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The *S*-genotyping of wild-grown apricots reveals only self-incompatible accessions in the Erzincan region of Turkey

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Abstract: The *S*-genotypes of 63 wild-growing Turkish apricots (*Prunus armeniaca* L.) were determined by PCR amplification of the *S-RNase* intron regions and *SFB* gene in order to characterise their sexual (in)compatibility phenotype. We 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 labelled S_X and S_Y) were identified in the genotypes. S_2 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. A total of 36 different *S*-genotypes were assigned to the tested accessions. The S_C-allele responsible for self-compatibility in apricot was not present, indicating that all accessions are self-incompatible. The analysis of *S*-allele frequencies allowed us to conclude the close relationship of wild-grown and cultivated apricots in Turkey and helped to raise hypotheses to explain high occurrences of S_2- and S_8-alleles.

Key words: Crop evolution, PCR analysis, *Prunus armeniaca*, self-(in)compatibility, *S*-haplotype–specific F-box, *S*-ribonuclease

1. Introduction

Apricots are grown in warm temperate to subtropical regions of all continents. Over a long period, cultivation moved westward from China to Middle Asia and, further, to Europe. Turkey dominates world apricot production with approximately 500,000 t of annual production. Apricot has been widely cultivated for its edible fruit throughout Turkey since ancient times, especially in Inner Anatolia (e.g., Malatya, Erzincan, Aras valley). Some parts of Turkey, especially the Erzincan plain, have huge native seedling apricot populations. Some of the seedlings genetically reveal late blooming and a dwarf growth habit. These forms may be important for the extension of the harvest period (Ercisli, 2004). In addition, improving the antioxidant capacity of fruits is among the most recent breeding efforts in a range of *Prunus* species (Hegedűs et al., 2010, 2013). This can be achieved by including wild accessions into the parental combinations since they accumulate higher levels of antioxidant polyphenolics in fruit compared to popular commercial cultivars (Yildiz et al., 2010; Hasanloo et al., 2011; Jahanban Esfahlan and Jamei, 2012; Leccese et al., 2012).

Species of the family *Rosaceae* show gametophytic self-incompatibility (GSI) to prevent inbreeding depression. This intercellular reaction is controlled by a single multiallelic locus, the *S*-locus (de Nettancourt, 1977). The *S*-gene product in styles is a ribonuclease enzyme (*S*-RNase) (McClure et al., 1989), while the pollen product is an F-box protein (Entani et al., 2003; Romero et al., 2004). Knowledge of the self-compatibility of commercial cultivars and selections from breeding programs is imperative for any apricot breeder hoping to design compatible combinations (Burgos et al., 1998).

In apricot, 7 *S*-alleles (S_1–S_7) were described in North American and Spanish apricot cultivars for self-incompatibility, while the S_C-allele was identified as responsible for self-compatibility (Alburquerque et al., 2002). Later, 9 additional alleles (S_8–S_{16}) were found using non-equilibrium pH gradient electrofocusing (NEpHGE) and polymerase chain reaction (PCR) analyses (Halász et al., 2005). From Chinese cultivars more than 50 *S*-alleles have been identified based on *S*-RNase activity staining, PCR, and sequencing (Jie et al., 2005; Zhang et al., 2008; Wu et al., 2009; Halász et al., 2012). In total, 17 cross-

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incompatibility groups (CIG) are known, including North American, European, Turkish, and Tunisian apricot cultivars (Szabó and Nyéki, 1991; Egea and Burgos, 1996; Halász et al., 2010; Milatovic et al., 2010; Lachkar et al., 2013).

The S_C-haplotype has been confirmed to be a pollen-part mutant of the S_8-haplotype (Halász et al., 2007) with a 358 bp insertion in the SFB_C gene (Vilanova et al., 2006). The loss of the pollen *S*-function was further supported by the identification of the original, nonmutated form of the apricot SFB_C-allele in Hungarian and Turkish apricots (Halász et al., 2007).

S-genotyping is also useful in the elucidation of crop evolution and propagation history of a given species (Halász et al., 2007, 2010). Previous results suggest that the mutation rendering the S_C-haplotype nonfunctional might have occurred somewhere east of Central Turkey. The aim of the present study was to evaluate the genetic diversity in the *S*-locus of wild-growing apricots in the Erzincan region, situated in the eastern-central part of Turkey. The results were expected to be suggestive for finding the region where self-compatibility emerged in apricot.

2. Materials and methods

2.1. Plant material

The 63 Turkish apricot genotypes used in the experiments were obtained from wild-grown populations in the Erzincan region of Turkey (Table).

2.2. DNA extraction

Genomic DNA was extracted from fully expanded young leaves using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). The quantity and quality of DNA were analysed by NanoDrop ND-1000 spectrophotometer (Bio-Science, Budapest, Hungary).

Table. Label, site of origin, and sizes of the first and second intron regions of the *S-RNase* gene; specific PCR for the $S_{C/8}$-*RNase* and $SFB_{C/8}$ alleles; and *S*-genotypes of the tested Turkish apricots.

Number	Site	First intron (bp)	Second intron (bp)	S_C/S_8-RNase	$SFB_{C/8}$	S-genotype
1	Merkez, Erzincan	269, 262	310, 370	–	–	S_3S_{12}
2	Merkez, Erzincan	332, 355	950, 2800	+	S_8	S_2S_8
3	Merkez, Erzincan	269, 203	310, 500	–	–	S_3S_9
4	Merkez, Erzincan	332, 203	950, 500	–	–	S_2S_9
5	Merkez, Erzincan	424, 305	1300, 1700	–	–	S_6S_{11}
6	Akyazı, Erzincan	424, 355	1300, 2800	+	S_8	S_6S_8
7	Akyazı, Erzincan	203, 334	500, 1980	–	–	S_9S_{19}
8	Akyazı, Erzincan	332, 379	950, 1250	–	–	S_2S_{13}
9	Akyazı, Erzincan	269, 332	310, 950	–	–	S_2S_3
10	Hançiftliği, Erzincan	355, 203	2800, 500	+	S_8	S_8S_9
11	Hançiftliği, Erzincan	401, 334	820, 1980	–	–	S_7S_{19}
12	Hançiftliği, Erzincan	262, 343	370, 700	–	–	$S_{12}S_Y$
13	Saztepe, Erzincan	332, 334	950, 1980	–	–	S_2S_{19}
14	Saztepe, Erzincan	379, 334	1250, 1980	–	–	$S_{13}S_{19}$
15	Saztepe, Erzincan	379, 334	1250, 1980	–	–	$S_{13}S_{19}$
16	Saztepe, Erzincan	332, 203	950, 500	–	–	S_2S_9
17	Bayırbağ, Erzincan	262, 334	370, 1980	–	–	$S_{12}S_{19}$
18	Bayırbağ, Erzincan	269, 334	310, 1980	–	–	S_3S_{19}
19	Bayırbağ, Erzincan	355, 203	2800, 500	+	S_8	S_8S_9
20	Bayırbağ, Erzincan	305, 379	1700, 1250	–	–	$S_{11}S_{13}$
21	Bayırbağ, Erzincan	305, 334	1700, 1980	–	–	$S_{11}S_{19}$
22	Bayırbağ, Erzincan	355, 334	2800, 1980	+	S_8	S_8S_{19}
23	Üzümlü, Erzincan	332, 979	950, 1250	–	–	S_2S_{13}

Table. (Continued).

24	Üzümlü, Erzincan	332, 262	950, 370	–	–	S_2S_{12}
25	Üzümlü, Erzincan	401, 262	820, 370	–	–	S_7S_{12}
26	Üzümlü, Erzincan	269, 355	310, 2800	+	S_8	S_3S_8
27	Üzümlü, Erzincan	305, 343	1700, 700	–	–	$S_{11}S_Y$
28	Üzümlü, Erzincan	332, 424	950, 1300	–	–	S_2S_6
29	Üzümlü, Erzincan	355, 334	2800, 1980	+	S_8	S_8S_{19}
30	Üzümlü, Erzincan	269, 424	310, 1300	–	–	S_3S_6
31	Üzümlü, Erzincan	401, 236	820, 1270	–	–	S_7S_X
32	Üzümlü, Erzincan	332, 203	950, 500	–	–	S_2S_9
33	Üzümlü, Erzincan	269, 262	310, 370	–	–	S_3S_{12}
34	Çukurkuyu, Erzincan	355, 334	2800, 1980	+	S_8	S_8S_{19}
35	Çukurkuyu, Erzincan	332, 424	950, 1300	–	–	S_2S_6
36	Çukurkuyu, Erzincan	401, 379	820, 1250	–	–	S_7S_{13}
37	Çukurkuyu, Erzincan	401, 305	820, 1700	–	–	S_7S_{11}
38	Yalnızbağ, Erzincan	355, 305	2800, 1700	+	S_8	S_8S_{11}
39	Yalnızbağ, Erzincan	269, 332	310, 950	–	–	S_2S_3
40	Yalnızbağ, Erzincan	424, 334	1300, 1980	–	–	S_6S_{19}
41	Yalnızbağ, Erzincan	424, 355	1300, 2800	+	S_8	S_6S_8
42	Işıkpınar, Erzincan	401, 305	820, 1700	–	–	S_7S_{11}
43	Işıkpınar, Erzincan	355, 379	2800, 1250	+	S_8	S_8S_{13}
44	Işıkpınar, Erzincan	332, 203	950, 500	–	–	S_2S_9
45	Işıkpınar, Erzincan	424, 401	1300, 820	–	–	S_6S_7
46	Bahçeliköy, Erzincan	424, 343	1300, 700	–	–	S_6S_Y
47	Bahçeliköy, Erzincan	332, 334	950, 1980	–	–	S_2S_{19}
48	Bahçeliköy, Erzincan	332, 355	950, 2800	+	S_8	S_2S_8
49	Bahçeliköy, Erzincan	332, 343	950, 700	–	–	S_2S_Y
50	Bahçeliköy, Erzincan	269, 262	310, 370	–	–	S_3S_{12}
51	Bahçeliköy, Erzincan	269, 355	310, 2800	+	S_8	S_3S_8
52	Yeniköy, Erzincan	379, 334	1250, 1980	–	–	$S_{13}S_{19}$
53	Yeniköy, Erzincan	269, 355	310, 2800	–	S_8	S_3S_8
54	Yeniköy, Erzincan	355, 262	2800, 370	+	S_8	S_8S_{12}
55	Elmaköy, Erzincan	332, 305	950, 1700	–	–	S_2S_{11}
56	Elmaköy, Erzincan	262, 334	370, 1980	–	–	$S_{12}S_{19}$
57	Elmaköy, Erzincan	269, 262	310, 370	–	–	S_3S_{12}
58	Gümüştarla, Erzincan	424, 262	1300, 370	–	–	S_6S_{12}
59	Gümüştarla, Erzincan	401, 355	820, 2800	+	S_8	S_7S_8
60	Çağlayan, Erzincan	401, 236	820, 1270	–	–	S_7S_X
61	Çağlayan, Erzincan	332, 355	950	+	S_8	S_2S_8
62	Çağlayan, Erzincan	401, 334	820, 1980	–	–	S_7S_{19}
63	Çağlayan, Erzincan	269, 332	310, 950	–	–	S_2S_3

2.3. Genomic PCR with *S-RNase* and *SFB*-specific primers

PCR was conducted according to Sutherland et al. (2004) using the degenerate primers EM-PC2consFD and EM-PC3consRD for the amplification of the second intron region of the *S-RNase* gene. To amplify the first intron, the fluorescently labelled ($_{JOE}$) forward primer SRc-F (Romero et al., 2004) was used in combination with the reverse primer SRc-R (Vilanova et al., 2005). For the identification of the S_C-haplotype, a 2-step approach was used. An allele-specific reverse primer, AprSC8R (Halász et al., 2010), was designed to selectively amplify the S_C/S_8-*RNase* allele and used in combination with PaConsI F (Sonneveld et al., 2003). SFB_C/SFB_8-specific primers, 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 designed based on the V2 and HVb variable region of the $SFB_{C/8}$ allele (Halász et al., 2007). The amplification was carried out using a temperature profile, according to Halász et al. (2010). PCR was carried out in a PTC 200 thermocycler (MJ Research, Budapest, Hungary). For amplification of the *S-RNase* first and second introns, we used the programs originally described for the primers (Sutherland et al., 2004; Vilanova et al., 2005). Approximately 20–80 ng of genomic DNA was used for PCR amplification in a 25 µL reaction volume containing 10X Dream*Taq* Green buffer (Fermentas, Szeged, Hungary) as well as KCl and $(NH_4)_2SO_4$ at a ratio optimised for robust performance of Dream*Taq* DNA Polymerase in PCR with final concentrations of 4.5 mM of $MgCl_2$, 0.2 mM of dNTPs, 0.2 µM of the adequate primers, and 0.75 U of Dream*Taq* DNA polymerase (Fermentas). PCR was carried out in a PTC 200 thermocycler (MJ Research, Budapest, Hungary).

2.4. Data evaluation

The second intron PCR products were separated by electrophoresis in 1.2% TAE agarose gels for 2 h at 100 V, and DNA bands were visualised by ethidium bromide staining. Fragment lengths were estimated by comparison with the 1-kb DNA ladder (Promega, Madison, WI, USA). To determine the exact size of the *S-RNase* first intron region fragments under 500 bp, the fluorescently labelled products were run on an automated sequencer ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Budapest, Hungary). For determination of size (genotyping), GENOTYPER 3.7 software and the GS500 LIZ size standard (Applied Biosystems) were used. In the case of unknown alleles, PCR products were cloned and sequenced in an automated sequencer and analysed as described by Halász et al. (2007).

3. Results

The determination of the *S*-genotypes of 63 wild Turkish apricot accessions was carried out using the SRc-F and SRc-R consensus primers (Vilanova et al., 2005) for the first intron and EM-PC2consFD and EM-PC3consRD primers (Sutherland et al., 2004) for the second intron analysis (Figure 1). The sizes of the PCR products obtained were compared with those previously published by Vilanova et al. (2005) and Halász et al. (2010). Primers

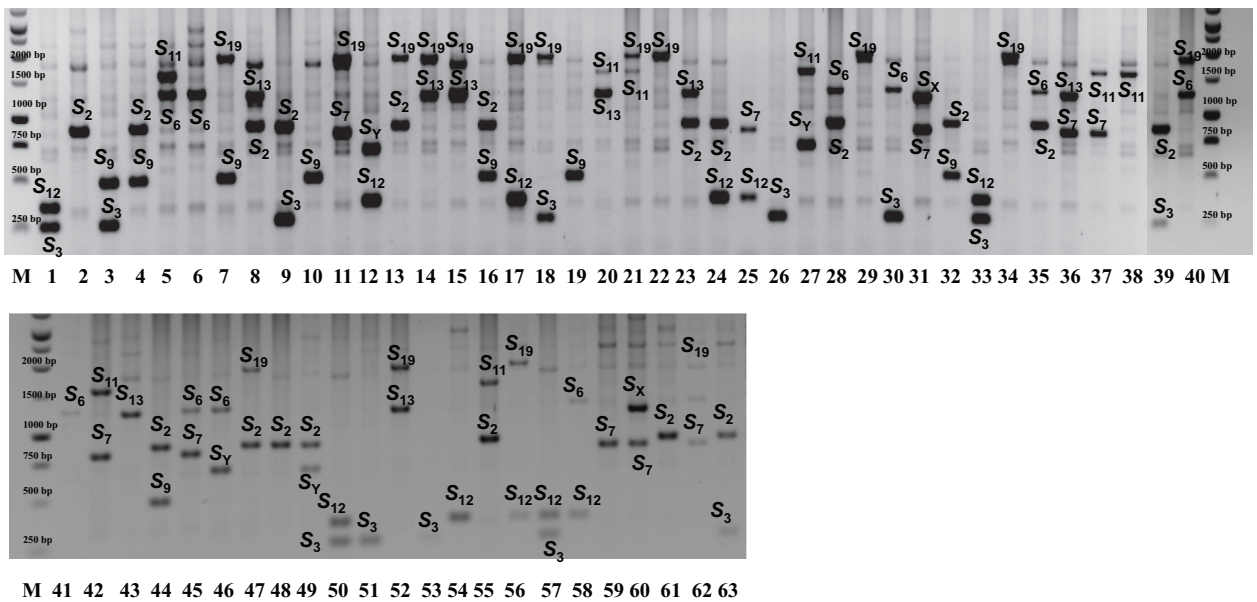

Figure 1. PCR products (in negative) in 63 Turkish apricot accessions using the second intron consensus primers of *Prunus S-RNase* gene. M: 1 kb + DNA ladder; numbers refer to samples shown in Table.

designed from conserved coding regions flanking the second intron yielded 2 fragments ranging from 310 to 1980 bp, except in 17 cultivars where only 1 fragment was amplified. For 19 accessions a fragment of approximately 900 bp was detected, which indicated the presence of allele S_2. A fragment of approximately 310 bp occurred in 13 accessions, which is the allele S_3. Ten accessions yielded a fragment of approximately 1300 bp; hence, this allele was labelled S_6 based on the formerly described size of this allele. The allele S_7 occurred in 10 accessions declaring a fragment of approximately 820 bp.

An approximately 500 bp fragment was detected in 8 accessions, which could be attributed to the allele S_9. An approximately 1700-bp fragment appeared in 8 accessions, indicating the presence of the S_{11}-allele. A fragment size characteristic for allele S_{12} was observed in 11 accessions. A band of approximately 1250 bp appeared in 8 accessions, suggesting that the S_{13}-allele is common to all. The allele S_{19} has a second intron region (approximately 1980 bp), which was found in 16 accessions.

To support the *S*-genotype determinations, precise first intron lengths were also determined for all accessions using fluorescently labelled primers and automated sizing on a capillary sequencer. Analysis of the first intron in all 63 apricot accessions showed 2 fragments that varied between 203 and 424 bp. These results indicated that all accessions were heterozygous in the *S*-locus.

A 355 bp fragment was present in 17 accessions. This fragment size was previously attributed to both the S_C- and S_8-*RNase* alleles (Halász et al., 2007). 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 358 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 (Halász et al., 2010), which amplifies a fragment of approximately 500 bp in the case of SFB_C-allele; genotypes carrying the SFB_8-allele show a fragment of approximately 150 bp. Our analysis revealed only the smaller fragment, indicating that each of the 17 accessions carries the SFB_8-allele, and hence they are self-incompatible.

The 1270 bp size of the second intron region in accessions 31 and 60 does not match the size of any known alleles. According to the DNA sequence of the first intron (236 bp) and the size of the second intron region, this allele, provisionally labelled S_X, is considered a new *S*-allele in apricot. Another putatively new allele (provisionally labelled S_Y) was demonstrated in 4 accessions (12, 27, 46, and 49) with a size of 700 bp for the second intron and 343 bp for the first intron. Sequence information for the second intron confirmed the novelty of this allele.

We determined the complete *S*-genotype of 63 wild-grown apricot seedlings by combining the results of different primer pairs (Table). Ten previously described and 2 new *S*-alleles were identified in the genotypes (Figure 2). S_2 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. In total, 36 different *S*-genotypes were assigned: the most frequent genotypes were S_2S_9, S_2S_{11}, and S_3S_{12} (4 accessions); while each of S_2S_3, S_2S_8, S_3S_8, S_8S_{19}, and $S_{13}S_{19}$ was carried by 3 accessions.

4. Discussion

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, we detected an uneven distribution of the S_C-allele in Turkish apricot cultivars: no self-compatible cultivar was found among 11 tested accessions in the eastern region, while 7 cultivars were self-compatible out of the 14 tested cultivars from the western part of the country (Halász et al., 2010). Although the 55 cultivars analysed in that study did not reveal a sound conclusion regarding the place of the origin of self-compatibility in apricot, the increasing number of SC cultivars from east to west was suggestive.

In the present study, we determined the *S*-genotype of 63 accessions growing wild in the Erzincan region of Turkey. Our most important finding is that self-compatible accessions were not found, although the wild-type allele, S_8, was one of the most frequent alleles in this region. The absence of the S_C-allele in the tested accessions can be explained in 3 ways: (1) the mutation might have been emerged in another region, (2) the S_C-allele is present in Erzincan but so rare that our sampling has not detected it, or (3) it had been present in Erzincan but was later removed by natural selection due to inbreeding depression associated with self-pollination. Since the S_C-allele was shown in only one Malatya cultivar and some other cultivars from Western Turkey (Halász et al., 2010), it might have emerged in another region, such as Southern Turkey. If S_C-allele was present in Erzincan, its frequency would be doubtful. Pollen grains carrying the S_C-haplotype would be compatible on each pistil; hence, its dissemination seems unimpeded. Although pollen grains carrying an S_C-allele will be free from balancing selection, the frequency of S_C might be decreased due to inbreeding depression, which was shown to result in low productivity in *Prunus* (Ortega et al., 2010). However, inbreeding depression has not been described for apricots harbouring the S_C-haplotype and known to be self-pollinated over several generations

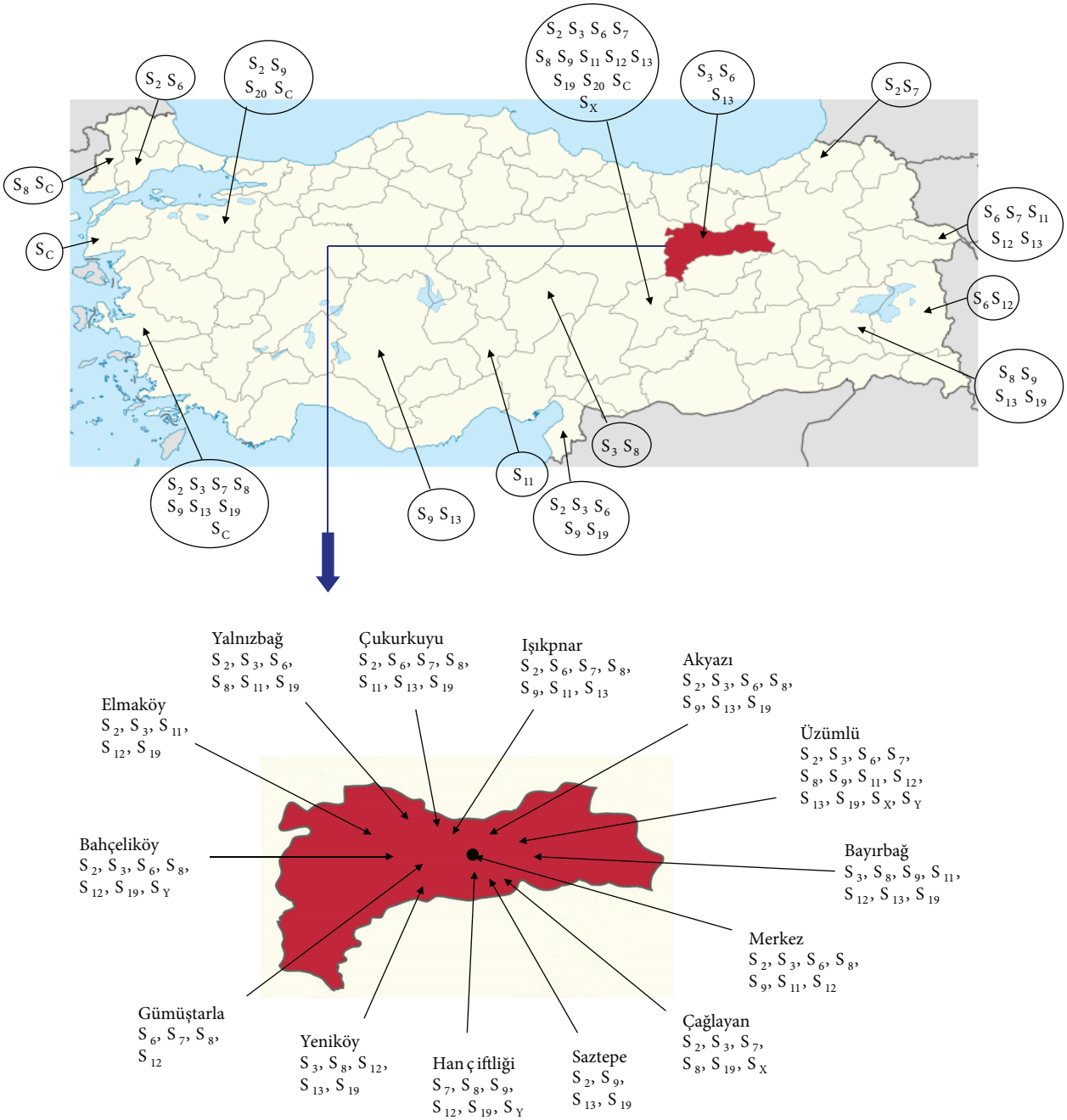

Figure 2. The spread of apricot self-incompatibility ribonuclease alleles in Turkey. The *S*-RNase alleles detected in commercial Turkish cultivars as described by Halász et al. (2010) (A) and wild-grown accessions (B) in the Erzincan region.

(Nyujtó and Surányi, 1981). In conclusion, none of the 3 scenarios can be ruled out at the moment. Our results seem to support that SC is not present in the Erzincan region, but additional experiments are needed to clarify this matter further.

Sixty-three seedlings carried 36 different *S*-genotypes, and 11 combinations of *S*-alleles have not yet been detected in commercial cultivars (Burgos et al., 1998; Halász et al., 2005, 2007, 2010; Lachkar et al., 2013). In such a diverse population, a selection pressure is required to significantly alter allele frequency. For example, unfavourable weather conditions might have exposed a selection pressure on apricot during its dissemination. The western part of Turkey receives more precipitation than the Erzincan region during the blooming period of apricot (http://www.mgm.gov.tr/files/en-US/climateofturkey.pdf), which must have resulted

in low activity of pollinator insects. In such an environment, self-compatibility is a favourable trait that allows reliable fruit set (Tao et al., 2007). Accordingly, we found a relatively high frequency of self-compatible cultivars grown in the more humid regions of Edirne, Çanakkale, İzmir, and Bursa (Halász et al., 2010). Since all tested accessions from these regions were commercial cultivars and landraces, human selection for the reliable cropping of apricot genotypes might also have a great influence.

Many (22 of 36) of the *S*-genotypes determined for wild-grown Turkish apricots have also been assigned to Turkish cultivars by Halász et al. (2010). Most (9 of 10) *S*-alleles were also detected in the Turkish apricot cultivars (Halász et al., 2010) with the exception of S_{20}, which is found only in landrace cultivars, not in wild apricots. We have also identified 2 putatively new *S*-alleles. Using DNA sequencing, we clarified that S_X is identical to the allele previously detected in the cultivar 'Güz Aprikozu' (Halász et al., 2010). For both of the new alleles, S_X and S_Y, sequencing a major part of the exon regions or open field controlled pollinations will be required for confirmation. A considerably overlapping *S*-allele pool of wild and cultivated apricots in Turkey indicates that selection from the rich apricot germplasm available in specific localities formed a major part of apricot breeding activity in this country; hence, traditional cultivars and the wild germplasm have close genetic relationships.

The over-dominance of some alleles (e.g., S_2 or S_8) is unexpected under the conditions of frequency-dependent balancing selection on the *S*-locus (Wright, 1939); however, uneven *S*-allele frequencies were also detected in wild cherry populations (De Cuyper et al., 2005; Schueler et al., 2006). Deviations from isoplethy at the *S*-locus might be explained by a range of reasons including founder effects, stochastic fluctuations around the equilibrium, or different levels of selection acting on non-*S* regions linked to specific *S*-alleles. Considering the high levels of heterozygosity under an operating GSI system, there is a relatively high chance of the recessive harmful alleles existing in the population. In *Solanum*, under the control of a very similar *S*-RNase-based self-incompatibility system, 2 of the 7 studied *S*-alleles showed a severe load of deleterious mutations (Stone, 2004).

It is interesting to realise that S_2 and S_8 were the most frequent alleles (their relative frequencies were 0.30 and 0.27, respectively) in the sampled wild-growing apricot population. It may indicate these alleles are free of *S*-linked genomic regions that are exposed to purifying selection. This is further supported by the fact that mutations resulting in self-compatibility were declared both in the S_8- (Halász et al., 2007) and S_2-haplotypes (Vilanova et al., 2006). Although the dissemination of SC accessions was strongly favoured by human-imposed selection, potentially harmful alleles linked to the S_2- or S_8-haplotypes must have been disclosed in the S_CS_C or S_2S_2 homozygotes or S_CS_8 heterozygotes. However, deleterious effects have not been manifested in such genotypes (Vilanova et al., 2006; Halász et al., 2007). In addition, inbreeding episodes are known to have occurred in the breeding history of a considerably homozygous (Nyujtó and Surányi, 1981; Pedryc et al., 2009) landrace cultivar group 'Magyarkajszi' (S_8S_C), confirming that S_8 should be free from purifying selection. Similarly, only 2 *S*-alleles have been maintained in peach populations since the emergence of self-compatibility (Tao et al., 2007) compared to the many *S*-alleles described in almond, a self-incompatible species closely related to peach. In fact, self-compatible almond showed signs of inbreeding depression after self-pollination (Ortega et al., 2010). However, experimental confirmation is still required to accept that purifying selection acts on close proximity to specific *S*-alleles of apricot.

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