International Journal of Horticultural Science 2006, 12 (2): 111–116
Agroinform Publishing House, Budapest, Printed in Hungary
ISSN 1585-0404

Review of sweet and sour cherry incompatibility

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Summary: Cherry incompatibility has widely been studied from the beginning of the twentieth century. As a consequence of the valuable results cherry has become a model for incompatibility research of other plant species. This study provides a detailed information about incompatibility of sweet and sour cherry based on several Hungarian and international literature sources from the last 100 years. The study gave details about the traditional and molecular base of incompatibility of sweet and sour cherry.

Key words: incompatibility, sweet cherry, sour cherry

Sweet cherry

(*Prunus avium* L.) is regarded as basically self-incompatible (*Garner*, 1914 cit. *Crane & Brown*, 1937) and cross-incompatibility among cultivars often occurs. Incompatibility studies of this species date back to 1929 when *Crane & Lawrence*, researchers at the John Innes Horticultural Institution, reported the first cross-incompatible cultivar pairs determined on the basis of outdoor pollination experiments. These authors were the first to attribute sweet cherry incompatibility to the gametophytically expressed factor *S*, that is multiallelic (with the series of so called *S*-alleles). Test pollinations by *Crane & Brown* (1937) aimed at demonstrating factor hypothesis in sweet cherry. Among the 66 cultivars tested they assigned 45 to 11 incompatibility groups within which all self- and cross-pollination fails. *Lewis* (1949) concluded that in sweet cherry the *S* factor has two parts – one expressed in the style and the other in the pollen – between which no recombination occurs.

Until recently sweet cherry compatibility was studied mostly by making traditional test crossings and monitoring seed set or pollen tube growth. In Switzerland, *Kobel* et al. (1938) had assigned alleles to cultivars; however, they used an allele labelling system that differs from the others published afterwards. *Matthews & Dow* (1969), drawing on test crossing results from the John Innes Institute and overseas, published the *S*-genotype of some 160 cultivars and reported the alleles from S_1 to S_6. This classic work became an important compilation for the scientists studying sweet cherry incompatibility. Attempts for assigning cultivars into incompatibility groups were made by researchers in other countries (e.g. *Nyéki*, 1989, Hungary; *Stösser*, 1966, Germany). By combining pollen tube growth and test-cross results the *S*-allele constitutions of several German cultivars were recently determined fully or partially (*Schmidt*, 1999). For pollen tube growth studies *Schmidt & Timmann* (1997) developed an *in vitro* method that was used for genotyping cultivars.

Sweet cherry was an entirely self-incompatible species until *Lewis & Crowe* (1954) raised the first self-compatible seedlings. Some of them were obtained by artificial mutation using X-irradiated pollen in nominally incompatible pollinations, others were derived from spontaneous mutation. Among mutated seedlings three were selected for further breeding work: the selections JI 2420 and JI 2434 were obtained from 'Emperor Francis' x 'Napoleon' (X-rayed pollen), whereas JI 2538 is a spontaneous mutant and came from selfing 'Merton 42' (*Matthews & Lapins*, 1967). In the selection JI 2420 the S_4 allele had mutated to S_4' where the prime symbol (') indicates a pollen part mutation (*Lewis & Crowe*, 1954; *Matthews*, 1970). In the case of JI 2434 there now appear to be two clones (the Ahrensburg clone and the East Malling clone - with different genotypes (*Schmidt* et al. 1999; *Bošković* et al., 2000).

The desirable aim of obtaining wholly self-compatible progenies could be achieved by using a self-compatible cultivar (e.g. Stella, S_3S_4') as pollen parent on a cultivar that has the same self-incompatible allele as the pollen parent (e.g. S_1S_3). *Bošković* et al. (1999) obtained hybrids homozygous for the self-incompatibility allele ($S_4'S_4'$) and when used as a pollen parent on any sweet cherry cultivar, the cross will yield only self-compatible seedlings.

In most cultivars it is the S_4' allele responsible for self-compatibility. 'Alex', a cultivar originating from Hungary (*Brozik & Apostol*, 2000) appeared to be the first self-compatible cultivar having S_3' conferring self-compatibility (*Sonneveld* et al. 2003).

The nature of the substance responsible for incompatibility interested several scientists. In cherry, *Mau* et al. (1982) from Melbourne University found a glycoprotein, "Antigen *S*" with two components which, it was proposed, corresponded to two *S*-alleles (cit. *Bošković & Tobutt*, 1996). An important milestone in sweet cherry

incompatibility studies was the work of *Bošković & Tobutt* (1996). At East Malling they extracted stylar proteins, separated them by isoelectric focusing (IEF) and stained for ribonuclease activity. Ribonuclease patterns of cultivars correlated with their *S*-genotypes. The correspondence of ribonucleases to *S*-alleles was supported by the report of *Bošković* et al. (1997) who analysed the segregation of stylar ribonucleases in six cherry progenies. The progeny of those parents having one allele in common segregated for two genotypes in a 1:1 ratio, whereas those having no common allele was found to segregate for four genotypes 1:1:1:1. On the basis of their earlier findings and the report of *McClure* et al. (1989) in solanaceous plants the authors concluded that ribonucleases in sweet cherry are indeed the products of the *S* locus. Continuing their work, *Bošković & Tobutt* (2001) by stylar ribonuclease analysis genotyped incompatibility groups X, XI, XII, the *S*-allelic constitutions of which had not previously been determined by *Matthews & Dow* (1969).

Tao et al. (1999) showed that the glycoproteins associated with *S*-alleles in sweet cherry have sequences consistent with *S*-RNases reported in *Solanaceae* (*Tsai* et al., 1992). The amino acid sequence of the alleles S_2, S_3 and S_6 were determined from cDNA clones (*Tao* et al. 1999) that was followed by sequencing the alleles S_1, S_4 and S_5 by *Sonneveld* et al. (2001) who designed allele-specific primers. PCR products obtained by these primers cosegregated with particular *S*-alleles in three cherry progenies analysed.

Primers based on the different conserved regions of the *S*-RNases amplifying the two intron regions (consensus primers) were designed. The primers amplifying the first intron of *Tao* et al. (1999) and *Wiersma* et al. (2001) are based on the C2 and C4 regions, whereas those designed by *Sonneveld* et al. (2003) on C2 and C5 (*Figure 1*). With the development of consensus and allele-specific primers by *Sonneveld* et al. (2003) and other methods mentioned here, identification of all known sweet cherry *S*-alleles became available.

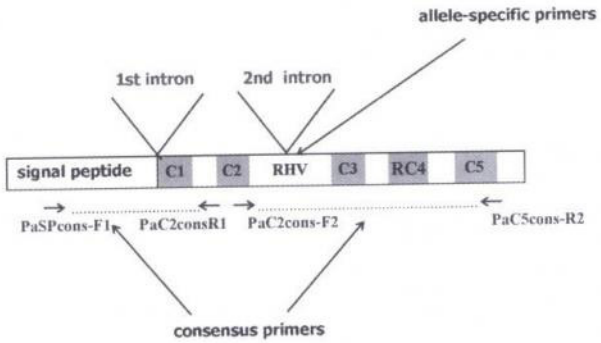

Figure 1 Structure of the *Rosaceae S*-RNase according to *Ushijima* et al. (1998) and primers designed by *Sonneveld* et al. (2001; 2003)

Early works on sweet cherry incompatibility resulted in the classic table of *Matthews & Dow* (1969) who reported six *S*-alleles (S_1 to S_6) and assigned cultivars into 13 incompatibility groups.

Molecular methods on the protein level aimed at identifying the alleles S_1, S_2 and S_6 (*Bošković & Tobutt*, 1996), but correlation of certain zymograms with S_4 and S_5 were confused by the incorrect genotypes assigned to Groups V and VII by *Matthews & Dow* (1969). The correct identification of S_4 and S_5 alleles was soon resolved (*Bošković* et al. 1997). The alleles S_1-S_5 could be distinguished by PCR analysis (*Tao* et al. 1999; *Wiersma* et al. (2001); however, their S_5 was actually S_9 as it turned out later (*Bošković & Tobutt*, 2001). Genuine S_5 allele can be identified with the primers of *Sonneveld* et al. (2001) as *Tao* et al. (1999) and *Wiersma* et al. (2001) used mistakenly genotyped cultivars when identifying S_5. Four putative new alleles were detected by *Wiersma* et al. (2001). However, among these their S_{13} is the same as S_{12} (*Bošković & Tobutt*, 2001) and S_{15} was identical to S_5 (*Tobutt* et al. 2001).

Later on additional five (S_7 to S_{11}), then three new alleles (S_{12} to S_{14}) were proposed (*Bošković* et al. 1997; *Bošković & Tobutt*, 2001). In the latter report the *S*-genotype of seventy cultivars that had been genotyped previously (*Matthews & Dow*, 1969) were checked, some were confirmed, the others were reassigned. The authors stressed the importance of choosing correctly genotyped cultivars as standards otherwise false results can be obtained.

Sonneveld et al. (2003) was able to identify all known *S*-alleles described until that time (S_1 to S_{14}). Some conflicting genotypes were clarified and *S*-genotypes were assigned to additional 18 cultivars. A new allele, labelled S_{16}, was identified, and two additional incompatibility groups were proposed.

Wünsch & Hormaza (2004) reported three putatively new alleles found in three local Spanish and Italian cultivars (labelled S_{23} to S_{25} as S_{17} to S_{22} was already found in wild cherries, as described later in this chapter). Their PCR products derived from amplification of the first and second introns of the *S*-RNase were cloned and sequenced. The fragment sizes obtained by the same consensus primer pairs used by *Tao* et al. (1999) and *Wiersma* et al. (2001) differed from the alleles S_1 to S_6 and S_9 therefore proposed as new alleles. However, the sequence of S_{23} matches that of S_{14} reported by *Bošković & Tobutt* (2001) and S_{25} corresponds to S_{21} (*De Cuyper* et al. 2005).

Tobutt et al. (2001, 2005) undertook the job of collating cultivar *S*-genotypes reported in recent years worldwide (East Malling, Ahrensburg, British Columbia, Kyoto, Michigan, New York, Zaragoza) and clarified confusing genotypes (*Table 1*). The latter paper gives the *S*-genotypes of 223 self-incompatible and 25 self-compatible cultivars (*Tobutt* et al. 2005). In this list there are 26 incompatibility groups, Group O of universal pollen donors, and Group SC, the self-compatible cultivars. This harmonisation table is an update that of *Matthews & Dow* (1969) providing useful information for growers and breeders. To date, 14 *S*-alleles have been found in cultivated sweet cherry - S_1 to S_{16} and S_{22} (*Bekefi* et al. 2003) among which S_7/S_{11}, S_3/S_8 and S_5/S_{15} are duplicates (*Sonneveld* et al. 2003). Additionally, a new incompatibility group, XXVII was proposed by *Bekefi* et al. (2003).

In recent years demand has arisen for *Prunus avium* as a

Table 1 (In)compatibility genotypes of sweet cherry cultivars (collated results from reports published until September 2003) – *Tobutt* et al. 2005[1]

Group I S_1S_2
Baumanns May A
Bedford Prolific A
Black Downton
Black Tartarian
Canada Giant
Carnation C
Early Rivers
Emperor Francis B
F1/3
Kastanka
Knight's Early Black
Nanni
Ronald's Heart
Roundel
Stark Hardy Giant
Sparkle
Summit
Ursula Rivers

Group II S_1S_3
Belle Agathe
Bigarreau de Schrecken
Black Elton
Caroon B
Cristalina
Erika
Frogmore Early
Gil Peck
Kouka-Nishiki
LaLa Star
Lamida
Merton Crane
Oktavia
Olympus
Regina
Ruby
Samba
Sonnet
Sumele
Tigre
Troprichterova
Valeska
Van
Venus
Vera
Victoria Black A
Waterloo
Windsor A

Group III S_3S_4
Angela
Belge
Bigarreau Esperen
Bing
Botond[2]
Büttners Späte Rote Kn.
Emperor Francis
Hedelfingen O[2]
Heinrichs Riesen
Kavics[2]
Kristin
Lambert
Late Maria
Marmotte
Münchebergi Korai[2]
Namare
Namosa
Napoleon
Querfurter Königskirsche
Solymári Gömbölyü[2]
Somerset
Star
Turkey Heart B
Ulster
Vernon
Yellow Spanish

Group IV S_2S_3
Allman Gulrod
Cavalier
Coralise
Kassins
Kentish Bigarreau
Knight's Bigarreau
Late Amber
Ludwig's Bigarreau
Merton Premier
Naresa
New Moon
Sue
Vega
Velvet
Victor
Viva
Vogue

Group V S_4S_5
Carmen[2]
Late Black Bigarreau
Turkey Heart

Group VI S_3S_6
Ambrusena
Anita[2]
Donnisens Gelbe Kn.
Durone Nero No. 3
Early Amber
Elton Heart
Governor Wood
Hartland
Kordia
Merton Heart
Merton Marvel
Nanyo
Pico Negro
Sasha
Satonishiki
Stark's Gold
Turkish Black

Group VII S_3S_5
Bigarreau Gaucher
Bilago
Black Eagle A
Bradbourne Black
Frühe Luxburger
Hedelfingen
Hooker's Black
Nadino
Tünde[2]

Group VIII S_2S_5
Malling Black Eagle
Mona BC
Vista

Group IX S_1S_4
Bada
Black Giant
Black Republican
Chinook
Dawson
Early Lyons
Garnet
Hudson
Merton Late
Merton Reward
Rainier
Rube
Republican
Salmo
Summer Jewel
Sylvia
Symphony
Viscount

Group X S_6S_9
Bigarreau de Jaboulay
Bigarreau de Mezel
Black Tartarian E
Early Lyons
Lyons
Penny
Ramon Oliva

Group XI S_2S_7
Cryall's Seedling
Early Purple (Hinode)
Gulgne d'Annonay

Group XII S_6S_{13}
Durona di Vignola III
Noble
Turca

Group XIII S_2S_4
Corum
Deacon
Mal Bigarreau
Namada
Noir de Schmidt
Ord
Patricia
Peggy Rivers
Royalton
Sam
Schmidt
Spalding
Szomolyai Fekete[2]
Tragana d'Edessis
Vic

Group XIV S_1S_5
Alma
Annabella
Basler Adler
Beta
Bianca
Noir de Guben
Secunda
Seneca
Valera

Group XV S_5S_6
Colney
Erianne
Trusenszkaja 2[2]
Zweitfrühe

Group XVI S_3S_9
Bigarreau Burlat
Bigarreau Moreau
Chelan
Mona MI
Nabigos
Naline
Naprumi
Precoce Bernard
Tieton
Winklerova Rana

Group XVII S_4S_6
Beni-Shuho
Elton Heart
Larian
Merton Glory
Nutberry Black

Group XVIII S_1S_9
Brooks
Earlise
Norbury's Early Black
Smoky Dun
Valerij Cskalov[2]

Group XIX S_3S_{13}
Reverchon
Sir Tom
Wellington A

Group XX S_1S_6
Alfa
Beni-Sakaya
Bowyer Heart
Hertford
Merla
Mermat
Rockport Big (Takasago)
Valery Chkalov

Group XXI S_4S_9
Inge
Merchant
Merpet
Summersun

Group XXII S_3S_{12}
Ferrovia
Germersdorfi 1[2]
Germersdorfi 3[2]
Linda[2]
Noir de Meched
Nordwunder
Princess
Schneider's Späte Kn.

Group XXIII S_3S_{16}
Strawberry Heart
Rodmersham Seedling

Group XXIV S_6S_{12}
Aida
Flamentiner

Group XXV S_2S_6
Arcina
Great Black Delicious
Knauffs Riesen

Group XXVI S_5S_{13}
Ferbolus
Goodnestone Black

Group XXVII S_4S_{12}
Katalin[2]
Margit[2]

Group O (Universal donors)
Castor S_1S_{12}
Charger S_1S_7
Dikkeloen S_5S_{14}
Krupnoplodnaja[2] S_5S_9
Orleans 171 S_7S_{10}
Rita[2] S_5S_{22}

Group SC (Self-compatibles, which are also universal donors)
Alex S_3S_3'
Blaze Star $S_4'S_6$
Celeste S_1S_4'
Columbia $S_4'S_9$
Cristobalina S_3S_6
Early Star $S_4'S_9$
Glacier $S_4'S_9$
Index S_3S_4'
Lapins S_1S_4'
Newstar S_3S_4'
Pál2 $S_4'S_9$
Peter S_3S_4'
Sándor[2] $S_4'S_9$
Sandra Rose S_3S_4'
Santina S_1S_4'
Sir Don $S_4'S_{13}$
Skeena S_1S_4'
Sonata S_3S_4'
Staccato S_3S_4'
Starkrimson S_3S_4'
Stella S_3S_4'
Sunburst S_3S_4'
Sumesi S_3S_4'
Sweetheart S_3S_4'
Tehranivee S_3S_4'
Temprana de Sot S_3S_6
Vandalay S_3S_4'

[1] For lack of space data are not published here sources by cultivar
[2] *Bekefi* et al. 2003

timber tree and for afforestation in Europe. Establishing seed orchards is essential, and thus, questions of pollination among wild cherry selections have become important. *De Cuyper* et al. (2005) genotyped 65 Belgian wild cherry accessions by using consensus and allele-specific primers developed by *Sonneveld* et al. (2001, 2003). 17 alleles were detected, among which six (S_{17} to S_{22}) appeared to be new. Among these wild accessions, 16 new incompatibility groups could be established. Interestingly, the alleles S_4 and S_5 were absent in wild cherries, whereas S_7, S_{10} and S_{12} to S_{16} were frequent in wild cherries but rare in sweet cherry cultivars grown for their fruit.

A brand new line in sweet cherry incompatibility studies is the identification and characterisation of the pollen part gene in which considerable achievements have been reached. *Yamane* et al. (2003a) found the pollen-part, the so-called F-box gene which is expressed specifically in the pollen. It found to be very close to the *S*-RNase gene and showed *S* haplotype-specifity (The term "haplotype" is used to mean variants of the *S*-locus, whereas alleles are variants of the genes).

Sonneveld et al. (2005) characterised the F-box gene in two self-compatible selections, namely JI 2420 (with S_4') and JI 2434 EM (with S_3'). It was shown that, unlike in certain Solanacea, self-fertility can not be attributed to duplication of the pollen-*S* gene in either selections. According to their findings it is more likely that a two component inhibitor model fits the SI reaction in sweet cherry, and perhaps in other genera, where a general inhibitor degrades all *S*-RNases, whereas *SFB* proteins protect self-RNases from inactivation. As the primers for amplifying the S_3-*SFB* and S_4-*SFB* are available, self-compatible seedlings can be selected soon after germination.

Sweet cherry incompatibility has been studied nearly for a century. However, since new molecular techniques appeared, knowledge on this research field has multiplied in the last ten years. Sweet cherry proved to be a very useful model for studies of incompatibility in *Rosaceae*, and significant achievements aimed at understanding better the genetics of incompatibility.

Sour cherry

(*Prunus cerasus* L.) is an allotetraploid species, a spontaneous hybrid between the diploid sweet cherry (*Prunus avium* L.) and tetraploid ground cherry (*Prunus fruticosa* Pall.). Some sour cherry cultivars are self-compatible, the others are fully or partially self-incompatible (*Crane & Lawrence*, 1929). Mutual and unilateral cross-incompatibility has either been reported (*Hruby*, 1963 cit. Tobutt et al. 2005; *Brozik & Nyéki*, 1975), even among self-compatible cultivars (*Nyéki* et al. 1992).

Inheritance of self-compatibility in sour cherry is not clear. For example, self-incompatible seedlings can be obtained when crossing two self-compatible selections (*Lansari & Iezzoni*, 1990).

The SI system in polyploid species are less clear-cut. Competitive interaction of the alleles in diploid pollen grains might be the explanation of the self-compatibility of some sour cherry cultivars. *Lewis & Modlibowska* (1942) presented evidence that, in pear, a heteroallelic pollen (e.g. S_1S_2) of a tetraploid plant would succeed on a style even if it has both alleles (e.g. $S_1S_1S_2S_2$) in common, whereas a homoallelic pollen (e.g. S_1S_1 or S_2S_2) fails.

The first study dealing with sour cherry *S*-RNases was of *Yamane* et al. (2001). In the 13 cultivars genotyped, RFLP analysis indicated the presence of S_1, S_4, S_6, S_9 and S_{12} sweet cherry alleles. Another five alleles were identified, distinct from S_1 to S_{12} sweet cherry alleles and labelled *Sa* to *Se*. Correspondence between self-compatibility and certain allele combinations could not be identified. In contrast to some solanaceous species, heteroallelic pollen alone does not cause self-compatibility in sour cherry.

Continuing their work, *Hauck* et al. (2002) made interspecific crosses between sour and sweet cherry cultivars and examined pollen tube growth. The cross of the sour cherry 'Crisana' ($S_1S_4S_d$) × the sweet cherry 'Rainier' (S_1S_4) was incompatible as was the reciprocal cross. This indicates that the stylar and pollen components in both species regarding these cultivars are functionally the same. The sequences of the S_4 and S_6-RNases in sour cherry were identical to the corresponding sweet cherry alleles.

Segregation analysis in a progeny from the cross 'Rheinische Schattenmorelle' ($S_aS_bS_cS_6$) × 'Érdi Bőtermő' ($S_aS_4S_{6m}$) helped understanding of the SI system in sour cherry (*Yamane* et al. 2001). On the basis of segregation data it was presumed that in 'Erdi Botermo' the allele S_4 is present in two copies, therefore its genotype is $S_aS_4S_4S_{6m}$. Interestingly, the S_{6m}-RNase allele was not present in the progeny. It is assumed that the S_{6m} *S*-RNase is not functionally active, in contrast to its pollen component, which is functional. This observation was confirmed (*Yamane* et al., 2003b) by expression analyses of the S_6-RNase and the pollen-part gene, SFB_6 (*Yamane* et al. 2003a). The pollen-component SFB_6 was found to be transcribed both in the S_6 and S_{6m} haplotypes. However, in the S_{6m} haplotype transcription of S_6-RNase failed, because of a 2600 bp insertion in the *S*-RNase gene that was not present in the fully functional S_6 allele. The S_{6m}-RNase in 'Erdi Botermo' derives from its pollen parent, 'Nagy Angol' and was ascribed to a natural mutation. Again, heteroallelic pollen did not seem to be universally compatible. None of the alleles segregated with SC, thus self-compatibility can not be attributed to a mutation in the *S*-RNase gene.

Another work on sour cherry incompatibility was performed by *Tobutt* et al. (2004). *S*-RNase pattern of 36 accessions were studied by IEF and NEPHGE. Four non sweet cherry alleles were found and labelled S_A, S_B, S_C and S_D. The allele S_B was found in several *P. fruticosa* accessions also studied, the remaining three were not. These alleles and derived genotypes could not be reconciled with the results and labelling of *Yamane* et al. (2001). Pollen tube growth and field test crosses in some sour x sweet cherry combinations proved that the observed *S*-RNases are functional. Sweet

cherry pollen was incompatible on those sour cherry styles having the same two *S* alleles. Thus the bands seen on the zymograms represented the corresponding *S* alleles in sour cherry. Progeny analysis from sour by sweet cherry crosses indicated disomic inheritance of *P. fruticosa* and *P. avium* genome in sour cherry.

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