

Incompatibility Alleles in *Corylus avellana* L. Cultivars*

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Summary. Pollen-stigma compatibility relationships are reported for 55 filbert cultivars (cvs) (*Corylus avellana* L.). A total of 11 S-alleles have been identified amongst 36 cvs for which one or both S-alleles have been established. For the 20 cvs with only one known allele and the 17 for which neither allele have been identified further information is provided as to which alleles can be excluded as possibilities.

Key words: *Corylus avellana* – Incompatibility – S-alleles – Filberts – Hazelnuts

Introduction

Self-incompatibility and cross-incompatibility were first reported for filberts (= hazelnuts), *Corylus avellana* L., by Schuster (1924) and Johansson (1927) and more recently by Thompson (1971) and Bergougnoux et al. (1978). Therefore, when selecting a cultivar (cv) to be used as a pollinizer in an orchard, or before attempting to make crosses for breeding, it is necessary to test pollen-stigma compatibility between potential combinations of cvs. This can be done rapidly and reliably by making pollinations on detached female flower clusters and subsequently squashing the styles and observing pollen tube growth by fluorescence microscopy. Knowledge of specific S-alleles associated with each cv, as well as the type of genetic control of incompatibility would greatly facilitate the choice of successful parental combinations. This paper consists of a progress report on the data accumulated thus far on S-alleles and compatibility relationships for 55 filbert cvs.

Materials and Methods

The cultivars (cvs) used for these studies are located at the Oregon State University Horticulture Research Farm, Corvallis, OR. Many are of European or Turkish origin; others are selections from chance seedlings in Oregon. Compatibility was determined by pollinating detached female flower clusters, placing them on moist filter paper in petri dishes, and allowing the pollen to germinate overnight in the laboratory (18-20°C). They were then stored in the freezer until it was convenient to prepare the squashes. For each pollen-pistil combination at least 3 pistillate clusters, each having 8-24 stigmatic styles, were pollinated and observed. The stigmatic styles were squashed directly in aniline blue (0.1 g aniline blue + 0.71 g K_3PO_4 + 100 ml distilled water) and pollen tubes were observed with a fluorescence microscope. Compatible crosses produce masses of long tubes while incompatible crosses form very short tubes which often terminate in a pronounced bulb. That these short tubes do not penetrate or adhere to the stigmatic cells is demonstrated by the fact that they are easily washed off if pollinated clusters are kept in a preserving fluid.

Much of the data was accumulated throughout 9 years of checking compatibility for possible hybridizations. However, as the study progressed and the identity of some S-alleles became established some of the undetermined cvs were tested with those having the known alleles. Cvs with 1 or 2 known alleles as well as those whose identity was completely unknown were used sometimes as the pistillate parent and sometimes as the pollen. As more S-allele genotypes become elucidated the series of tester cvs will expand. Thus, identification of new types will be facilitated.

Results

Partial or complete S-allele genotypes are given in Table 1 for some of the cvs studied. Initially I arbitrarily assigned the genotype S_1S_2 to 'Barcelona', the major U.S. cv. While both alleles were expressed in the pistil, S_1 was found to be dominant in the pollen. As additional alleles were identified in other cvs they were assigned succeeding numbers. The S-alleles of 'Extra Ghiagli' were designated S_xS_y temporarily because this cv was used in a parent and progeny diallele for genetic studies and the 2 distinct S-alleles which segregated have not been tested against the

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Table 1. Compatibility relationships for 55 clones of filberts, including for each clone 1) S-allele genotype, if established, 2) distinct pollen specificities and clones whose pollen specificity is unknown which are accepted by pistils, and 3) specific S-alleles in pistils and clones in which one or both pistil alleles are unknown which accept the pollen

Clone	Genotype ^a	Pistil accepts	Pollen accepted by
<i>C. avellana fusco-rubra</i>	<u>S₆</u>	S ₃	S ₁ , S ₂ , S ₃ , S ₅ , S ₁₁ , Daviana Ennis, Hall's Giant
Badem Barcelona	<u>S₁S₂</u>	S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _x , Badem, Bandnuss, Buchanan, DuBearn, Fitz- gerald, Gem, Henneman # 2, Imperial de Trebizonde, Luisen, Neue Riesennuss, Nooksack, Nottingham, Potomac, Tonda Rossa, Segorbe	S ₁ , S ₂ , S ₃ , S ₆ , S ₉ , S ₁₀ , S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₁₀ , S ₁₁ , Bandnuss, Bollwiller, Compton, Daviana, Gem, Gironenc, Hall's Giant, Imperial de Trebizonde, Negret, Neue Riesennuss, Nooksack, Tombul Ghiaghli, Tonda di Giffoni
Bellhusker # 2	<u>S₂S₃</u>	S ₁ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , Italian Red, Segorbe	S ₁ , S ₂ , S ₅ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Ennis, Gem, Hall's Giant, Negret, Tonda Bianca
Brixnut Buchanan	<u>S₁</u>	S ₅	S ₁ , S ₂ , S ₃ , Daviana
Butler	<u>S₂S₃</u>	S ₁ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _x	S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₁₀ , S ₁₁ , Bollwiller, Ennis, Gem, Hall's Giant, Negret, Tonda Bianca, Tonda di Giffoni
Campanica Compton	<u>S₁S₂</u> <u>S₃</u>	S ₃ , S ₆ , S ₇ S ₁ , S ₅ , S ₆ , S ₇	S ₂ , S ₃ , S ₇ , S ₁₁ S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₈ , S ₁₀ , S ₁₁ , Ennis, Goodpasture, Hall's Giant, Tombul Ghiaghli
Cosford Creswell	<u>S₃</u> <u>S₂S₁₀</u>	S ₁ , S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , Sivri Ghiaghli, Imperial de Trebizonde	S ₁ , S ₂ , S ₅ , S ₆ , S ₉ , S ₁₀ , S ₁₁ S ₁ , S ₂ , S ₃ , S ₅ , S ₉ , S ₁₁ , Bollwil- ler, Daviana, Ennis, Gem, Tonda Bianca
Daviana	<u>S₃</u>	S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _x , Badem, Buchanan, Gem, Imperial de Trebizonde, Italian Red, Mortarella, Neue Riesennuss, Nottingham, Pallaz, Potomac, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₁₀ , S ₁₁ , Ennis, Hall's Giant, Ryan
DuBearn Ennis	<u>S₁</u>	S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₁₀ , S _x , Neue Riesennuss, Nottingham, Potomac, White Aveline	S ₁ , S ₂ , S ₃ , Imperatrice Eugenie S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₁₀ , S ₁₁ , Compton, Daviana, Hall's Giant
Extra Ghiaghli	<u>S_xS_y</u>		S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Daviana, Ennis, Negret, Tonda di Giffoni
Fitzgerald 20	<u>S₂S₁₁</u>	S ₁ , S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _x , Gem, Imperial de Trebizonde, Italian Red, Mortarella, Neue Riesennuss, Nottingham, Potomac, Ribet, Segorbe, Sivri Ghiaghli, White Aveline	S ₁ , S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₁₀ , Compton, Daviana, Ennis, Hall's Giant, Ryan, Tombul Ghiaghli
Gassoway Gem	<u>S₃</u> <u>S₂</u>	S ₁ , S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , Badem, Imperial de Trebizonde, Italian Red, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₇ , Ennis S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Daviana, Negret, Neue Riesennuss, Tonda di Giffoni
Gironenc		S ₁	

Table 1 (Continuation).

Clone	Genotype ^a	Pistil accepts	Pollen accepted by
Hall's Giant	<u>S₅</u>	S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₈ , Mortarella, Nottingham	S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Brixnut, Compton, Daviana, Ennis, Gem, Neue Riesennuss, Ryan, Tonda Bianca
Henneman # 3	<u>S₆S₁₀</u>	S ₁ , S ₂ , S ₃ , S ₅ , S ₇ , S ₉ , S _X , Badem, Gem, Italian Red, Mortarella, Neue Riesennuss, Pallaz, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₃ , S ₅ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Compton, Daviana, Ennis, Gem, Hall's Giant, Negret, Neue Riesennuss, Ryan, Tonda Bianca, Tonda di Giffoni
Imperatrice Eugenie	<u>S₃</u>	S ₁ , S ₂ , Nottingham, White Aveline	
Imperial de Trebizonde		S ₁	S ₁ , S ₂ , S ₃ , S ₅ , S ₇ , S ₉ , S ₁₀ , Bollwiller, Daviana, Gem, Neue Riesennuss, Tonda di Giffoni
Italian Red			S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Daviana, Gem, Neue Riesennuss, Negret, Tonda di Giffoni
Jemtegaard 5	<u>S₂S₃</u>	S ₁ , S ₆ , S ₈ , Italian Red, Mortarella, Neue Riesennuss, Potomac, White Aveline	S ₁ , S ₂ , S ₅ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Ennis, Hall's Giant, Ryan
Jemtegaard 20			S ₁ , S ₂ , S ₇ , S ₁₀ , S ₁₁ , Negret
Jemtegaard 21	<u>S₁</u>		S ₂ , S ₃ , S ₇ , Gironenc, Imperatrice Eugenie, Luisen, Nottingham, Tonda di Giffoni
Kruse	<u>S₁S₂</u>	S ₃ , S ₅ , S ₆ , S ₇ , S ₈ ,	S ₂ , S ₃ , S ₇ , S ₁₀ , S ₁₁
Lansing	<u>S₁S₃</u>	S ₂ , S ₅ , S ₆ , S ₇ , S ₈ , W4-6	S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Ennis, Hall's Giant
Montebello	<u>S₁S₂</u>	S ₃ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , Badem, Segorbe	S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₁₀ , S ₁₁ , Compton, Daviana, Hall's Giant, Tonda di Giffoni
Mortarella			S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₉ , S ₁₀ , S ₁₁ , Daviana, Hall's Giant, Negret
Negret	<u>S₁₀</u>	S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₈ , S _X Badem, Gem, Italian Red, Jemtegaard 20, Mortarella, Neue Riesennuss, Potomac, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₃ , S ₇ , S ₉ , S ₁₁ , Daviana, Ennis, Gem, Neue Riesennuss, Tonda di Giffoni
Neue Riesennuss		S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₁₀ , Gem, Imperial de Trebizonde, Italian Red, Pallaz, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₃ , S ₆ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Daviana, Ennis, Negret
Nonpareil	<u>S₁S₃</u>	S ₂ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _X , Badem, Gem, Imperial de Trebizonde, Italian Red, Mortarella, Neue Riesennuss, Pallaz, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Ennis, Gem, Negret, Neue Riesennuss, Tonda Bianca, Tonda di Giffoni
Nooksack Nottingham		S ₁	S ₁ , S ₂ , S ₁₁ , Ennis S ₁ , S ₂ , S ₃ , S ₅ , S ₁₁ , Daviana, Ennis, Hall's Giant, Imperatrice Eugenie
Pallaz			S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₉ , S ₁₀ , Bollwiller, Daviana, Negret, Tonda di Giffoni
Pearcy 14	<u>S₁S₃</u>	S ₂ , S ₅ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _X , Badem, Gem, Imperial de Trebizonde, Italian Red, Neue Riesennuss, Pallaz, Segorbe, Sivri Ghiaghli	S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Gem, Negret, Tonda Bianca

Table 1 (Continuation).

Clone	Genotype ^a	Pistil accepts	Pollen accepted by
Potomac			S ₁ , S ₂ , S ₃ , S ₁₀ , S ₁₁ , Daviana, Ennis, Negret
Ribet			S ₂ , S ₁₁
Riccia di Talanico	<u>S₁</u> S ₂	S ₃ , S ₆ , S ₇ , S ₁₀ , S _X , Badem, Gem, Imperial de Trebizonde, Jemtegaard 20, Mortarella, Neue Riesennuss, Potomac, Segorbe, Sivri Ghiaghli	S ₂ , S ₃ , S ₅ , S ₇ , S ₁₁ , Hall's Giant
Rode Zeller	<u>S₆</u>	S ₁ , S ₇	S ₁ , S ₂ , S ₃ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Daviana, Gem, Negret, Tonda Bianca
Royal	<u>S₃</u>		S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Gem, Neue Riesennuss, Tonda di Giffoni
Ryan	<u>S₁</u>	S ₂ , S ₃ , S ₅ , S ₆	S ₂ , S ₃ , S ₅ , S ₇ , S ₈ , S ₁₀ , S ₁₁ , Compton, Daviana, Hall's Giant, Tombul Ghiaghli
Segorbe			S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Daviana, Gem, Neue Riesennuss, Tonda di Giffoni
Sivri Ghiaghli			S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Neue Riesennuss, Tonda Bianca, Tonda di Giffoni
Tombul			S ₁ , S ₂ , S ₃ , S ₇
Tombul Ghiaghli	<u>S₄</u> <u>S₈</u>	S ₁ , S ₂ , S ₃ , S ₇	S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Daviana, Ennis, Gem, Hall's Giant, Imperatrice Eugenie, Negret, Tonda di Giffoni
Tonda Bianca	<u>S₁</u>	S ₃	S ₂ , S ₃ , S ₇ , S ₁₀ , S ₁₁ , Negret, Tonda Bianca
Tonda di Giffoni	<u>S₂</u>	S ₁ , S ₃ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , S _X , Badem, Gem, Imperial de Trebizonde, Italian Red, Pallaz, Segorbe, Sivri Ghiaghli, White Aveline	S ₁ , S ₃ , S ₅ , S ₆ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Daviana, Ennis, Hall's Giant, Imperatrice Eugenie, Negret, Neue Riesennuss, Tonda Bianca
Tonda Gentile Delle Langhe	<u>S₂</u> <u>S₇</u>	S ₁ , S ₃ , S ₅ , S ₆ , Jemtegaard, 20, Luisen, Tombul	S ₁ , S ₂ , S ₃ , S ₅ , S ₆ , S ₈ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Compton, Daviana, Ennis, Gem, Hall's Giant, Imperatrice Eugenie, Negret, Neue Riesennuss, Rode Zeller, Tonda di Giffoni, Tombul Ghiaghli
White Aveline			S ₁ , S ₂ , S ₃ , S ₁₁ , Ennis, Imperatrice Eugenie, Tonda di Giffoni
Woodford	<u>S₃</u>		S ₁ , S ₂ , S ₅ , S ₆ , S ₇ , S ₉ , S ₁₀ , S ₁₁ , Bollwiller, Negret, Tonda di Giffoni
Wunder von Bollwiller ^b	<u>S₅</u>	S ₁ , S ₂ , S ₃ , S ₆ , S ₇ , S ₈ , S ₉ , S ₁₀ , Badem, Gem, Imperial de Trebizonde, Neue Riesennuss, Pallaz, Sivri Ghiaghli, W4-6	S ₁ , S ₂
W4-6	<u>S₆</u>		S ₁ , S ₂ , S ₃ , S ₅ , S ₇ , S ₉ , S ₁₀ , S ₁₁

^a Pistil genotypes were established on the basis of rejection of pollen bearing specific alleles. The underlined allele is dominant in the pollen

^b Wunder von Bollwiller equals Bollwiller

11 established alleles. The recessive alleles in 'Fitzgerald 20' (S_{11}) and in 'Tombul Ghiaghli' (S_4), while not discovered in pollen of any clone as yet, are known to exist because they segregated in progeny of crosses involving these cvs ('Fitzgerald 20' \times 'Lansing' and 'Barcelona' \times 'Tombul Ghiaghli'). By intercrossing sibs bearing these recessive alleles it will be possible to produce homozygotes, S_4S_4 and $S_{11}S_{11}$ in the next generation and thus pollen of S_4 and S_{11} specificity.

Additional information is also provided which permits the exclusion of certain S-alleles as possibilities for specific cvs. This is based on the assumption that whenever pistils accept pollen these pistils do not contain the S-allele borne by that pollen. Likewise, if the pollen of an unknown cv is accepted by a pistil with known alleles, or a clone with unknown alleles, it follows that the pollen specificity can not be identical to the alleles in those pistils. In all clones studied to date, whether 1 or both alleles have been identified, pollen has borne only 1 specificity, which implies dominance. However, in many cvs 2 specificities have been recognized in the pistils, indicating independent action of the 2 alleles. In those clones whose pistils have, as yet, revealed only 1 specificity, 3 explanations are possible: 1) there is dominance, 2) the plant is homozygous for the S-allele, or 3) the allele has not been identified because a clone bearing pollen with the same specificity has not been tried on the pistils. In 'Daviana', only 1 specificity (S_3) has been identified in both pollen and pistil although pollen of numerous clones has been tried on 'Daviana' pistils. It can be concluded that, unless S_3 is dominant in the pistil, the second S-allele cannot be S_1 , S_2 , S_5 , S_6 , S_7 , S_8 , S_9 , S_{10} , or S_x , nor can it have identity with the pollen of several cvs whose specificities are unknown, namely 'Badem', 'Buchanan', 'Gem', 'Imperial de Trebizonde', 'Italian Red', 'Mortarella', 'Neue Riesennuss', 'Nottingham', 'Pallaz', 'Potomac', 'Segorbe', or 'Sivri Ghiaghli'. Unless a second allele is identified in 'Daviana' by screening pollen of additional clones, progeny tests will be necessary to distinguish the 3 alternative explanations.

In 'Gem', only the allele which is recessive in the pollen has been identified. 'Gem' pistils reject S_2 pollen from other cvs but 'Gem' pollen is not rejected by pistils known to have S_2 . Because 'Gem' pollen is not rejected by pistils bearing S_1 , S_2 , S_3 , S_5 , S_6 , S_7 , S_9 , S_{10} , S_{11} or by 'Bollwiller', 'Daviana', 'Negret', 'Neue Riesennuss', and 'Tonda di Giffoni' (cvs having 1 or both unknown S-alleles) its specificity cannot be the same as these alleles or the same as any allele in the unknown cvs. For certain cvs such as 'Italian Red', 'Mortarella', 'Nottingham', and 'Pallaz' which have been tested as pollen only, conclusions have been drawn only about which particular S-allele specificity the pollen cannot possess. All clones tested thus far are self-incompatible.

Discussion

Early in this study, considerable cross-incompatibility was found amongst cvs and selections being used for breeding. It became evident that there was a preponderance of S_1 , S_2 , and S_3 . Therefore, it was concluded that many of the named selections originating in Oregon as chance seedlings were related to 'Barcelona' (S_1S_2) and/or 'Daviana' (S_3S_7), the 2 most common cvs in this region. Included are 'Bellhusker 2' (S_2S_3), 'Brixnut' (S_1S_7), 'Compton' (S_3S_7), 'Creswell' (S_2S_{10}), 'Ennis' (S_1S_7), 'Fitzgerald 20' (S_2S_{11}), 'Gassoway' (S_3S_7), 'Gem' (S_2S_7), 'Jemtegaard 5' (S_2S_3), 'Jemtegaard 21' (S_1S_7), 'Kruse' (S_1S_2), 'Lansing' (S_1S_3), 'Nonpareil' (S_1S_3), 'Nooksack' (S_1S_7), 'Pearcy 14' (S_1S_3), 'Royal' (S_3S_7), 'Ryan' (S_1S_7), and 'Woodford' (S_3S_7). Less clear is why 6 of the 7 Italian cvs examined also have S_1 and/or S_2 , e.g. 'Campanica' (S_1S_2), 'Montebello' (= 'Santa Maria de Gesu') (S_1S_2), 'Riccica di Talanico' (S_1S_2), 'Tonda Bianca' (S_1S_7), 'Tonda di Giffoni' (S_2S_7), and 'Tonda Gentile Delle Langhe' (S_2S_7). For the other Italian cv, Mortarella, whose S-alleles have not been identified, S_1 and S_2 can be excluded, at least as the pollen specificity.

Thus far, although only 11 S-alleles have been confirmed, I expect that as the identity of the undetermined cvs in this study becomes established several more S-alleles will become evident. Further, additional cvs as well as representatives from wild populations in diverse geographic regions should provide even more S-alleles. Since this species ranges widely throughout Europe from Ireland and Portugal in the west to the Caucasian region and the Ural Mountains in the east (Kasaplilgil 1968) it should contain considerable diversity in S-alleles as in other genetic traits.

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