

## Molecular S-genotyping of sweet cherry (*Prunus avium* L.) genetic resources

JOSEF PATZAK<sup>1\*</sup>, ALENA HENYCHOVÁ<sup>1</sup>, FRANTIŠEK PAPRŠTEIN<sup>2</sup>, JIŘÍ SEDLÁK<sup>2</sup>

<sup>1</sup>Hop Research Institute, Žatec, Czech Republic

<sup>2</sup>Research and Breeding Institute of Pomology, Holovousy, Czech Republic

\*Corresponding author: patzak@chizatec.cz

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**Abstract:** Sweet cherries are self-incompatible, which is determined by a gametophytic self-incompatibility system (GSI). The self-incompatibility is controlled by a multi-allelic S-locus. Knowledge about the S-allele constitution of the cultivars is essential for fruit growers and breeders. Recently, molecular PCR-based methods have been developed to distinguish all S-alleles in sweet cherries. In our work, we analysed S-locus genotypes by 13 universal and allele-specific PCR primer combinations within 117 registered, old and local sweet cherry cultivars from the Czech genetic resources of the Research and Breeding Institute of Pomology in Holovousy, the Czech Republic. We confirmed the previous S-genotyping for 66 accessions except for Drogans Gelbe, Hedelfinger, Erika, Meckenheimer Frühe, Badeborner, Bing, Alfa, Gamma, Huldra, Rivan, Valerij Tschkalov, Viola and Winkler's Frühe. It could be due to either mislabelling or mistakes in the previous analyses. Newly, S-genotyping was determined for 51 accessions in which we found 4 new S-loci combinations. We detected the S-locus combinations in 19 incompatibility groups. The most frequent incompatibility groups were III (S<sub>3</sub>S<sub>4</sub>), II (S<sub>1</sub>S<sub>3</sub>), IV (S<sub>2</sub>S<sub>3</sub>), and VI (S<sub>3</sub>S<sub>6</sub>) with 22, 20, 12 and 12 genotypes, respectively.

**Keywords:** self-incompatibility; S-RNase alleles; incompatibility groups; cultivars

The sweet cherry (*Prunus avium* L.) is an important fruit species in the temperate zone. Sweet cherries are generally self-incompatible, which is determined by a gametophytic self-incompatibility system (GSI). The incompatible phenotype is determined by a ribonuclease called S-RNase (TAO et al. 1999) and the specificity of the pollen is determined by the product of the F-box gene *SFB* (YAMANE et al. 2003). The S-RNase locus is multi-allelic and the cloning and sequence characterisation of it has allowed the development of PCR and RFLP based methods (DIRLEWANGER et al. 2009). These S-RNase sequences have two introns varying in length for each different allele and, conse-

quently, the PCR amplification with those primers enables the differentiation of the different S-alleles according to the size of the amplified fragments. Subsequently, other sweet cherry S-RNases were cloned and other PCR methods were developed using conserved sequence primers (WIERSMA et al. 2001) and allele specific primers (SONNEVELD et al. 2003). Recently, SCHUSTER (2012) compiled the S-genotype of 734 sweet cherry accessions and reported 18 different S-alleles (S<sub>1</sub> to S<sub>7</sub>, S<sub>9</sub>, S<sub>10</sub>, S<sub>12</sub> to S<sub>14</sub>, S<sub>16</sub>, S<sub>17</sub>, S<sub>19</sub>, S<sub>21</sub>, S<sub>22</sub>, S<sub>24</sub>), 47 incompatibility groups, a group '0' of unique S-genotypes (15 cultivars or universal pollen donors) and a group of 44 self-compatible cultivars. Additionally, another

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six S-alleles have been described in the wild cherry only, these are  $S_{27}$  to  $S_{32}$  (DE CUYPER et al. 2005; VAUGHAN et al. 2008). The knowledge about the S-allele constitution of the cultivars is very important for fruit growers and breeders regarding the planning of new orchards, for artificial hybridisations and as a genetic marker (SCHUSTER 2012).

The aim of this study was to identify the S-allele combinations within the set of the Czech and world registered, old and local cherry cultivars by PCR molecular markers.

## MATERIAL AND METHODS

In our experiment, we used 117 cherry accessions of the registered, old and local cultivars in total (Table 1) from the cherry genetic resources of the Research and Breeding Institute of Pomology in Holovousy in the Czech Republic. 1 g of the collected young green leaves were powdered with liquid nitrogen and used for DNA isolation by the SDS isolation method according to GOULÃO et al. (2001). The isolated DNAs were afterwards cleaned by a ChargeSwitch® gDNA Plant Kit (Invitrogen, ThermoFisher Scientific, Waltham, USA). For the PCR identification of the S-locus sequence, we used universal primer pairs for Intron 1 and 2, and the allele-specific primer pairs  $S_2$ ,  $S_3$ ,  $S_4$ ,  $S_7$ ,  $S_9$ ,  $S_{10}$ ,  $S_{12}$ ,  $S_{13}$ ,  $S_{14}$  and  $S_{16}$  (SONNEVELD et al. 2003; IEZZONI 2008; SHARMA et al. 2014). In a typical PCR reaction (*Taq* PCR master mix kit, Qiagen, Hilden, FRG), we used the following amplification conditions: 2 min at 94°C, 35 cycles/ (30 s at 94°C; 60 s at 50–60°C, 90 s at 72°C); 10 min at 72°C, in a TGradient thermocycler (Biometra, Goettingen, FRG). The annealing temperatures were used according to the references. The amplification products were resolved via electrophoresis in horizontal 1–2 % agarose gels and visualised by ethidium bromide staining according to PATZAK (2001). The products were scored for the presence or absence in each accession, based on the size measured with the pGEM DNA marker and a 100 bp ladder (Promega, Madison, USA).

## RESULTS AND DISCUSSION

The introduction of molecular methods in sweet cherry S-allele typing has allowed for the rapid

confirmation of the S-alleles and incompatibility groups of different cultivars, the identification of the S-genotype of new varieties and the identification of putative new S alleles by their correlation with the new PCR products (DIRLEWANGER et al. 2009). Currently, the specific allele primer pairs for the  $S_2$ ,  $S_3$ ,  $S_4$ ,  $S_7$ ,  $S_9$ ,  $S_{10}$ ,  $S_{12}$ ,  $S_{13}$ ,  $S_{14}$  and  $S_{16}$  alleles have been useful (SONNEVELD et al. 2003; IEZZONI 2008; SHARMA et al. 2014) for the identification of the S locus sequence. All of them we used for the identification of the S-genotypes within 117 cherry accessions of the registered, old and local cultivars (Table 1). Therefore, there are more than ten other S-alleles, so it was also necessary to use universal primer pairs for Intron 1 and 2 of the S-RNase gene. The sizes of the genomic amplification products of both introns corresponded with different S-alleles (Sonneveld et al. 2003; Schuster et al. 2007) for their useful identification. Overall, the results are summarised in Table 1. In total, we detected 13 different S-alleles in 24 S-locus combinations for 19 individual incompatibility groups. The most frequent S-alleles were  $S_3$  (74 genotypes),  $S_1$  (43 genotypes) and  $S_4$  (39 genotypes), followed by  $S_2$  (27 genotypes) and  $S_6$  (24 genotypes) (Fig. 1a). The rare alleles were  $S_7$ ,  $S_{13}$ ,  $S_{14}$ ,  $S_{16}$  and  $S_{19}$  (Table 1, Fig. 1a). These results were in accordance with published data for the European germplasm (DE CUYPER et al. 2005; CACHI, WÜNSCH 2014; LISEK et al. 2015). Among 734 sweet cherry cultivars, the frequencies were in the order  $S_3$  (383 cultivars),  $S_4$  (227 cultivars),  $S_1$  (221 cultivars),  $S_6$  (190 cultivars),  $S_2$  (112 cultivars),  $S_9$  (98 cultivars) and  $S_5$  (81 cultivars) (SCHUSTER 2012). The most frequent incompatibility groups were III ( $S_3S_4$ ), II ( $S_1S_3$ ), IV ( $S_2S_3$ ) and VI ( $S_3S_6$ ) with 22, 20, 12 and 12 genotypes, respectively (Fig. 1b).

We confirmed the previous S-genotyping for 66 accessions except for Drogans Gelbe, Hedelfinger, Erika, Meckenheimer Frühe, Badeborner, Bing, Alfa, Gamma, Huldra, Rivan, Valerij Tschkalov, Viola and Winkler's Frühe. This could be due to the mislabelling or mistakes in our previous analyses. The published results of the S-genotypes have not been based on the PCR markers only, but also on previously reported data and breeders' knowledge (SCHUSTER 2012). Newly, S-genotyping was determined for 51 accessions when we found 4 new S-loci combinations  $S_4S_x$  (Těchlovická),  $S_{19}S_x$  (Drogans Gelbe),  $S_2S_{13}$  (Szwecija) and  $S_1S_{16}$  (Buketova). It is also known that there are difficult to detect S-alleles

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Table 1. Identification of S-alleles and incompatibility groups (IG) within 117 registered, old and local sweet cherry cultivars

Cultivar	Origin <sup>1</sup>	Detected S-alleles	Published S-alleles	IG <sup>2</sup>
Raná Černá Edra	BGR	S <sub>1</sub> S <sub>2</sub>		I
Raná Laskovská	BGR	S <sub>1</sub> S <sub>5</sub>		XIV
Sam	CAN	S <sub>2</sub> S <sub>4</sub>	S <sub>2</sub> S <sub>4</sub>	XIII
Star	CAN	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Stella	CAN	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Sue	CAN	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Summit	CAN	S <sub>1</sub> S <sub>2</sub>	S <sub>1</sub> S <sub>2</sub>	I
Sunburst	CAN	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Sweetheart	CAN	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Van	CAN	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Vega	CAN	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Velvet	CAN	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Venus	CAN	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Vic	CAN	S <sub>2</sub> S <sub>4</sub>	S <sub>2</sub> S <sub>4</sub>	XIII
Vineland	CAN	S <sub>3</sub> S <sub>6</sub>		VI
Viva	CAN	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Vogue	CAN	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Buketova	CZE	S <sub>1</sub> S <sub>16</sub>		0
Černá špička	CZE	S <sub>1</sub> S <sub>3</sub>		II
Černá z Hořan	CZE	S <sub>4</sub> S <sub>12</sub>		XXVII
Děkanka	CZE	S <sub>3</sub> S <sub>6</sub>		VI
H 21/40 Černá	CZE	S <sub>1</sub> S <sub>6</sub>		XX
Holovouská chrupka	CZE	S <sub>1</sub> S <sub>3</sub>		II
Chlumecká Černá	CZE	S <sub>1</sub> S <sub>3</sub>		II
Karešova	CZE	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Kordia	CZE	S <sub>3</sub> S <sub>6</sub>	S <sub>3</sub> S <sub>6</sub>	VI
Ladeho pozdní	CZE	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Libějovická raná	CZE	S <sub>3</sub> S <sub>4</sub>		III
Moravská rychlice	CZE	S <sub>2</sub> S <sub>3</sub>		IV
Mramorovaná chrupka	CZE	S <sub>1</sub> S <sub>5</sub>		XIV
Pivka	CZE	S <sub>1</sub> S <sub>3</sub>		II
Pivovka	CZE	S <sub>3</sub> S <sub>7</sub>		XLIV
Plavečský granát	CZE	S <sub>3</sub> S <sub>6</sub>	S <sub>3</sub> S <sub>6</sub>	VI
Samofertilní	CZE	S <sub>3</sub> S <sub>4</sub>		III
Semenáč č.13	CZE	S <sub>4</sub> S <sub>12</sub>		XXVII
Srdcovka přeúrodná	CZE	S <sub>3</sub> S <sub>6</sub>		VI
Šakvická	CZE	S <sub>1</sub> S <sub>6</sub>		XX
Těchlovan	CZE	S <sub>3</sub> S <sub>6</sub>	S <sub>3</sub> S <sub>6</sub>	VI
Těchlovická	CZE	S <sub>4</sub> S <sub>x</sub>		0
Vanda	CZE	S <sub>1</sub> S <sub>6</sub>	S <sub>1</sub> S <sub>6</sub>	XX

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Table 1. To be continued

Cultivar	Origin <sup>1</sup>	Detected S-alleles	Published S-alleles	IG <sup>2</sup>
Vlachova	CZE	S <sub>1</sub> S <sub>2</sub>		I
Vosenka	CZE	S <sub>2</sub> S <sub>4</sub>		XIII
Žalanka	CZE	S <sub>1</sub> S <sub>4</sub>		IX
Alma	DEU	S <sub>1</sub> S <sub>5</sub>	S <sub>1</sub> S <sub>5</sub>	XIV
Badeborner	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>5</sub>	III
Büttner's späte Knorpelkirsche	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Dönissens Gelbe	DEU	S <sub>3</sub> S <sub>6</sub>	S <sub>3</sub> S <sub>6</sub>	VI
Drogans Gelbe	DEU	S <sub>19</sub> S <sub>x</sub>	S <sub>1</sub> S <sub>5</sub>	0
Emperor Francis	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Erika	DEU	S <sub>4</sub> S <sub>6</sub>	S <sub>1</sub> S <sub>3</sub>	XVI
Frühe von Boppard	DEU	S <sub>3</sub> S <sub>6</sub>		VI
Germersdorfer	DEU	S <sub>3</sub> S <sub>12</sub>	S <sub>3</sub> S <sub>12</sub>	XXII
Grolls Schwarze Knorpelkirsche	DEU	S <sub>3</sub> S <sub>4</sub>		III
Hedelfinger	DEU	S <sub>1</sub> S <sub>3</sub>	S <sub>3</sub> S <sub>5</sub>	II
Hildesheim	DEU	S <sub>1</sub> S <sub>3</sub>		II
Kassins Frühe	DEU	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Knauffs Schwarze	DEU	S <sub>2</sub> S <sub>6</sub>	S <sub>2</sub> S <sub>6</sub>	XXV
Leopoldskirsche	DEU	S <sub>2</sub> S <sub>4</sub>		XIII
Meckenheimer Frühe	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>1</sub> S <sub>4</sub>	III
Müncheberger	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Napoleon	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Německá rychlice	DEU	S <sub>2</sub> S <sub>3</sub>		IV
Oktavia	DEU	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Querfurter Königskirsche	DEU	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Rebekka	DEU	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Regina	DEU	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Simonis	DEU	S <sub>3</sub> S <sub>4</sub>		III
Spitze Braune	DEU	S <sub>3</sub> S <sub>14</sub>		XXXI
Thurn Taxis	DEU	S <sub>3</sub> S <sub>12</sub>		XXII
Tropfichters Schwarze Knorpelkirsche	DEU	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Valeska	DEU	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Velká Černá Chrupka	DEU	S <sub>1</sub> S <sub>6</sub>		XX
Viola	DEU	S <sub>4</sub> S <sub>12</sub>	S <sub>3</sub> S <sub>6</sub>	XXVII
Winkler's Frühe	DEU	S <sub>2</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub> , S <sub>3</sub> S <sub>9</sub>	IV
Zeisberger	DEU	S <sub>2</sub> S <sub>4</sub>		XIII
Bigarreau Charmes	FRA	S <sub>3</sub> S <sub>9</sub>		XVI
Burlat	FRA	S <sub>3</sub> S <sub>9</sub>	S <sub>3</sub> S <sub>9</sub>	XVI
Ramon Oliva	FRA	S <sub>6</sub> S <sub>9</sub>		X
Early Rivers	GBR	S <sub>1</sub> S <sub>2</sub>	S <sub>1</sub> S <sub>2</sub>	I
Merchant	GBR	S <sub>4</sub> S <sub>9</sub>	S <sub>4</sub> S <sub>9</sub>	XXI
Merla	GBR	S <sub>1</sub> S <sub>6</sub>	S <sub>1</sub> S <sub>6</sub>	XX

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Table 1. To be continued

Cultivar	Origin <sup>1</sup>	Detected S-alleles	Published S-alleles	IG <sup>2</sup>
Mermet	GBR	S <sub>3</sub> S <sub>6</sub>		VI
Merton Favourite	GBR	S <sub>3</sub> S <sub>6</sub>		VI
Merton Glory	GBR	S <sub>4</sub> S <sub>6</sub>	S <sub>4</sub> S <sub>6</sub>	XVII
Merton Premier	GBR	S <sub>2</sub> S <sub>3</sub>	S <sub>2</sub> S <sub>3</sub>	IV
Baltavarská	HUN	S <sub>3</sub> S <sub>4</sub>		III
Alfa	CHE	S <sub>3</sub> S <sub>4</sub>	S <sub>1</sub> S <sub>6</sub>	III
Basler Adlerkirche	CHE	S <sub>1</sub> S <sub>5</sub>	S <sub>1</sub> S <sub>5</sub>	XIV
Basler Langstieler	CHE	S <sub>1</sub> S <sub>2</sub>	S <sub>1</sub> S <sub>2</sub>	I
Beta	CHE	S <sub>1</sub> S <sub>5</sub>	S <sub>1</sub> S <sub>5</sub>	XIV
Delta	CHE	S <sub>5</sub> S <sub>6</sub>	S <sub>5</sub> S <sub>6</sub>	XV
Gamma	CHE	S <sub>1</sub> S <sub>6</sub>	S <sub>3</sub> S <sub>5</sub>	XX
Schöne von Marien	CHE	S <sub>1</sub> S <sub>2</sub>		I
Zweitfrühe	CHE	S <sub>5</sub> S <sub>6</sub>	S <sub>5</sub> S <sub>6</sub>	XV
Durone Nero 1	ITA	S <sub>1</sub> S <sub>3</sub>		II
Nero 1	ITA	S <sub>1</sub> S <sub>3</sub>		II
Nero 2	ITA	S <sub>3</sub> S <sub>4</sub>		III
Kišiněvskaia	MDA	S <sub>1</sub> S <sub>3</sub>		II
Skierniewice 1	POL	S <sub>2</sub> S <sub>3</sub>		IV
Skierniewice 3	POL	S <sub>2</sub> S <sub>3</sub>		IV
Skorospielka	RUS	S <sub>2</sub> S <sub>3</sub>		IV
Asenova raná	SRB	S <sub>3</sub> S <sub>9</sub>		XVI
Ladzanská 1	SVK	S <sub>1</sub> S <sub>13</sub>		0
Medňanská	SVK	S <sub>4</sub> S <sub>6</sub>		XVII
Huldra	SWE	S <sub>3</sub> S <sub>6</sub>	S <sub>1</sub> S <sub>3</sub>	VI
Rivan	SWE	S <sub>2</sub> S <sub>4</sub>	S <sub>1</sub> S <sub>2</sub>	XIII
Szwecija	SWE	S <sub>2</sub> S <sub>13</sub>		0
Valerij Tschkalov	UKR	S <sub>3</sub> S <sub>9</sub>	S <sub>1</sub> S <sub>9</sub>	XVI
Bing	USA	S <sub>1</sub> S <sub>3</sub>	S <sub>3</sub> S <sub>4</sub>	II
Gil Peck	USA	S <sub>1</sub> S <sub>3</sub>	S <sub>1</sub> S <sub>3</sub>	II
Hudson	USA	S <sub>1</sub> S <sub>4</sub>	S <sub>1</sub> S <sub>4</sub>	IX
Kristin	USA	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Lambert	USA	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Lapins	USA	S <sub>3</sub> S <sub>4</sub>	S <sub>3</sub> S <sub>4</sub>	III
Mona Cherry	USA	S <sub>3</sub> S <sub>4</sub>		III
Seneca	USA	S <sub>1</sub> S <sub>5</sub>	S <sub>1</sub> S <sub>5</sub>	XIV
Starking Hardy Giant	USA	S <sub>1</sub> S <sub>2</sub>	S <sub>1</sub> S <sub>2</sub>	I

<sup>1</sup>three-letter country codes, according to ISO3166-1 alpha-3; <sup>2</sup>incompatibility group, according to SCHUSTER (2012); IG 0 groups together different unique S-genotypes

by PCR markers in some S-genotype combinations (HANADA et al. 2014). Although the S-genotype must be hetero-allelic we did not detect a second

allele of the S-locus in Těchlovická and Drogans Gelbe. Another disadvantage of the PCR markers is that they cannot distinguish wild type S-alleles

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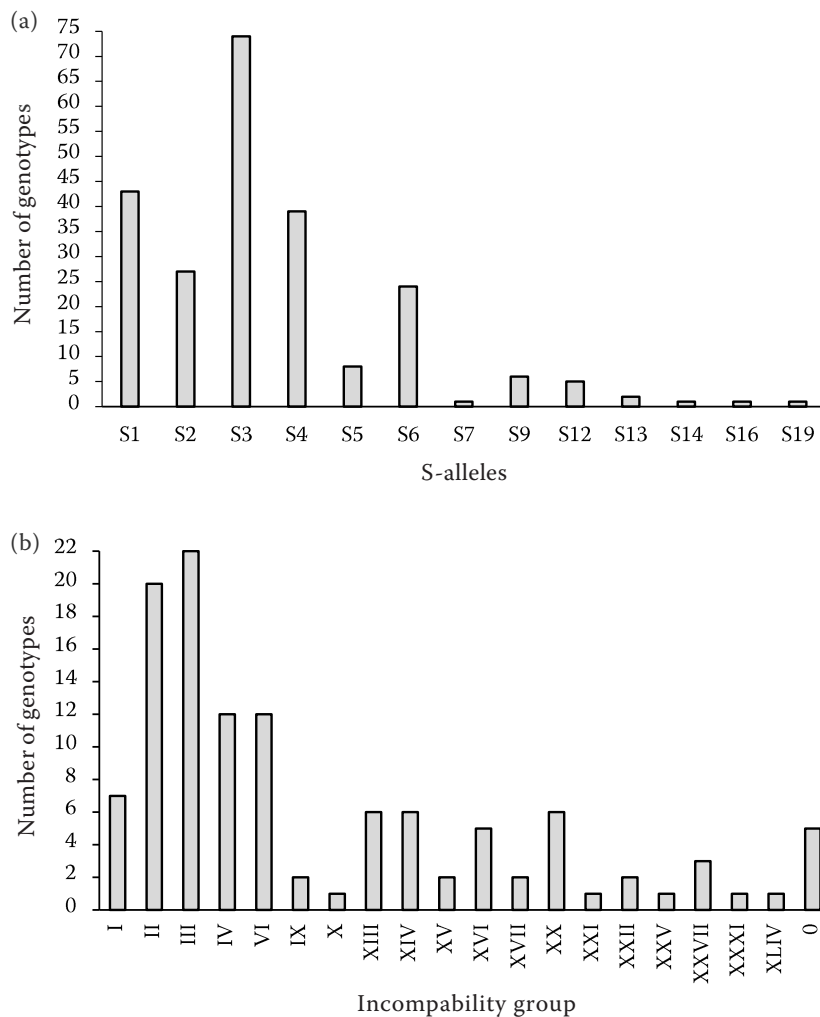


Fig. 1. The S-allele (a) and incompatibility group (b) frequencies within the studied cherry cultivars

from mutated S-alleles. Therefore, we could not exactly determine if the newly S-genotyped accessions were self-incompatible or self-compatible.

In our study, we proved that molecular PCR methods can be used for S-allele genotyping and for the rapid determination of the incompatibility groups in sweet cherry cultivars. It is mainly useful for the evaluation of old and local cherry cultivars and information for the breeders and growers.

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