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Identification of *S*-Allele Based Self-incompatibility of Turkish Pear Gene Resources

Merve Dilek KARATAŞ[a], Nahid HAZRATI[b], Ezgi OĞUZ[b], Canan YÜKSEL ÖZMEN[b], Serdar ALTINTAŞ[c], M. Emin AKÇAY[d], Ali ERGÜL[b*]

[a]*Van Yüzüncü Yıl University, Faculty of Agriculture, Department of Agricultural Biotechnology, 65090 Tuşba, Van TURKEY*

[b]*Ankara University, Biotechnology Institute, 06135 Keçiören, Ankara-TURKEY*

[c]*Siirt University, Faculty of Agriculture, Department of Agricultural Biotechnology, 56100 Siirt, TURKEY*

[d]*Republic of Turkey Ministry of Agriculture and Forestry, Atatürk Horticultural Central Research Institute, Yalova, TURKEY*

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Corresponding Author: Ali ERGÜL, E-mail: ergul@ankara.edu.tr
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ABSTRACT
Self-incompatibility is considered to be a growth-limiting factor in fruit plants. In species with hermaphrodite flowers, *S*-locus (*S*-allele) has been accepted to control self-incompatibility, and the genetic control of this locus is provided by multiple genes (alleles). Pear (*Pyrus communis* L.) belongs to the *Pomoideae* from the *Rosaceae* family and is found to have great genetic potential in terms of ecological features in Turkey. To protect these cultivation features, national garden collections have been established across the country and *Atatürk Horticultural Central Research Institute–Yalova* collection is considered as genes bank. Identification of the different features of this collection (fruit quality, stress tolerance, self-incompatibility, grafting incompatibility, etc.) is of great importance for its utilization in pear breeding and cultivation. However, to our knowledge, this collection has not been characterized for self-incompatibility trait. In the current study, PCR (Polymerase Chain Reaction)-based amplification of the *S*-allele regions (S_1, S_6, S_7, S_8) causing the self-incompatibility in 180 pear genotypes obtained from the national pear germplasm was investigated by molecular biological methods based on the comparison of amplified products. In 180 pear genotypes, the S_6 allele was the most prevalent one with 63% frequency, while the S_8 allele was the least common allele with a rate of 4%. In allele combinations, the S_1-S_6 allele combination was the most common allele combination with a rate of 18%, and trilateral allele combinations (S_1-S_6-S_7 and S_1-S_6-S_8) were observed at a rate of 1%. Findings of the current research will enable the classification of the materials and the analysed material is likely to be used in breeding studies as well as pear cultivation.

Keywords: Pear genotypes, self -incompatibility, *S*-allel, PCR amplification

1. Introduction

Pear (*Pyrus communis* L.), is common fruit grown in almost all moderate climates especially in Europe and Asia. In Turkey, Anatolia area is considered as the homeland and/or diversity centre for many fruit trees. About 640 different pear genotypes have been found in the country. To protect these gene sources, local nominated genotypes in different eco-geographical regions have been collected and protected within this area (Akçay et al. 2014).

Self-incompatibility (SI) in flower-bearing plants is known as a failure in self-fertilization, which may be controlled genetically. Self-incompatibility is known as an unfavourable feature in successful fertilization and fruit set. This phenomenon has been found in more than 100 plant families and has been reported in nearly 40% of plant species (Igic et al. 2008) involving some major crop plants like pome, potato, canola, cocoa, olive, stone fruits, coffee, etc. and/or wild relatives of the mentioned crops. In the majority of plants, genetic control of self-incompatibility is done by a single multiallelic locus named *S*-locus however, control of the systems by two or more loci in some crops like grasses has also been identified (De Nettancourt 2001). Determinants of both female and male specificity which their products are expected to interact and operate the function of self or non-self-distinction are encoded by the *S*-locus (Iwano & Takayama 2012; Muñoz-Sanz et al. 2020).

Depending on the function time of the gene in the stamen, most SI types can be categorized as gametophytic or sporophytic. In sporophytic self-incompatibility (SSI), determination of the SI phenotype is defined by the diploid genotype of parental or pollen-donor plant (sporophyte) and in gametophytic SI (GSI), the SI phenotype is determined by the pollen gametophytic haploid genotype (gametophyte) (Hiscock & Tabah 2003). At the molecular level, three mechanisms of the SI have been identified. In *Brassicaceae*, sporophytic self-incompatibility (SSI) has been identified while two separate types of gametophytic self-incompatibility (GSI) including *S-RNase*-based SI widely elucidated in *Solanaceae* and *Rosaceae*, and the Papaver based system relating to the programmed cell death (PCD) (Muñoz-Sanz et al. 2020).

In GSI which is considered to be the most prevalent type of SI, the cross becomes completely compatible when the male parent (haploid pollen genome) and female parent (diploid pistil genome) contain entirely disparate *S*-genotypes without any common *S*-allele (for instance S_1S_2 x S_3S_4). In case one *S*-allele is shared by the parents (for instance S_1S_2 x S_1S_3), proceeding of the pollen tube containing the similar allele is inhibited by pistil and consequently, the cross is considered to be semi-compatible. Accordingly, in case the same *S*-alleles are carried by the parents at the self-incompatibility locus (for instance S_1S_2 x S_1S_2), growth of the pollen cannot be happened on stigma. In other words, in case pistil-pollen couples do not include the same alleles, include at least one similar allele, or include several alleles, full compatibility, semi-compatibility or incompatibility is encountered, respectively. In crosses with the semi-compatible behaviour, half of the existing pollens are inhibited and could affect the yield and fruit set significantly, for example in Japanese plums, European pears and apple (Schneider et al. 2005; Zisovich et al. 2005; Goldway et al. 2008; Sapir et al. 2008). Results of the incompatibility are observed in minimum seed set and consequently, higher rates of small fruit formation, and yield loss.

Though GSI system applies similar genes in different taxa to specify the pollen rejection system, the mechanism elaboration differs significantly. Moreover, in all families, at least two linked genes or often more, are involved in *S*-locus consisting of a set of pollen-expressing *SFBB* genes (*S-locus F-Box Brothers*) and a pistil-expressed *S-RNase* gene. Pistil-expressed glycoproteins which show ribonuclease activity are encoded by *S-RNase* and they function as extremely selective cytotoxins which result in inhibition of pollens germination and growth when pollen single *S*-haplotype corresponds to one of the diploid pistil *S*-haplotypes (Sanzol & Robbins 2008; Gao et al. 2015; Claessen et al. 2019; Muñoz-Sanz et al. 2020). Another is an F-box protein gene which is distinctly expressed in pollen, is named *SFB* or *SLF* according to the family (De Franceschi et al. 2012; Bagheri & Ershadi 2019; Muñoz-Sanz et al. 2020).

Ability to predict the genomic structure of the pear *S*-locus has been performed using BAC cloning and sequencing in the Japanese pear (*Pyrus pyrifolia*) (Sassa et al. 2007). This was the first study to reveal the existence of several *SFBB* genes surrounding the *S-RNase*. Comparing the genomic sequence surrounding the *S2*- and *S4-RNases*, elucidated meaningful changes in the orientation and position of the *SFBB* genes in pear *S*-haplotypes compared to the *S-RNase* gene (Okada et al. 2011; Claessen et al. 2019).

In *Rosaceae* and *Solanaceae*, *S*-haplotypes have 16 to 20 *SLF* gene sequences which collectively contribute to SI function of the pollen (Kubo et al. 2010; Kakui et al. 2011; Williams et al. 2014; Muñoz-Sanz et al. 2020). Sequence alignment of the *S-RNase* amino acid revealed five regions with the conserved characteristics (i.e. C1, C2, C3, C4, and C5) along with a highly variable region. In addition, a highly polymorphic intron located between the C2 and C3, is found in the hyper variable region (De Franceschi et al. 2012; Bagheri & Ershadi 2019).

2D-PAGE (Two-dimensional Polyacrylamide Gel Electrophoresis) technique has been used to determine mentioned *S*-genotypes earlier. Despite being a fast technique, it is not preferred by plant breeders because it is not a reliable and easy method (Ishimizu et al. 1996). In the following years, PCR technique was applied to identify protected nucleotide sequences of *S-RNase*. Zuccherelli et al. (2002) isolated 2 *S*-allele DNA fragments in Japanese pear and proved that their sequences are similar to that of databank sequences. Among them, 6 *S*-allele fragments (S_a, S_b, S_c, S_d, S_e and S_h) have been cloned and sequenced. Using these alleles, the *S*-allele genotyping was performed in 10 pear genotypes (Barlett, Cascade, Doyennedu Comice, Abbé Fétel, Beurré Hardy, Passe Crassane, Conference, Beurré Bosc, Max Red Bartlett, Eletta Morettini), and the molecular data obtained were confirmed by field crossing results. In the study, PCR based *S*-allele genotyping at molecular level has been shown to be more fast and valid method for European pears.

A similar result was reported by Sanzol & Robbins (2008), that partially *S*-genotyped European pear cultivars and semi compatible test-crosses of these cultivars resulted in the identification of 14 *S*-alleles (S_1 to S_{14}) at the phenotypic level and allele-specific PCR led to the distinction across *S-RNases* that yielded amplification products with similar size using appropriate primers. The authors concluded that these two procedures presented a system for discrimination of all fourteen *S*-alleles in European pear at the molecular level.

Although self-pollination could have occurred in pear, the commercial-scale production depends on the existence of at least two simultaneously flowering compatible cultivars to enable appropriate and effective cross-fertilization so, exploiting of self and inter-compatible cultivars are important for economic fruit set (Zisovich et al. 2010; Goldway et al. 2012). In addition, in last decades, repeated use of scant numbers of cultivars in fruit breeding programs led to increase in cross-incompatibility property as well as a narrow genetic base in new pear varieties (Sanzol & Herrero 2002; Bagheri & Ershadi 2019). In this point of view, identification of the *S*-genotypes of the given species is important for revealing the species and inter-species fertilization biology to proper utilization in breeding programs (Quinet et al. 2014).

Although the incompatibility has been investigated in many pear germplasms, no findings relating to the self-compatibility/incompatibility have been encountered in genotypes of Turkey. In this paper, we evaluated the *S*-allele profiles of the pear genotypes of Turkey national collection in terms of fertilization biology.

2. Material and Methods

2.1 Plant material

180 pear (*Pyrus communis* L.) genotypes were obtained from the Atatürk Horticultural Central Research Institute, Yalova, Turkey, as plant material (Supplementary Table 1).

Table 1- Primer sequences for allele-specific PCR

Primer	*Forward (5'-3')*	*Reverse (5'-3')*	*PCR product size*
*PyrusS$_1$***	aatgtaagactacagccctg	tccaccagtggcctgtttg	367bp
*PyrusS$_6$**	gtttgtggccttcaaacgacg	gtgatcctttaaaagaactgc	347bp
*PyrusS$_7$***	tcacccagaaaattgcactaatgc	ccagtggcctttgtattcccaa	352bp
*PyrusS$_8$***	gtcattgacggggtttgaaccc	ccaactgggctttgagtgat	218bp

*: Ishimizu et al. (1999); **: Nashima et al. (2015)

2.2 Polymerase chain reactions (PCR)

Genomic DNA was isolated from the pear leaves according to Lefort et al. (1998). Determination of the DNA quantity was performed using Nanodrop ND-100 spectrophotometer and extracted DNA was checked on 1% agarose gel.

Allele-specific primers were applied for identifying the single alleles (S_1, S_6, S_7, S_8). Nucleotide sequences of *PyrusS$_1$*, *PyrusS$_6$*, *PyrusS$_7$*, and *PyrusS$_8$* primers were obtained according to Ishimizu et al. (1999) and Nashima et al. (2015), respectively (Table 1). Optimization of PCR (BioRad T100^{TM}) was conducted for used primers as follows: 5X PCR reaction buffer, 25 mM $MgCl_2$, 100 µM dNTP, 5 pmol primer, 5U Taq polymerase and 50-250 ng of genomic DNA was performed at a total volume of 15 µL. Negative control was conducted for controlling each PCR contamination. PCR program was performed as follows; 3 minutes pre-denaturation at 94 °C, 10 cycles (94 °C 1 min; 65 °C 1 min 45s; 72 °C 2 min; reducing the annealing temperature by 1 °C each cycle), 20 cycles (94 °C 1 min; 50 °C 1 min 45s; 72 °C 2 min) and final extension was performed at 72 °C for 10 minutes.

2.3. Evaluation of S-alleles according to band profiles

Amplified PCR products were separated by 2% agarose gel electrophoresis along with DNA marker (Solis Byodyne) in 100 V for 1 hour and thereafter, DNA bands were visualized using a visualization system (Gene Genius Bio Imaging System) (Figure 1).

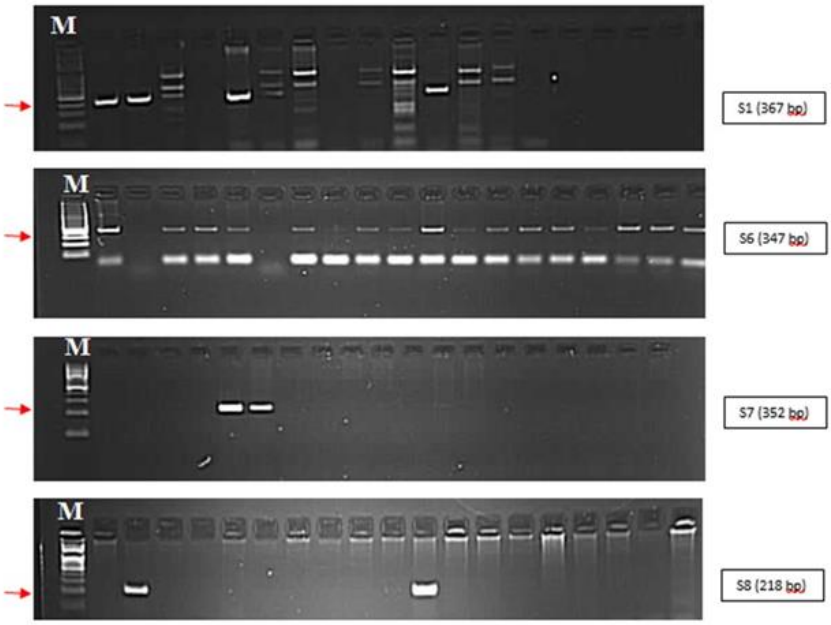

Figure 1- Examples of *S*-allele-specific PCR amplification images (S_1, S_6, S_7 and S_8 respectively). M: 100bp DNA ladder

After agarose gel visualization, genotypes with 367 bp (base pairs) in *PyrusS*$_1$ primer, 347 bp in *PyrusS*$_6$ primer, 352 bp in *PyrusS*$_7$ primer, and 218 bp in *PyrusS*$_8$ primer were considered self-incompatible for the relevant *S*-allele. Allele distribution features determined by Broothaerts et al. (1996) and Ishimizu et al. (1999) have been considered in evaluation of the results.

Among four *S*-alleles, genotypes with at least one-two of which were accepted as semi-compatible, genotypes without amplified fragments were introduced as compatible, and the genotypes with three *S*-alleles are considered to be incompatible.

3. Results and Discussion

By identifying self-incompatibility in genotypes at molecular levels using *S*-alleles, findings of the pear gene resources have been revealed in Turkey (Supplementary Table 1).

3.1. Relationship of compatibility and genetic similarity

Two homonyms of Yalova pear genotypes named "Göksulu (Malatya)" and "Göksulu" (Akçay et al. 2014), showed to possess no similar *S*-alleles and were determined to be semi-compatible.

According to Akçay et al. (2014), "150 887 (1-5)" and "240 887 (3-3)" genotypes with a similarity rate of 91.7% were observed to contain same *S* allele (S_6). Also, in "Bey Armudu" and "16" genotypes, with 91.7% similarity, the first genotype contained S_6 allele while the other one was identified to be whole compatible (Supplementary Table 1).

3.2. Relationship of compatibility and triploidy

In a trial, genetic analyses using 18 SSR loci in 11 pear genotypes revealed presence of three alleles in 4-10 loci, and these genotypes have been identified as potential triploid genotypes (Akçay et al. 2014). In the current study, high variation of SSR alleles detected earlier, was not observed in incompatibility alleles and the S_6 allele was the most observed allele in these triploid incompatible genotypes and while there was no incompatibility allele observed in other 5 genotypes (A 2411, E. Buzbağ, A 2407, 265 GFAE, 140 887 (2-2)) the rest showed at least one incompatible allele (Table 2).

Table 2- Self-incompatibility states of triploid genotypes in SSR analyses

Triploids pear genotypes in SSR analysis	***Incompatibility allele***	***PCR based- Incompatibility status***
190 887 (3-7)	S_6S_6	Semi-compatible
140 887 (2–1)	S_6S_6	Semi-compatible
A 2412	S_1S_6	Semi-compatible
A 2404	S_6S_6	Semi-compatible
A 2401	S_6S_7	Semi-compatible
A 2411	-	Compatible
E. Buzbağ	-	Compatible
A 2407	-	Compatible
265 GFAE	-	Compatible
140 887 (2-2)	-	Compatible

Table 3- *S*-Alleles, self-incompatibility cases and numbers

S allele	***Number of genotypes***	***PCR based-Incompatibility status***
S_6S_6	69	Semi-compatible
S_6S_7	4	Semi-compatible
S_6S_8	2	Semi-compatible
S_7S_7	5	Semi-compatible
S_8S_8	3	Semi-compatible
S_1S_1	14	Semi-compatible
S_1S_6	33	Semi-compatible
-	46	Compatible
$S_1S_6S_8$	2	Incompatible
$S_1S_6S_7$	2	Incompatible

3.3. Identification of alleles and compatibility

To improve the knowledge of self-incompatibility and its relations to many new pear genotypes, we elucidated *S*-genotype of 180 pear genotypes and arranged them based on their *S-RNase* alleles in 10 incompatibility groups (Table 3). Our results revealed incompatibility relations among a great number of pear genotypes in Turkey with unknown previous pollination requirements. These findings of given genotypes will be beneficial for indicating the potential of fertilization and fruit set, establishing the isolated gardens, and selecting as pollinizer.

In this research, four different *S*-alleles (S_1, S_6, S_7, S_8) whose primers have been identified in similar work (Kim et al. 2002; Nashima et al. 2015) were optimized and band size of 180 pear genotypes was determined. 130 out of 180 genotypes which contained at least one *S*-allele were identified as semi-compatible. From the rest, 4 of which containing three *S*-allele were determined as incompatible. In 46 genotypes, it was not observed any *S*-allele and being different from the others, they were identified as compatible genotypes (Table 3).

S_6 allele was observed with 63% rate followed by S_1 with 28% rate. S_8 was the less observed *S*-allele with 4% rate. The highest bilateral *S*-allele combination was observed in S_1-S_6 (18%), and the highest trilateral combinations were S_1-S_6-S_7 and S_1-S_6-S_8 (1%). Quadripartite combination was not observed in any genotype.

In terms of S_1, S_6, S_7, and S_8 alleles, 46 genotypes (25%) contained none of them, 91 genotypes (50%) contained one of them, 39 genotypes (21%) contained two of them, and 4 genotypes (2%) contained three of them. No genotype containing all of the mentioned alleles was observed (Table 3).

Similar to our work, 14 Japanese pear genotypes were investigated using 11 *S*-alleles including S_1, S_6, S_7, and S_9 alleles, and these alleles are applicable effectively for rapid identification of *S*-genotypes in similar pear breeding studies, and marker-assisted selection (MAS) performing (Nashima et al. 2015). Low sequence similarity of allele introns (average 43%) and high polymorphism in exon regions have been shown as the causes of high performance features of these *S*-alleles (Nashima et al. 2015). Nashima et al. (2015) identified existence of peculiar amplification (especially between 55-61 °C) through various PCR optimization trials of the S_1, S_6, S_7, and S_9 primers, and observed undesirable fragments on agarose gel in all primer pairs under 100 bp. In our research, these primers were similarly optimized using Touch Down PCR (*Tm* between 55-65 °C) program and some non-specific band was observed among PCR products.

Nowadays, *S*-allele genotyping trials at molecular level have been accelerated. Up until now, *S*-allele cloning and sequencing has been performed in about 26 European pear genotypes. In addition, genotyping of *S-RNase* genes in more than 150 pear genotypes has been carried out (Sanzol & Herrero 2002; Zuccherelli et al. 2002; Zisovich et al. 2004; Sanzol et al. 2006; Takasaki et al. 2006; Sanzol & Robbins 2008; Goldway et al. 2009; Sanzol 2009 a, b; Nashima et al. 2015).

In our study, since the high numbers of genotypes possess S_6 allele, so this allele was chosen as the prevalent one. The high ratio of genotypes bearing the S_6 allele (112 out of 180 genotypes) in comparison to genotypes bearing S_1 and other two alleles, could be explained by a plausible hypothesis that the S_6-locus is linked to another gene or genes encoding an important trait for pear cultivation or quality so, it could be mentioned that the S_6 allele involved a selective preference during breeding. A previous study on European pears revealed that certain *S*-alleles have considerably more frequency, and selection for commercial traits was proposed to describe this result. In this regard, Sanzol & Robbins (2008) noted that the majority of selected offspring of "Williams Bon Chrétien" cultivar with *PcS101* and *PcS102 S*-alleles comprised the *PcS101* allele rather than the *PcS102* allele. The authors suggested that the *PCS101* allele is of interest throughout selection. In addition, genetic analyses of species belonging to distant taxa are quite consistent with this feasibility (Burke et al. 2002; Gandhi et al. 2005). Nevertheless, it could be mentioned that the high use of certain genotypes as parent in breeding programs could also be one of the reasons for the abundance of certain alleles.

In our study, Williams cultivar was employed as a reference genotype and displayed an incompatible feature similar to previous studies (Sanzol & Herrero 2002). *S*-allele-specific PCR analysis (S_1, S_6, S_7 and S_8, respectively) are given in Figure 1 and the Williams cultivar representing reference genotype with known *S-RNase*s (S_1S_6), gave the expected PCR products corresponding to each allele and after electrophoresis, the higher frequency of S_6 allele was sensibly distinct among studied genotypes (Figure 1). Orcheski & Brown (2012) noted that, since specific reference cultivars are often used as parent in breeding programs of new cultivars so, their related *S*-alleles are found frequently in new developed commercial cultivars.

In the current study, three alleles were found in the four genotypes, namely 'E2480 Kızıl Bıldırcın' and 'E 2481 Kaymak' from Central Anatolian region and '21' and '52' from Marmara regions using these primers (Supplementary Table 1). According to 46 self-compatible genotypes, considering the proportion of regional samples, the highest proportion (40%) with 13 out of 32 genotypes was assigned to the Marmara region and the lowest percentage with 3 out of 24 genotypes (12% of the region samples) allocated to the Central Anatolian region so, more attention should be paid to contrivance, regarding the commercial production and orchard design in this region. The results confirmed that the self-incompatibility feature tends to

increase in species, which is contrary to the former reports indicating that most cultivars were compatible (Mehlenbacher et al. 1991; Herrera et al. 2018).

Although much progress has been gained in understanding how the SI system works, many points of ambiguity remain still unclear. It has been recently illustrated that the *Pyrus* SI response begins with the uptake of the *S-RNase* protein from the style transmitter tissue by the pollen tube in a non-allelic specific manner. The entry of both non-self and self *S-RNase*s into the pollen tube, support that the process of self-recognition takes place inside the pollen tube and subsequently results in inhibition of the non-self *S-RNase*s activity (Goldraij et al. 2006; De Franceschi et al. 2012; Meng et al. 2014a; Meng et al. 2014b, Williams et al. 2015). In *Malus* and *Pyrus* species, the simultaneous attendance of multiple *SFBB* genes on the *S*-locus as the pollen *S*-detectors (Sassa et al. 2007) indicates that each of the SFBB proteins may detect one or more non-self *S-RNase*s, targeting them for proteasome degradation (De Franceschi et al. 2012).

The recognition system has been proposed to occur *via* two models for GSI in *Pyrus* species. In the first model, the SFBB protein which identifies specifically the self *S-RNase*, relinquishing the self *S-RNase* intact to reject extension of the incompatible (self) pollen tube while mark all non-self *S-RNase*s (Williams et al. 2015). In the second model which functions in the non-self-recognition way, the multiplex *SFBB*s that each distinguish and target a subset or unique non-self *S-RNase*s, resulted in *S-RNase* decomposition so, the self *S-RNase*s which are not prohibited led to the inhibition of self-incompatible pollen growth (Kubo et al. 2010).

It should be noted that in nature, true rejection of pollen is not only controlled genetically but also is affected by various external agents, like the environmental factors and pollination grade resulting in selfed seeds in self-incompatible varieties (Visser & Marcucci 1984). Interestingly, in cases where pollination occurs by non-self pollen, the evolvement possibility of ovule or fruit is higher than in case of self-pollination, which indicates the attendance of additional post-zygotic inhibitors that inhibit the selfed seed formation (Martin & Lee 1993). It is concluded that this abortion could be caused by recessive homozygous alleles combination or accumulation of low alleles that occur as a result of self-fertilization (Pannell & Labouche 2013) or due to the lower intake strength of plant sap for energy attainment.

Similarly, crosses between two semi-compatible lines could also lead to adversities. In semi-compatible crosses, half of the pollens bearing certain *S*-genotype are inhibited, resulting in a limited number of possible *S*-genotype compositions in the progeny. This “artificial selection” significantly affects the diversity of *S*-alleles, leading to a reduction in biological and genetic diversity as well as the loss of interesting traits in pear cultivars (Claessen et al. 2019).

According to the contents, examination of the pear SI mechanism reveals that in most commercial cultivars, the fruit set is highly depend on cross-pollination and successful fertilization. For these reasons, incompatibility is a system that nature has developed to prevent the accumulation of adverse homozygous allele damages and to provide a way to create varieties with diverse characteristics while maintaining viability over the years.

4. Conclusions

S-genotyping has made it possible to classify cultivars in relevant incompatibility groups considering their compatibility relations. Self-incompatibility is displayed when the pollen genotype corresponds to one of the pistil *S*-alleles. Therefore, self-incompatible lines bearing the similar *S*-alleles by classification in the identic incompatibility category, are considered to be inter-incompatible, while lines from other categories containing at least one different *S*-allele are accepted to be inter-compatible (Muñoz-Sanz et al. 2017).

It should be noted that standardization of the *S*-alleles identification criteria is essential in various laboratories, including the full sequencing of *S* alleles and utilization of the identic primer pairs. This will lead to easy *S*-allele identification without confusion and will provide valuable information for pear breeders (Herrera et al. 2018). Obtained results in this study make it possible to organize the incompatibility relationships between pear genotypes with former unknown pollination knowledge and provide the possibility to select suitable parents in designing new crosses in pear production and breeding programs. Besides, this work could be helpful for other *Rosaceae* fruit products with the same challenges encountered by pear.

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Supplementary Table 1- *S*-allele compositions of pear cultivars

No.	*Cultivar name*	*S-Genotype*	*PCR based- Compatibility status*	*Region*
1	190 887 (3-2)	S_6S_6	Semi-compatible	Unknown
2	190 887 (3-1)	S_8S_8	Semi-compatible	Aegean
3	240 887 (3-1)	-	Compatible	Aegean
4	22	-	Compatible	Marmara
5	38	S_6S_6	Semi-compatible	Marmara
6	A-48	-	Compatible	Unknown
7	133	S_1S_6	Semi-compatible	Marmara
8	200 GFAE	S_6S_6	Semi-compatible	Black Sea
9	207 BF(G)	-	Compatible	Black Sea
10	221 GFAE (G)	S_6S_8	Semi-compatible	Black Sea
11	223 GFAE (G)	S_6S_6	Semi-compatible	Black Sea
12	A-2406	S_1S_6	Semi-compatible	Unknown
13	Azdavay	S_6S_6	Semi-compatible	Black Sea
14	Bağ (G)	-	Compatible	Black Sea
15	Bal Armut (Malatya)	S_6S_6	Semi-compatible	Unknown
16	Bey Armudu	S_6S_6	Semi-compatible	Unknown
17	Çankaya1	S_6S_6	Semi-compatible	Unknown
18	Cennet (G)	S_6S_6	Semi-compatible	Black Sea
19	E 2473 Cinci	S_8S_8	Semi-compatible	Central Anatolian
20	E 2501 Eğrişap	S_6S_6	Semi-compatible	Central Anatolian
21	E 2507 Pamukap	S_1S_1	Semi-compatible	Central Anatolian
22	E Rize	S_6S_6	Semi-compatible	Unknown
23	Fakaz (G)	S_1S_6	Semi-compatible	Black Sea
24	Gümüşhane (G)	S_1S_6	Semi-compatible	Black Sea
25	Gürpınar (G)	S_1S_6	Semi-compatible	Black Sea
26	İğnesi (Malatya)	S_7S_7	Semi-compatible	Unknown
27	İncir (Malatya)	-	Compatible	Unknown
28	Kantartopu	S_1S_1	Semi-compatible	Black Sea

Supplementary Table 1 (Continue)- *S*-allele compositions of pear cultivars

No.	*Cultivar name*	*S-Genotype*	*PCR based- Compatibility status*	*Region*
29	Karagöynük	-	Compatible	Marmara
30	Karpuz	S_6S_6	Semi-compatible	Black Sea
31	Kiraz	S_1S_1	Semi-compatible	Black Sea
32	Küpdüşen (Malatya)	S_6S_6	Semi-compatible	Unknown
33	Küre (G)	S_6S_6	Semi-compatible	Black Sea
34	Laliye	S_1S_1	Semi-compatible	Marmara
35	Malatya Limon	S_1S_6	Semi-compatible	Unknown
36	Mis (G)	S_1S_1	Semi-compatible	Black Sea
37	Turşu (G)	S_6S_6	Semi-compatible	Black Sea
38	174W (G) D.dAngulume	S_1S_1	Semi-compatible	Unknown
39	E Santa Maria	-	Compatible	Unknown
40	Williams	S_1S_6	Semi-compatible	Unknown
41	Akça	S_1S_1	Semi-compatible	Marmara
42	E. Buzbağ	-	Compatible	Marmara
43	Çiçek	-	Compatible	Marmara
44	Göksulu	S_1S_6	Semi-compatible	Marmara
45	Göksulu (Malatya)	S_1S_1	Semi-compatible	Marmara
46	Malatya (Malatya)	S_6S_6	Semi-compatible	Unknown
47	205 AF (G)	S_6S_6	Semi-compatible	Black Sea
48	188 BK (G)	S_6S_6	Semi-compatible	Black Sea
49	130 887 (1-3)	S_1S_1	Semi-compatible	Unknown
50	130 887 (3-7)	S_1S_6	Semi-compatible	Unknown
51	140 887 (1-1)	S_6S_6	Semi-compatible	Unknown
52	140 887 (2-3)	S_6S_6	Semi-compatible	Aegean
53	150 887 (1-3)	S_6S_6	Semi-compatible	Aegean
54	150 887 (1-5)	S_6S_6	Semi-compatible	Unknown
55	150 887 (2-3)	S_6S_6	Semi-compatible	Aegean
56	172 887 (2-2)	S_6S_6	Semi-compatible	Aegean
57	190 887 (2-6)	S_6S_6	Semi-compatible	Unknown
58	180 887 (4-3)a	S_6S_6	Semi-compatible	Aegean
59	180 887 (9-7)	S_6S_6	Semi-compatible	Aegean
60	190 887 (3-3)	S_1S_6	Semi-compatible	Unknown
61	190 887 (3-5)	S_1S_6	Semi-compatible	Aegean
62	190 887 (3-7)	S_6S_6	Semi-compatible	Aegean
63	190 887 (4-1)	S_6S_6	Semi-compatible	Aegean
64	190 887 (6-2)	S_1S_6	Semi-compatible	Aegean
65	200 887 (2-1)	S_6S_6	Semi-compatible	Aegean
66	200 887 (2-3)	S_8S_8	Semi-compatible	Aegean
67	200 887 (2-4)	S_1S_6	Semi-compatible	Aegean
68	200 887 (11-6)	S_6S_6	Semi-compatible	Aegean
69	210 887 (2-2)	S_1S_1	Semi-compatible	Aegean
70	210 887 (2-3)	S_1S_6	Semi-compatible	Aegean
71	210 887 (4-4)	S_6S_6	Semi-compatible	Unknown
72	210 887 (4-6)	S_6S_6	Semi-compatible	Aegean
73	220 887 (2-3)	S_1S_6	Semi-compatible	Aegean
74	220 887 (3-3)	S_1S_6	Semi-compatible	Aegean
75	230 887 (3-3)	S_6S_6	Semi-compatible	Aegean
76	240 887 (3-3)	S_6S_6	Semi-compatible	Aegean
77	A33	S_1S_6	Semi-compatible	Unknown
78	A 129	S_1S_6	Semi-compatible	Unknown
79	A 2401	S_6S_7	Semi-compatible	Unknown
80	A 2407	-	Compatible	Unknown
81	A 2409	S_1S_6	Semi-compatible	Unknown
82	A 2411	-	Compatible	Unknown
83	A 2412	S_1S_6	Semi-compatible	Aegean
84	E 2470 Kokmuş Armut	S_6S_6	Semi-compatible	Unknown
85	E 2444 Arpa	S_6S_6	Semi-compatible	Aegean
86	E 2462 Bıldırcın	S_6S_7	Semi-compatible	Central Anatolian
87	E2480 Kızıl Bıldırcın	$S_1S_6S_7$	Incompatible	Central Anatolian
88	E 2481 Kaymak	$S_1 S_6S_8$	Incompatible	Central Anatolian
89	E 2493 Kışlık Şalgam	S_1S_6	Semi-compatible	Central Anatolian
90	E 2516	S_1S_6	Semi-compatible	Central Anatolian
91	E 2539 Baymaz	S_1S_6	Semi-compatible	Central Anatolian
92	E 2540 Dalkıran	S_1S_6	Semi-compatible	Unknown
93	E 2542 Ağa	S_1S_6	Semi-compatible	Central Anatolian
94	E 2547 Armut	S_6S_6	Semi-compatible	Central Anatolian

Supplementary Table 1 (Continue)- *S*-allele compositions of pear cultivars

No.	*Cultivar name*	*S-Genotype*	*PCR based- Compatibility status*	*Region*
95	E 2556 Hocacul	-	Compatible	Unknown
96	E 2557 Mustafabey	S_6S_6	Semi-compatible	Central Anatolian
97	E Ankara	S_6S_6	Semi-compatible	Central Anatolian
98	E Giresun	S_6S_6	Semi-compatible	Central Anatolian
99	10	S_6S_6	Semi-compatible	Marmara
100	13	S_6S_6	Semi-compatible	Unknown
101	14	S_1S_6	Semi-compatible	Unknown
102	18	S_1S_1	Semi-compatible	Marmara
103	19	S_6S_6	Semi-compatible	Unknown
104	20	S_6S_6	Semi-compatible	Marmara
105	21	$S_1S_6S_8$	Incompatible	Marmara
106	30	S_6S_6	Semi-compatible	Marmara
107	37b	S_1S_1	Semi-compatible	Marmara
108	41	S_1S_6	Semi-compatible	Unknown
109	43	S_6S_6	Semi-compatible	Marmara
110	136	-	Compatible	Marmara
111	139	S_1S_1	Semi-compatible	Marmara
112	231 BC	S_1S_6	Semi-compatible	Unknown
113	P5-9	S_6S_6	Semi-compatible	Unknown
114	P5-23	-	Compatible	Unknown
115	Thompson (Malatya)	S_6S_6	Semi-compatible	Unknown
116	Andre Desportes	-	Compatible	Unknown
117	150 887 (1-1)	-	Compatible	Aegean
118	E 2545	-	Compatible	Unknown
119	140 887 (2-5)	-	Compatible	Unknown
120	140 887 (2-2)	S_6S_7	Semi-compatible	Aegean
121	E 2533 Sarı Armut	-	Compatible	Central Anatolian
122	E 509 Kış Armudu	-	Compatible	Central Anatolian
123	E 224 K. Armut	S_1S_6	Semi-compatible	Central Anatolian
124	52	$S_1S_6S_7$	Incompatible	Marmara
125	200 887 (2-1)b	-	Compatible	Aegean
126	210 887 (4-5)	S_6S_6	Semi-compatible	Unknown
127	P5 11	-	Compatible	Unknown
128	64	-	Compatible	Marmara
129	44	-	Compatible	Marmara
130	134	-	Compatible	Marmara
131	E 2537 Bulap	S_6S_6	Semi-compatible	Central Anatolian
132	220 887 (3-1)	-	Compatible	Unknown
133	213 GFAE	-	Compatible	Karadeniz
134	236 GFAE	-	Compatible	Karadeniz
135	A 2404	S_6S_6	Semi-compatible	Unknown
136	190 887 (3-6)	S_6S_6	Semi-compatible	Unknown
137	31	S_6S_6	Semi-compatible	Marmara
138	190 887 (2-3)	S_6S_6	Semi-compatible	Aegean
139	16	-	Compatible	Marmara
140	P5-2	S_6S_6	Semi-compatible	Unknown
141	14	-	Compatible	Unknown
142	A 129	S_1S_6	Semi-compatible	Unknown
143	P 522	S_6S_6	Semi-compatible	Unknown
144	A 2410	S_1S_6	Semi-compatible	Unknown
145	E 2462 Bıldırcın	-	Compatible	Central Anatolian
146	E 2480 Kızıl Bıldırcın	S_6S_6	Semi-compatible	Mediterranean
147	E 2542 Ağa	S_6S_6	Semi-compatible	Central Anatolian
148	150 887 (3-1)	-	Compatible	Aegean
149	21	-	Compatible	Marmara
150	190 887 (1-1)	-	Compatible	Aegean
151	200 887 (2-1)	S_1S_1	Semi-compatible	Aegean
152	E Ankara	S_6S_6	Semi-compatible	Central Anatolian
153	220 887 (2-3)	S_7S_7	Semi-compatible	Aegean
154	Giresun	S_7S_7	Semi-compatible	Unknown
155	150 887 (1-1)	S_6S_7	Semi-compatible	Aegean
156	240 887 (3-2)	S_7S_7	Semi-compatible	Aegean
157	200 887 (2-1)a	-	Compatible	Aegean
158	140 887 (2-1)	S_6S_6	Semi-compatible	Aegean
159	140 887 (2-2)	-	Compatible	Aegean
160	265 GFAE	-	Compatible	Karadeniz

Supplementary Table 1 (Continue)- *S*-allele compositions of pear cultivars

No.	***Cultivar name***	***S-Genotype***	***PCR based- Compatibility status***	***Region***
161	E 2533 Sarı Armut	S_6S_8	Semi-compatible	Central Anatolian
162	E 2509 K. Armut	S_1S_6	Semi-compatible	Unknown
163	190 887 (3-4)	S_6S_6	Semi-compatible	Unknown
164	200 887 (2-1)b	-	Compatible	Aegean
165	E 2525 Ekşi Armut	S_6S_6	Semi-compatible	Central Anatolian
166	44	S_6S_6	Semi-compatible	Marmara
167	134	S_6S_6	Semi-compatible	Marmara
168	E 2537 Bulap	S_6S_6	Semi-compatible	Central Anatolian
169	220 887 (3-1)	S_6S_6	Semi-compatible	Unknown
170	235 P	-	Compatible	Unknown
171	A 2404	-	Compatible	Unknown
172	31	S_1S_6	Semi-compatible	Marmara
173	M 2404	-	Compatible	Unknown
174	190 887 (2-3)	S_7S_7	Semi-compatible	Aegean
175	180 887 (4-3)b	S_6S_6	Semi-compatible	Aegean
176	220 887 (4-1)	S_6S_6	Semi-compatible	Aegean
177	45	-	Compatible	Marmara
178	32	-	Compatible	Marmara
179	138	-	Compatible	Marmara
180	A 135	-	Compatible	Unknown