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S-Genotype Profiles of Azerbaijan Apricot Germplasm

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Abstract

Apricot is one of the important export products of Azerbaijan. Some studies showed that unproductiveness problem of apricots together with increasing production areas arises because of self-incompatibility. In flowering plants, gametophytic self-incompatibility, controlled by a single locus with several allelic variants, is one of the major problems preventing self-fertilization. Among fruit trees, apricots show a high degree self-incompatibility, especially in Middle-Asian and Iranian-Caucasian eco-geographical groups. In this study, the S-genotypes of a set of 61 Azerbaijan apricot (*Prunus armeniaca* L.) cultivars were determined by polymerase chain reaction (PCR) amplification of their S-RNase intron regions. In addition, the S-genotyping method was extended to the S haplotype-specific F-box (SFB) gene to detect the non-functional SC-haplotype and hence identification of self-compatible apricot cultivars were carried out by using four primer pairs (SRc-F and SRc-R, EM-PC2consFD and EM-PC3consRD, AprSC8-R and PaConsI-F, AprFBC8-F and AprFBC8-R). A total of 9 S-RNase alleles (S_2, S_3, S_6, S_7, S_8, S_{11}, S_{12}, S_{13} and S_c) were determined in the 61 apricot genotypes. As Azerbaijan apricot genotypes are determined to be mostly self-incompatible, the data obtained hereby might be of good use for apricot breeding programs and more practically, for new apricot plantations; thus, pollinator cultivars should be considered when self-incompatible apricot cultivars are being used.

Keywords: alleles, *Prunus armeniaca* L., primers, self-(in)compatibility

Introduction

Apricot is thought to have originated in China, from where it was disseminated to Europe through central Asia and Asia Minor (Faust et al., 1998). According to

Kostina (1969), apricot cultivars are classified into four major eco-geographical groups: central Asian, Irano-Caucasian, European, and Dzhungar-Zailing (Tien-shan area). The central Asian and Irano-Caucasian (encompassing Turkish cultivars) groups show the richest phenotypic variability, while the European group (including cultivars grown in North America, Australia, and South Africa) is said to have the least diversity (Mehlenbacher et al., 1991). Apricot cultivars originating in the eastern Europe cultivar group can be clearly distinguished in their pomological characteristics from other cultivars within the European origin (Faust et al., 1998; Kostina, 1970).

In Rosaceae, many fruit species such as Japanese pear (*Pyrus pyrifolia*), apple (*Malus* × *domestica*), sweet cherry (*Prunus avium*), almond (*Prunus dulcis*) and apricot (*Prunus armeniaca*) exhibit selfincompatibility (SI) and require pollination with pollen from compatible SI genotypes for stable fruit production. Aside from this practical importance, SI of Rosaceae is interesting from an evolutionary point of view, because the common ancestor of Asterid and Rosid is thought to exhibit S-RNase-based gametophytic self-incompatibility (Yilmaz et al., 2016).

Similar to other Prunus L. species, apricots reportedly demonstrate gametophytic self-incompatibility controlled by a single locus with multiple variants, termed S-haplotypes (de Nettancourt, 2001). The Irano-Caucasian apricots were described as predominantly self-incompatible (SI), while most European apricots are self-compatible (SC) (Hala´sz et al., 2005; Kostina, 1970). Cross-incompatibility, resulting in the mutual failure of fruit set between a pair of cultivars, occurs frequently in predominantly SI species. In apricot, the first cross-incompatibility group was described among the North American cultivars, Goldrich, Hargrand, and Lambertin-1 (Egea and Burgos, 1996), while the second group encompassed giant-fruited Hungarian apricots (Szab´o and Ny´eki, 1991).

In new apricot plantations, self-incompatibility is one of the important problems and in order to solve this issue, molecular techniques are being used to determine self-(in) compatibility alleles in apricot cultivars (Burgos et al., 1998; Halasz et al., 2005, 2007; Yilmaz, 2008; Yilmaz et al., 2013). Genetically, SI of Rosaceae is controlled by a single S locus with multiple alleles (Sonneveld et al., 2003). The S-gene product is a ribonuclease enzyme, while the pollen product is an F-box protein (Entani et al., 2003; Romero et al., 2004). The conventional methods to determine self-incompatibility are time consuming and can be affected by environmental factors (Zhang et al., 2003). Even more, molecular markers have been developed in recent years to determine the self-incompatibility of genotypes (Yaegaki et al., 2001). The Sc-haplotype was long suspected to be a pollen-part mutant of the S8-haplotype (Halasz et al., 2007) with a 353-bp insertion in the SFBC gene (Vilanova et al.,

2005). Although most apricot cultivars are self-compatible, self-incompatibility is present in some interesting cultivars (Hormaza et al., 2007). Up to 2010, a total of 20 SI (self-incompatible) alleles and one SC (self-compatible) allele were determined among European eco-geographical group of apricot (Burgos et al., 1998; Halasz et al., 2005, 2007, 2010) and studies undertaken to determine new SI alleles in apricot have been continuing (Halasz et al., 2013).

The aim of this study was to identify S-allele constitution of 61 apricot genotypes from apricot germplasm in Azerbaijan using polymerase chain reaction (PCR) with specific primer pairs.

Materials and Methods

Materials

A total of 61 apricot genotypes distributed in Nakhchivan, Tartar, Goranboy and Agdash regions of Azerbaijan were used in this study (Table 1).

DNA Isolation

Genomic DNA was extracted from full-expanded young apricot leaf samples, using the Cetyltrimethyl Ammonium Bromide (CTAB) method (Doyle and Doyle, 1987).

PCR studies with S-RNase and SFB-specific primers

For first intron region, SRc-R (Vilanova et al., 2005) and SRc-F (Romero et al., 2004) primer pair were used to determine Sc allele, which yielded bands at 353 bp at apricot cultivars (Vilanova et al., 2005). PCR products were separated on an ABI 3500 capillary electrophoresis instrument (Applied Biosystems, Foster City, CA, USA) at the core laboratory of the Genome and Stem Cell Centre (GENKOK) in Erciyes University, Kayseri, Turkey. For the identification of the SC-haplotype, a 2-step approach was used. An allele-specific reverse primer, AprSC8R (Halasz et al., 2010), was designed to selectively amplify the Sc/ S_8 -RNase allele and used in combination with PaConsI F (Sonneveld et al., 2003). AprFBC8-F (5′- CAT GGA AAA AGC TGA CTT ATG G -3′) and AprFBC8-R (5′- GCC TCT AAT GTC ATC TAC TCT TAG -3′) were used for detecting $SFB_{C/8}$ allele (Halász et al., 2007). The amplification was carried out using a temperature profile according to Halász et al. (2010).

For the second intron, PCR was conducted according to Sutherland et al. (2004) using the degenerate primers EMPC2consFD and EM-PC3consRD. For PCR amplification in a 20-mL reaction volume, containing 1X PCR buffer (Thermo) with the final concentrations of 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 2.0 mM MgCl2, 0.2 mM of dNTPs, 0.3 mM of each primer, and 1.0 U of Taq DNA polymerase (Thermo). The PCR products were electrophoresed in 1.5% (w/v) agarose gel, stained with ethidium bromide (0.5 lg/mL) using 1×TAE buffer, at 110 V for 2 h and visualized under UV light. Molecular size of the amplified fragments was estimated using a 100-bp ladder (Thermo). PCR's were repeated three times to determine the clear band size from apricot DNA.

Evaluation of data

To determine the exact size of the S-RNase first intron region fragments under 100 bp DNA ladder (Invitrogen), the fluorescently labelled products were run on an automated sequencer ABI Prism 3500 Genetic Analyzer. For the determination of size (genotyping), GENEMAPER software and the GS600 LIZ size standard (Applied Biosystems) were used.

The second intron PCR products were separated by electrophoresis in 1.2% TAE agarose gels for 2 h at 100 V, whereas DNA bands were visualised by ethidium bromide staining. Fragment lengths were estimated by comparison with the 1-kb DNA ladder (Promega, Madison, WI, USA). In the case of unknown alleles, PCR products were cloned and sequenced in an automated sequencer and analysed as described by Halász et al. (2010).

Results and Discussion

The determination of the S-genotypes of 61 Azerbaijan apricot genotypes was carried out using the SRc-F and SRcR consensus primers (Vilanova et al., 2005) for the first intron and EM-PC2consFD / EM-PC3consRD primers (Sutherland et al., 2004) for the second intron analysis of the S-RNase gene (Table 1). AprFBC8 F and R primers were used for discrimination of SFBC/8 allele (Halász et al., 2007). The size of the PCR products was compared with those previously published by other researchers (Vilanova et al., 2005; Halász et al., 2007, 2010). For S_8 and Sc alleles, although Vilanova et al. (2005) and Halasz et al. (2010) reported as 353 and also, Halasz et al. (2013) reported as 355 bp, the hereby result obtained was 354 bp band size. These differences might be explained by the genetic analyzers that affect the sensitivity of the method (Cachi and Wünsch, 2014). The sizes of the PCR products

obtained were compared with those previously published by Vilanova et al. (2005) and Hala´sz (2007).

A total of nine accessions failed to produce bands for

the second intron. The bands with the sizes of 310, 370, 500, 820, 900, 1200, 1250,

1300, 1700, 1980, and 2800 bp were produced by 11, 5, 15, 18, 10, 2, 12, 10, 5, 6,

and 12 accessions, respectively (Table 3).

In the present study a total of twenty accessions failed to produce bands for the second intron. The bands with the sizes of 280, 310, 370, 820, 900, 1250, 1300 and 1700 were produced by 10, 3, 3, 7, 4, 27, 4 and 8 accessions, respectively (Table 1). Previous studies have found that allele sizes of 310, 370, 500, 820, 900, 1250, 1300 and 1700 indicate S_3, S_{12}, S_9, S_7, S_2, S_{13}, S_6, S_{11}, respectively. In the present study, "Zeynabi", "Yeni forma" 1, "Gaysi", "Maychicheyi", "Yeni forma 2", "Shalakh 1", "Abu Talibi", “Teberze 2”, “Shalakh 3” and “Qırmiziyanag” produced by 280 bp sizes were not assigned to any known S locus. Four Azerbaijan cultivars (Jir Zeferani, Gaysi, Mayovka 1, Mayovka 2) a fragment of 900 bp was detected that indicated the presence of allele S_2. A fragment of 310 bp occurred in three Azerbaijan cultivars (Shemsi, Agja Nabad 2, Göyje Nabad confirming this allele as S_3. Four cultivars (Hampa, Yay Sherefi, Gecyetishen, Ordubad Sherefi) yielded a fragment of 1300 bp was detected that indicated the presence of allele S_6. The allele S_7 occurred in seven cultivars (Maychicheyi, Yeni forma 2, Teberze 1, Agja Nabad 2, Hagverdi 2, Alcha erik, Abu Talibi) as a fragment of 820 bp. Eight cultivars (Jir Zeferani, Gaysi, Mayovka 1, Mayovka 2) a fragment of 1700 bp was detected that indicated the presence of allele S_{11}. Fragment size characteristic for S_{12} allele was observed in three cultivars (Hampa, Jir Nakhchivan, Yay Sherefi). A fragment of 1250 bp occurred in twenty-seven cultivars (Ag erik Gülnar, Yeni forma 1, Balyarim, Shalakh 1, Teberze 1, Gecyetishen, Badami 1, Helena, Ag badami, Forma 1, Ag erik (early ripening), Ordubad eriyi, Ag erik, Shemsi, Göyje Nabad, Hagverdi 2, Heydari, Shalakh 2, May Goranboy, Badami 2, Limon erik 2) confirming this allele as S_{13}.

A total 9 S-RNase alleles (S_2, S_3, S_6, S_7, S_8, S_{11}, S_{12}, S_{13} and S_c) were determined in the 61 apricots genotypes (Table 1). Altogether, two cultivars (Forma 2, Mayovka 1) proved to be self-compatible. All apricot samples (except Forma 2, Mayovka 1) distributed in Azerbaijan used in the study showed self-incompatibility without SC-haplotype. Halasz et al. (2010) conducted a study to determine the S genotypes of a set of Turkish and Hungarian apricot cultivars by amplification of their S-RNase intron regions. A specific primer (AprSC8) for S_C and S_8 was designed to anneal

within the second intron region of the S_C- and S_8-RNase alleles. This primer pair amplified a fragment in the case of S_8/S_C-alleles. They reported that the presence of S_8/S_C-alleles was confirmed among the tested 18 cultivars. Some of them ('Canakkale', 'Ethembey', 'Kayisi Erigi', 'Mektep', 'Sam' and 'Yerli Izmir') were proved as self-compatible (ScSc). Two Turkish cultivars shared the S_CS_8-genotype ('Ethembey' and 'Mektep'). It was reported in their study that AprSC8 primer could distinguish between the SI and SC cultivars.

Nine previously described S-alleles were identified among the Azerbaijan cultivars. S_{13} was the most frequent S-allele in the tested Azerbaijan germplasm (occurring in 27 cultivars), followed by S_{11} (8), S_7 (7), S_2 (4), S_6 (4), S_{12} (3), S_3 (3), S_8 (3), S_c (2), while S_C-allele was only found in two cultivars.

In the present study, 'Ag erik Gülnar' ($S_{11}S_{13}$), 'Hampa' (S_6S_{12}), 'Yay Sherefi' (S_6S_{12}), 'Teberze 1' (S_7S_{13}), 'Gecyetishen' (S_6S_{13}), 'Ag erik' ($S_{11}S_{13}$), 'Shemsi' (S_3S_{13}), 'Agja Nabad 2' (S_3S_7), 'Göyje Nabad' (S_3S_{13}), 'Hagverdi 2' (S_7S_{13}), 'Ordubad Sherefi' (S_6S_{13})), 'Heydari' ($S_{11}S_{13}$), 'Shalakh 2' ($S_{11}S_{13}$), 'Alcha ərik' (S_7S_{13}), 'Badami 2' ($S_{11}S_{13}$), 'Limon erik 2' ($S_{11}S_{13}$), 'Mayovka 1' (S_CS_2), 'Forma 2' (S_CS_8) 18 S genotype combinations were determined.

Table 1. S-genotype profiles of apricot germplasms distributed in Nakhchivan, Tartar, Goranboy, Agdash regions of Azerbaijan

Cultivar	First intron (bp) of S-RNase gene	Second intron (bp) S-RNase gene	Paconsl-F/AprSC8R	AprFBC8-R/AprFBC8-F	S genotype
Zeynebi	268,268	280,280	-	150	
May Natig	-,-	-,-	-	150	
Ag erik Gülnar	378,304	1250,1700	-	150	$S_{11}S_{13}$
Yeni forma 1	268,378	280 ,1250	-	150	S_{13}
Jir Zeferani	332,332	900,900	550	150	S_2S_2
Jir erik	353,378	-,-	550	150	S_8
Gaysi	268,332	280,900	-	150, 500	S_2
Maychicheyi	268,402	280,820	-	150, 500	S_7
Balyarim	378,378	1250,1250	550	150	$S_{13}S_{13}$
Hampa	262,424	370,1300	-	150, 500	S_6S_{12}
Yeni forma 2	268,402	280,820	-	150, 500	S_7

Jir Nakhchivan	262,262	370,370	-	150, 500	$S_{12}S_{12}$
Yay Sherefi	262,424	370,1300	-	150, 500	S_6S_{12}
Shalakh 1	268,378	280,1250	-	150, 500	S_{13}
Teberze 1	402,378	820,1250	-	150,500	S_7S_{13}
Tokhum Shemsi	262,424	-,-	-	150,500	
Gejyetishen	378,424	1250,1300	-	150,500	S_6S_{13}
Badami 1	378,378	1250,1250	-	150	$S_{13}S_{13}$
Helena	378,402	1250,-	-	150	S_{13}
Mehmani	268,402	-,-	-	150	
Hagverdi 1	268,402	-,-	-	150	
Ag Nabati	378,378	-,-	-	150	
Kürdeshi	268,378	-,-	-	150	
Talibi	268,402	-,-	-	500	
Genotip 1	378,378	-,-	-	500	
Ag badami	378,378	1250,1250	-	-	$S_{13}S_{13}$
Agjanabad 1	378,402	-,-	-	150,500	
Limon erik 1	268,402	-,-	-	150,500	
Forma 1	378,378	1250,1250	-	-	$S_{13}S_{13}$
Ag erik (late ripening)	332,402	-,-	-	150,500	
Ağ erik (early ripening)	304,378	-,1250	-	150	S_{13}
Ordubad eriyi	304,378	-,1250	-	150,500	S_{13}
Ag erik	304,378	1700,1250	550	150	$S_{11}S_{13}$
Badam erik 1	304,304	1700,1700	,600	150	$S_{11}S_{11}$
Shemsi	268,378	310,1250	-	150	S_3S_{13}
Badam erik 2	304,402	-,-	-	150,500	
Agja Nabad 2	268,402	310,820	-	150,500	S_3S_7
Göyje Nabad	268,378	310,1250	-	150,500	S_3S_{13}
Hagverdi 2	402,378	820,1250	-	150,500	S_7S_{13}
Genotip 3	304,378	-,-	-	-	
Ordubad Sherefi	378,424	1250,1300	-	150	S_6S_{13}
Heydari	304,378	1700,1250	-	150,500	$S_{11}S_{13}$
Ordubad jiri	268,378	-,-	-	150	

Forma 2	304,353	-,-	-	150,500	S_CS_8
Genotip 2	304,378	-,1250	-	150,500	S_{13}
Ordubad Nabati	268,378	-;-	-	150	
Yeni forma 3	268,378	-,1250	-	150	S_{13}
Shalakh 2	304,378	1700,1250	-	150	$S_{11}S_{13}$
Alcha erik	402,378	820,1250	-	150	S_7S_{13}
Abu Talibi	268,402	280,820	-	-	S_7
Teberze 2	268,378	280,1250	-	-	S_{13}
Ag erik Elchin	304,424	-,-	-	150	
May Goranboy	304,353	1700,-	550	150	S_8S_{11}
Mayovka 1	332,353	900,-	550	500	S_CS_2
Badami 2	304,378	1700,1250	-	150,500	$S_{11}S_{13}$
Shalakh 3	268,378	280,1250	-	-	S_{13}
Girmiziyanag	-,-	280,1250	-	150,500	S_{13}
İrevan eriyi	-,-	-,-	-	-	
Mayovka 2	332,378	900,-	-	500	S_2
Limon erik 2	304,378	1700,1250	-	150	$S_{11}S_{13}$
Esgerabat	268,402	-,-	-	-	

Mehlenbacher et al. (1991) reported that the European group of apricot (Europe, North America, South Africa and Australia are included) may be described as self-compatible. It was reported by Halasz et al. (2013) to support the S-genotype determinations, as first intron lengths were also determined for all genotypes using fluorescently labelled primers and automated sizing on a capillary sequencer. Analysis of the first intron in 63 wild-grown apricot accessions from Turkey showed that 17 of 63 apricot accessions had 355 bp fragment. This fragment size was previously attributed to both the S_C- and S_8-RNase alleles (Halasz et al., 2007).

Vilanova et al. (2005) used SRc-R and SRc-F primer pair for 10 apricot cultivars to determine their S alleles. Six of 10 apricot genotypes were obtained via reciprocal crossing. They determined apricot genotypes that had Sc allele, which yielded at 353 bp. It was reported with previous studies that most of the European cultivars had Sc allele, whereas old Turkish cultivars were self-incompatible (Yilmaz, 2008; Halasz et al., 2010).

Since coding regions of the S_8- and S_C-RNase alleles are identical, discrimination between the 2 alleles was not possible. In apricot, self-compatibility is attributed to

a pollen-part mutation: a 353 bp insertion in the SFB gene. To distinguish between the self-incompatible (SI) and self-compatible (SC) accessions, a previously designed specific primer pair (AprFBC8) can be used (Halasz et al., 2010), which amplifies a fragment of approximately 500 bp in the case of SFB_C-allele, while genotypes carrying the SFB_8-allele show a fragment of approximately 150 bp (Halasz et al., 2013). Thus, Halasz et al. (2013) determined 17 apricot accessions carrying SFB8-allele among 63 apricots from Turkey using AprFBC8 primer pair and they were stated as self-incompatible.

Based on the structure of S-RNase, many pairs of primers have been developed for Prunus species, such as Pru-C2 and PCE-R (Tao et al., 1999a; Yamane et al., 2001), SRc-F and EMPC5consRD, SRc-F and PM-C5 (Vilanova et al., 2005; Sutherland et al., 2004; Habu et al., 2008), ASIII and AmyC5R (Tamura et al., 2000), EM-PC2consFD and ED-PC3cons-RD 70 (Sutherland et al., 2004), PaConsI-F and PaConsI-R, PaConsII-F and PaConsII-R (Sonneveld et al., 2003). Yaegaki et al. (2001) first determined S-RNase genotypes using the primer pair Pru-C2 and Pru-C5. Tao et al. (2002) cloned novel S8-RNase and Sc-RNase using Pru-C2 and PCE-R. Recently, the S-genotypes of 14 Japanese apricot cultivars native to Japan were determined using Pru-C2 and PCE-R, SRc-F and EM-PC5consRD, SRc-F and PM-C5 (Habu et al., 2008). The primer pair Pru-C2 and PCE-R was developed from C2 and C3 in Prunus by Tao et al. (1999) and Yamane et al. (2001) and is considered as the universal primer pair for determining the S-genotypes in Japanese apricot (Habu et al., 2008).

Halasz et al. (2013) carried out a study to determine S genotypes of wild-growing Turkish apricots by PCR amplification of the S-RNase intron regions and SFB gene, in order to characterize their sexual (in) compatibility phenotype. The authors determined the complete S-genotype of 63 wild-grown apricot accessions that originated in the Erzincan region. Ten previously described and 2 new S-alleles (provisionally labeled S_X and S_Y) were identified in the studied genotypes. S2 was the most frequent S allele in the tested germplasm (occurred in 19 accessions), followed by S_8 (17), S_{19} (16), S_3 (13), S_{12} (11), S_6 (10) and S_7 (10), while S_9-, S_{11}- and S_{13}-alleles were found in 8 accessions each. A total of 36 different S-genotypes were assigned to the tested accessions. The SC-allele responsible for self-compatibility in apricot was not present, indicating that all accessions were self-incompatible. The analysis of S-allele frequencies allowed to conclude the close relationship of wild-grown and cultivated apricots in Turkey and helped to raise hypotheses that may explain the high occurrences of S_2- and S_8-alleles.

One of the most important factors in apricot crop evolution was the emergence of self-compatibility, which has resulted in a serious loss of genetic diversity in Europe

and the Mediterranean Basin (Pedryc et al., 2009; Bourguiba et al., 2012). In a previous study, Halasz et al. (2010) detected an uneven distribution of the S_C-allele in Turkish apricot cultivars: no self-compatible cultivar was found among 11 tested genotypes in the Eastern Region, while 7 out of 14 tested cultivars from the Western part of the country were self-compatible. Although the 55 cultivars analyzed in their study did not reveal a sound conclusion regarding the place of the origin of self-compatibility in apricot, the increasing number of S_C cultivars from East to West was suggestive.

Conclusion

The development of apricot production in Azerbaijan is expanding day by day. There are also apricot growing areas with wide genetic diversity. Determining the S allele structure of apricot germplasm is very important for orchard management and breeding programs. Within the framework of this research, the S-allele structure of apricot germplasm in Azerbaijan was determined and the results showed that there are great differences between the studied apricot genetic materials according to the S allele formation.

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