performed using the CTAB (cetyl trimethyl ammonium bromide) protocol according to Doyle and Doyle [22] with minor modifications.[23] The concentration of isolated DNA was determined by comparison with λ-DNAs quantified by agarose gel electrophoresis (Thermo Electron Corporation EC135-90, Madison, WI, USA).

S-allele PCR amplification

Primer pairs developed by Romero et al. [24] and Vilanova et al. [25] were used as listed in Table 1 in order to determine the S-alleles by PCR analysis. Each PCR reaction of 25 μL contained 75 mmol/L of Tris-HCl (pH 8.8), 20 mmol/L of $(NH_4)_2SO_4$, 2 mmol/L of $MgCl_2$, 0.1% Tween 20, 100 μmol/L of each deoxyribonucleoside triphosphate, 0.2 μmol/L of each primer, 1.0 units of *Taq* DNA polymerase (Thermo, Waltham, MA, USA) and 50 ng of DNA. For PCR amplification, the samples were pre-denatured at 94 °C for 3 min, followed by 35 cycles in which the samples were denatured for 45 s at 94 °C, annealed for 45 s at 54 °C and extended for 60 s at 72 °C. For the final extension step, the samples were kept at 72 °C for 10 min. The PCR products were separated by electrophoresis in a 3% agarose gel with 0.5X TBE (Tris-borate-ethylenediaminetetraacetic acid) buffer based on band sizes and were visualized under ultraviolet light (Vilber Lourmat Infinity 1100, Collégien, France) by staining with ethidium bromide.

DNA sequencing

DNA sequence analysis of PCR products was performed by Sanger sequencing at Medsantek Company (İstanbul, Turkey). The S-alleles of the parents were determined by comparing the sequences using BLAST (basic local alignment search tool) with those available in the NCBI (National Center for Biotechnology Information) databases.

Table 1. The primers used to determine S-alleles of apricots.

Primers	Primer sequence	Reference
SRc-R	5'-GGC CAT TGT TGC ACA AAT TG-3'	Vilanova et al.[25]
SRc-F	5'-CTC GCT TTC CTT GTT CTT GC-3'	Romero et al.[24]

Data analysis

All results were analysed using the SPSS (version 15) statistical analysis package and the data are mean values with standard deviation (±SD) from three replications. Data were analysed by analysis of variance and significant differences between the groups were determined by the multiple comparison procedure according to Duncan.[26] Differences were considered statistically significant at ($P < 0.05$).

Results and discussion

PCR amplifications using the SrcF−SrcR primer combination detected an allele of 353 bp in Paviot genotype, which corresponds to the self-compatibility S_c allele reported by Vilanova et al.[25] According to Tao et al., [27] all genotypes without S_c alleles did not fructify, and they were self-incompatible. In addition to the S_c allele, three other alleles were identified: two in Paviot (328 and 267 bp) and one in Kabaasi (373 bp) (Figure 1).

The Paviot and Kabaasi S-allele genotypes showed homology with the allele sequences from *Prunus armeniaca* with S_c (353 bp), S_2 (328 bp), S_1 (373 bp) and S_9 (267 bp) available in the NCBI database.[23,28] The Paviot genotype was found to have S_cS_2 alleles and to be self-compatible due to the presence of S_c alleles. It was reported that the Kabaasi genotype has the S_9 allele, and it is the most common allele found in the local Turkish apricot varieties such as Adilcevaz 5, Akcadag Gunay, Cataloglu, Cekirge 52, Cologlu, Dortyol 2, Haci Haliloglu, Hasanbey, Ismailaga, Kadıoglu, Kamelya, Kurukabuk, No 2 Zerdali, Ozal, Seftalioglu, Soganci and X3 Zerdali.[2]

Previous selfing studies carried out under specific conditions showed that the Kabaasi cultivar is self-compatible,[16] whereas others have found it to be self-incompatible.[14,15] In this study, the Kabaasi cultivar had S_1S_9 alleles and was determined to be self-incompatible. Halasz et al. [2] reported that the Kabaasi cultivar had S_9S_{13} alleles, and it was self-incompatible. In that study, the alleles carried by individuals were identified based on the band sizes in electrophoresis gel images. The band sizes were estimated by separating the PCR products by agarose gel electrophoresis; however, it was sometimes very difficult to estimate such bands when the sizes of the alleles were very close to each other. In this study, to overcome this problem, the bands in

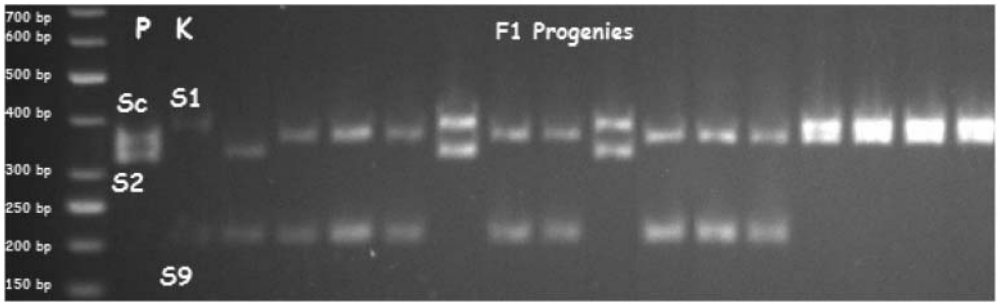

Figure 1. Electrophoregram of S-alleles of parents and F_1 progenies amplified with the SrcF and SrcR primers for the first intron region. P: Paviot, K: Kabaaşı. DNA molecular size marker: Thermo Generuler 50 bp DNA ladder (Waltham, MA, USA).

Kabaasi and Paviot cultivars were bidirectionally sequenced, BLAST searched in NCBI GenBank and in them, the S-alleles were determined as S_1S_9.

Apricots belonging to the Iran−Caucasian eco-geographical group have been reported to be mostly self-incompatible, those in the European eco-geographical group, mostly self-compatible and 60% of the varieties in Turkey have been found to be self-incompatible. [16,29−31] In this study, the Kabaasi cultivar, which is in the Iran−Caucasian eco-geographical group, was found to be self-incompatible, whereas the Paviot cultivar, which belongs to the European eco-geographical group, was found self-compatible.

Of the 77 F_1 progenies tested, 34 samples did not have S_c alleles and were identified to be self-incompatible (Table 2). According to Halasz et al.,[2] there was absence of an S_c allele in 44 of 51 apricot genotypes grown in Turkey and they were found to be self-incompatible. Halasz et al. [31] also found that 60% of the varieties grown in Turkey are self-incompatible. In this study,

Table 2. S-genotypes of parents and F_1 progenies in this study.

Progenies	Allele	Progenies	Allele	Progenies	Allele	Progenies	Allele
Paviot	S_cS_2	PK 19	S_1S_2	PK 39	S_2S_9	PK 59	S_cS_1
Kabaasi	S_1S_9	PK 20	S_cS_1	PK 40	S_1S_2	PK 60	S_cS_1
PK 1	S_1S_2	PK 21	S_cS_1	PK 41	S_cS_1	PK 61	S_cS_1
PK 2	S_cS_1	PK 22	S_1S_2	PK 42	S_cS_1	PK 62	S_2S_9
PK 3	S_cS_1	PK 23	S_1S_2	PK 43	S_cS_1	PK 63	S_1S_2
PK 4	S_cS_1	PK 24	S_cS_9	PK 44	S_2S_9	PK 64	S_2S_9
PK 5	S_2S_9	PK 25	S_2S_9	PK 45	S_cS_1	PK 65	S_cS_9
PK 6	S_1S_2	PK 26	S_2S_9	PK 46	S_cS_1	PK 66	S_cS_1
PK 7	S_1S_2	PK 27	S_2S_9	PK 47	S_2S_9	PK 67	S_cS_1
PK 8	S_1S_2	PK 28	S_1S_2	PK 48	S_cS_9	PK 68	S_1S_2
PK 9	S_2S_9	PK 29	S_cS_9	PK 49	S_cS_9	PK 69	S_2S_9
PK 10	S_cS_1	PK 30	S_1S_2	PK 50	S_cS_9	PK 70	S_cS_1
PK 11	S_cS_1	PK 31	S_1S_2	PK 51	S_1S_2	PK 71	S_cS_9
PK 12	S_2S_9	PK 32	S_cS_9	PK 52	S_cS_9	PK 72	S_cS_1
PK 13	S_cS_9	PK 33	S_1S_2	PK 53	S_cS_9	PK 73	S_1S_2
PK 14	S_1S_2	PK 34	S_cS_1	PK 54	S_1S_2	PK 74	S_cS_9
PK 15	S_cS_1	PK 35	S_cS_9	PK 55	S_cS_9	PK 75	S_cS_9
PK 16	S_cS_9	PK 36	S_cS_9	PK 56	S_cS_9	PK 76	S_1S_2
PK 17	S_cS_1	PK 37	S_cS_1	PK 57	S_cS_9	PK 77	S_1S_2
PK 18	S_2S_9	PK 38	S_1S_2	PK 58	S_cS_1		

Note: P, Paviot; K, Kabaasi; PK, Paviot × Kabaasi.

43 of the F_1 progenies had either S_cS_1 or S_cS_9 alleles, and they were self-compatible. On the other hand, 34 F_1 progenies were found to have S_1S_2 and S_2S_9 incompatibility alleles (Table 3). Burgos et al. [10] reported that the self-compatibility allele was dominant over the self-incompatibility allele. Similarly, in their study conducted on the self-incompatibility status of apricot F_1 populations in, Chen et al. [32] found that the self-compatibility allele was dominant over the self-incompatibility allele; and the S-genotype in Katy, the main individual, was heterozygous (S_cS_8).

The distribution of alleles in the F_1 progenies was observed to be as follows: S_cS_1 in 31.2%, S_1S_2 in 27.3%, S_cS_9 in 24.7%, and S_2S_9 in 16.8%. Two alleles were identified in the Paviot genotype with sizes of 353 and 328 bp, and two other alleles were found in the Kabaasi genotype with sizes of 267 and 373 bp. Comparison of the DNA sequences of all the four different alleles with those in GenBank showed that the S_c and S_2 alleles were found in the Paviot genotype, whereas S_1 and S_9 were identified in the Kabaasi genotype. In total, 43 F_1 progenies were found to have an S_c allele and thus, to be self-compatible, whereas 34 F_1 progenies were self-incompatible due to the absence of an S_c allele.

Table 3 shows the pomological features of some F_1 progenies that had high quality in 2011−2013. F_1 progenies Nos. 17, 20, 58, 67 and 72 were found to have high yield and high quality fruit in pomological studies. At the same time, they were determined to be self-compatible, too (Table 2). These progenies can be used as parents in breeding programmes or as cultivar candidates in commercial apricot orchards.

Conclusions

In this study, S-allele specific PCR was used to identify the S-alleles of 77 F_1 progenies and their parents. The DNA sequences of four alleles were obtained and compared in the NCBI GenBank database. S_c and S_2 alleles were found in the Paviot genotype, whereas S_1 and S_9

Table 3. Fruit characteristics of some F_1 progenies.

Progenies	Fruit weight (g)	Kernel weight (g)	Brix (%)	Fruit shape	Peel colour	Flesh colour
PK 10	32.1 ± 1.2^{c}	3.1 ± 0.01^{b}	23.8 ± 1.1^{b}	Oval	Yellow	Yellow
PK 12*	28.0 ± 0.2^{d}	3.4 ± 0.06^{b}	21.0 ± 1.6^{c}	Oval	Green	Yellow
PK 13	42.3 ± 2.3^{ab}	3.6 ± 0.06^{ab}	26.5 ± 1.2^{a}	Oblong	Orange	Orange
PK 14	35.2 ± 0.8^{c}	3.6 ± 0.05^{ab}	23.0 ± 1.7^{b}	Oval	Orange	Orange
PK 17**	35.7 ± 0.6^{c}	2.8 ± 0.05^{c}	23.5 ± 1.3^{b}	Round	Orange	Orange
PK 20**	39.8 ± 0.5^{b}	3.6 ± 0.01^{ab}	25.0 ± 1.3^{a}	Elliptic	Yellow	Yellow
PK 33	23.7 ± 0.2^{e}	2.6 ± 0.03^{c}	23.8 ± 1.2^{b}	Oval	Yellow	Cream
PK 38	37.7 ± 1.1^{b}	2.8 ± 0.02^{c}	21.5 ± 1.7^{c}	Round	Yellow	Yellow
PK 41	39.3 ± 0.4^{b}	3.4 ± 0.02^{b}	21.0 ± 1.8^{c}	Elliptic	Yellow	Cream
PK 46	48.2 ± 0.5^{a}	4.0 ± 0.09^{a}	21.6 ± 1.5^{c}	Oval	Yellow	Yellow
PK 52	38.6 ± 0.2^{b}	3.4 ± 0.02^{b}	26.2 ± 1.6^{a}	Oval	Yellow	Yellow
PK 58**	45.3 ± 0.7^{a}	3.3 ± 0.07^{b}	26.8 ± 1.4^{a}	Round	Yellow	Cream
PK 59	44.5 ± 0.9^{a}	3.2 ± 0.07^{b}	23.3 ± 1.1^{b}	Elliptic	Orange	Orange
PK 63	35.2 ± 0.1^{c}	3.2 ± 0.07^{b}	21.5 ± 1.4^{c}	Round	Yellow	Yellow
PK 65	28.5 ± 0.2^{d}	2.8 ± 0.02^{c}	22.0 ± 1.9^{b}	Oval	Yellow	Yellow
PK 67**	40.4 ± 1.3^{ab}	3.1 ± 0.05^{b}	17.1 ± 1.7^{d}	Elliptic	Green	Cream
PK 70	46.5 ± 0.4^{a}	3.5 ± 0.04^{ab}	22.8 ± 1.4^{b}	Oval	Yellow	Yellow
PK 72**	43.8 ± 1.9^{ab}	3.8 ± 0.06^{a}	24.5 ± 0.05^{b}	Elliptic	Yellow	Yellow
PK 74	33.2 ± 1.2^{c}	3.4 ± 0.08^{b}	26.6 ± 1.2^{a}	Oval	Orange	Orange
PK 77	41.8 ± 1.1^{ab}	3.7 ± 0.03^{a}	20.5 ± 1.0^{c}	Round	Yellow	Yellow

Note: Values are means (±SD) of three replications. Data followed by different letters are significantly different from each other ($P < 0.05$) according to Duncan's test [26].
*High yield. **Very high yield.

alleles were identified in the Kabaasi genotype. It was determined that 43 F_1 progenies had the S_c allele; and thus they were self-compatible. On the other hand, 34 F_1 progenies had no S_c allele; therefore, they were self-incompatible. The distributions of the detected alleles in the F_1 progenies in Paviot (S_cS_2) and Kabaasi (S_1S_9) parents were determined as follows: S_cS_1 31.2%, S_1S_2 27.3%, S_cS_9 24.7% and S_2S_9 16.8%. In breeding studies, the development of new genotypes with the desired characteristics and with known compatibility pattern of parents is of crucial importance in terms of both the required time and the cost of manpower. Therefore, the results from this study are relevant based on the data obtained in apricot breeding programmes in the selection of crossing combinations and in the establishment of commercial orchards.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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