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Revised dominance hierarchy for S-alleles in *Corylus avellana* L.

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Abstract Pollen-stigma compatibility was studied in cultivars and more than 1800 seedlings of the European hazelnut (*Corylus avellana* L). Four new S-alleles were identified, bringing the total to 25 unique alleles within *C. avellana*. The new alleles are the recessive alleles in 'Tonda di Giffoni' and 'Segorbe' (S_{23}), in 'Neue Riesennuss' (S_{25}), in 'Gasaway' (S_{26}), and a dominant allele in a seedling of Turkish origin (S_{24}). Dominance relationships in 233 of the possible 300 pairs of alleles were determined in both pistil and pollen. All alleles exhibited independent action in the pistil, whereas in the pollen either dominance or codominance was exhibited. The dominance hierarchy of alleles in the pollen was revised in light of the new information obtained. All 25 alleles have been assigned to a level in the hierarchy that is linear and now has eight levels. S_6 and S_9 were reassigned to lower levels in the hierarchy. Thirteen of the alleles are on the level of S_1, while S_4, S_6, S_{11}, and S_{23} occupy unique positions in the hierarchy. Improved pollen tester clones were identified for several S-alleles. The alleles in 55 cultivars were determined. The alleles identified in 'DuChilly' (S_{10} S_{14}) did not agree with previous reports. Four cultivars have the same alleles as 'Römische Nuss' (S_{10} S_{18}) and are morphologically indistinguishable from it: 'Fruttogrosso', 'Istarski Okrogloplodna', 'Payrone', and 'Romai'. 'Belle di Giubilino' and 'Tonda di Biglini' are both S_1 S_{10} and appear to be synonyms for the same cultivar.

Key words Incompatibility · Hazelnut · Filbert · S-alleles · Corylus

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Introduction

Self-incompatibility in hazelnut (*Corylus avellana* L.) is of the sporophytic type and under the control of a single locus with multiple alleles (Thompson 1979a). One-locus sporophytic incompatibility is common in the Compositae and Cruciferae; examples include *Ageratum houstonianum* Mill. (Stephens et al. 1982), *Carthamus flavescens* Spreng (Imrie and Knowles 1971), and *Brassica campestris* L. (Richards and Thurling 1973). Ockendon (1974) identified more than 40 S-alleles in *Brassica olearacea* L. In hazelnut, the stigmatic surface is the site of the incompatibility reaction (Hampson et al. 1993). In incompatible pollinations, pollen germination is delayed, and pollen tubes are distorted and fail to penetrate the stigma.

In a previous report (Thompson 1979b), 11 alleles were identified in hazelnut. Mehlenbacher and Thompson (1988) reported 10 additional alleles from *C. avellana* and S_{13} from the interspecific hybrid Chinese Trazel Gellatly #4. All alleles were found to be codominant in the pistil, whereas in the pollen alleles exhibited either dominance or codominance. The dominance relationship of alleles in the pollen was linear with seven levels. The objective of the study presented here was to locate additional S-alleles, to determine the dominance relationships among all known S-alleles in *C. avellana*, and to identify the S-alleles in additional cultivars.

Materials and methods

The seedling trees used in this study resulted from controlled crosses made as part of the breeding program at Oregon State University (OSU), Corvallis, Ore. Trees of named cultivars were in the collection at the OSU Smith Horticulture Research Farm or at the nearby United States Department of Agriculture's National Clonal Germplasm Repository in Corvallis. The cultivars were imported from Europe and constitute a very diverse gene pool.

Branches were marked for emasculation and staminate catkins clipped in early to mid-December. Emasculated branches were bagged with Tyvek housewrap (DuPont, Wilmington, Del.) to protect female inflorescences from wind-borne pollen when they emerged 2–10 weeks later (Smith and Mehlenbacher 1994). A second bag of either polyester muslin or Tyvek was used to cover and protect the inner bag from damage by wind. In a few cases, small emasculated trees were enclosed in wooden frames covered with white polyethylene for the purpose of making controlled pollinations. In all cases, only females from bagged branches or enclosed trees were used, as unprotected flowers are often pollinated prior to collection under field conditions and do not allow reliable discrimination between compatible and incompatible pollinations.

When staminate catkins had elongated and were about to shed, they were collected, placed on a sheet of paper in the laboratory, and allowed to dry overnight at room temperature (20°C). The following morning, the catkins were discarded and the pollen collected and stored in cotton-stoppered vials in the freezer (− 20°C). Pollen was collected from seedling trees and tester parents whose alleles had been previously identified (Table 1).

Female clusters were detached from bagged limbs when styles protruded 2–6 mm and placed in petri dishes on a double layer of moist filter paper. Pollinations were performed in the laboratory as soon as possible after collection by dipping the stigmatic styles in the appropriate vial of pollen, shaking off excess pollen, and leaving the flowers in the covered petri dish overnight. Two flower clusters, each consisting of several styles, were used for most of the pollinations. The stigmatic styles were detached from the buds and squashed the following morning (about 16 h after pollination) in aniline blue dye [0.1 g aniline blue (methyl blue No. M-5528, Sigma Chemical Company, St. Louis, Mo), 0.71 g K_3PO_4, 100 ml distilled water] and examined with a fluorescence microscope. In an incompatible cross, pollen germination is often reduced, and the pollen grains that do germinate produce short tubes that fail to penetrate the stigmatic surface. Many of these tubes terminate in a pronounced bulb. Compatible pollen germinates well, and the tubes penetrate the stigmatic surface and produce a mass of long parallel tubes with strongly fluorescing callose plugs. When fresh, unpollinated female flowers and viable tester pollen are used, the two reactions are quickly and easily distinguished (Thompson et al. 1996).

Fresh female clusters were used whenever possible. Occasionally, female flowers were held on moist filter paper in petri dishes in the refrigerator for 1 or 2 days prior to pollination. Flower quality declines when they are held for longer periods. Similarly, some flowers were pollinated, incubated overnight at room temperature, and refrigerated for up to 2 days until time permitted microscopic examination. Pollinated flowers were never frozen, as this leads to a darkening of stylar tissue and difficulty in reading the results.

The seedlings used in this study resulted from controlled pollinations. Many of the crosses were made for the specific purpose of creating new combinations of S-alleles. The search for new combinations began by bagging the branches of about 15 precocious seedlings in each progeny when they started to flower, 3 or 4 years after planting in the field. Pollen was collected from these seedlings as well as from the testers listed in Table 1. The female inflorescences collected from the seedlings were pollinated with four tester pollens, one for each allele present in the parents. When a seedling representing a new pair of S-alleles was identified, its pollen was placed on female inflorescences that expressed one of the seedling's two alleles, the other allele being different. If one of these pollinations was compatible and the other incompatible, the allele common to both parents in the incompatible pollination was dominant to the other allele in the seedling. If both pollinations were incompatible, the two alleles in the seedling were considered to be codominant in its pollen. Females of a third genotype expressing different alleles were pollinated to verify that the seedling's pollen was viable. For example, female inflorescences from seedlings of the cross 'Brixnut' (S_1 S_{14}) × 'Segorbe' (S_9 S_{23}) were tested with pollen from testers for S_1, S_9, S_{14}, and S_{23}. S_9 and S_{14} pollen were incompatible on seedling 552.167, but S_1 and S_{23} were compatible. Seedling 552.167 thus had genotype S_9 S_{14}. Pollen of 552.167 was incompatible on 'Gem' (S_2 S_{14}) but compatible on 456.005 (S_3 S_9); thus S_{14} was dominant to S_9. The dominance relationship for each new pair of alleles was confirmed by testing a second seedling with the same pair of alleles or by retesting the same tree the following year.

Table 1 Pollen testers for incompatibility alleles in hazelnut

Alleles	Tester	Alleles in tester	
1	Barcelona	1	2
	Montebello	1	2
2	OSU 20.058	2	2
3	Nonpareil	1	3
	Willamette	1	3
4	OSU 194.001	4	4
5	Badem	2	5
6	Henneman #3	6	10
	OSU 179.061	2	6
7	Tonda G. d. Langhe	2	7
	OSU 278.095	4	7
8	Tombul Ghiaghli	4	8
9	Segorbe	9	23
10	Imp. de Trebizonde	2	10
11	OSU 278.121	4	11
12	Extra Ghiaghli	4	12
13	USOR 98–83	6	13
14	Gem	2	14
15	OSU 39.044	11	15
	GN 66(3)AF5	11	15
16	OSU 485.010	11	16
17	Mortarella	2	17
18	Neue Riesennuss	18	25
19	OSU 452.026	4	19
20	Kadetten	20	25
21	OSU 168.026	2	21
22	OSU 219.133	4	22
23	OSU 385.003	4	23
24	OSU 54.041	4	24
25	Ordu	4	25
26	OSU 447.015	26	26

Alleles expressed in the pollen are underlined.

Cultivars carrying an unknown allele were crossed with selections carrying S_4 or S_{11} which Mehlenbacher and Thompson (1988) had shown to be low in the dominance hierarchy, and the resulting seedlings were tested with the expectation of confirming the presence of a new S-allele and identifying a tester for it. Reciprocal crosses were made to determine if the new allele was expressed in the pollen of the seedling. A seedling was a suitable tester if it expressed the new allele in its pollen. Testers that expressed a single allele in their pollen were preferred over testers with codominant alleles. The production of pollen in abundance during the first half of the season was also desired.

The identification of alleles in cultivars was conducted similarly. As cultivars were added to the collection, branches were emasculated and bagged, female inflorescences were collected when fully receptive, and 2 were dipped in the pollen of each tester. If 2 of the 25 pollens gave incompatible reactions, while the remaining 23 were compatible, the 2 alleles had been identified. Some tests were inconclusive and the number of flowers was limited, so completion of these tests on a single cultivar often required 2–3 years. A single incompatible reaction and 24 compatible reactions indicated either the presence of 1 known and 1 unknown allele or homozygosity.

Results

An additional four S-alleles have been identified since our last report (Mehlenbacher and Thompson 1988),

bringing the total number within *C. avellana* to 25. S_{13} from the interspecific hybrid Chinese Trazel Gellatly #4 was not included in this study. The second allele in 'Tonda di Giffoni' was unknown at the start of this study. A seedling from the cross 'Extra Ghiaghli' (S_4 S_{12}) × 'Tonda di Giffoni' (S_2 $S_?$) which carried S_4 but not S_2 or S_{12} was found, and its pollen was incompatible on 'Tonda di Giffoni' but compatible on 'Barcelona' (S_1 S_2). This seedling, OSU 385.006, was assigned alleles S_4 S_{23} and is now our tester for S_{23}. Use of this tester indicated that S_{23} was present as the recessive allele in both 'Segorbe' and 'Tonda di Giffoni'. S_{24} is the dominant allele in OSU 54.041, a selection grown from seed collected on the Black Sea coast of Turkey. Pollen of this selection is compatible on all other testers. S_{25} was identified as the dominant allele in a Turkish selection designated 'Ordu' imported from the University of Torino, Italy. Use of 'Ordu' pollen confirmed the presence of S_{25} in 'Neue Riesennuss', 'Pallagrossa', 'Kadetten', and selection B-3 from the former Yugoslavia. A tester for S_{26} was identified in a seedling from the backcross of selection VR 15–14 to its parent 'Gasaway'. Pollen of this tester, OSU 447.015, confirmed the presence of S_{26} in the Spanish cultivar 'Sant Pere'.

Seedlings or cultivars were identified that represent 233 of the 300 possible pairs of alleles (Table 2), a marked increase from the 75 pairs studied by Mehlenbacher and Thompson (1988). The number of pairs was limited for the most recently identified alleles S_{24}, S_{25}, and S_{26}, but nearly all combinations were observed for the other alleles. Nevertheless, the number of crosses was sufficient to allow assignment of all alleles, including the 3 most recently identified, to levels in the dominance hierarchy (Fig. 1). This hierarchy consists of eight levels in hazelnut pollen. Of the 25 alleles 13 are on the same level, while S_6, S_{19}, S_{23}, and S_4 occupy unique levels in the hierarchy. S_4 is particularly useful in developing testers for new S-alleles, as it is recessive to all known alleles and would likely be recessive to any newly identified allele. Of the 5 most recently identified testers 4 carry S_4 in addition to the new allele. Two of these were found in Turkish selections; the other 3 were identified in seedlings segregating for S_4 and the previously unidentified allele.

In light of the new information acquired in this study, S_6 and S_9 were reassigned to lower levels in the dominance hierarchy. The hierarchy presented by Mehlenbacher and Thompson (1988) was based on a much smaller number of pairs of alleles. S_6 was known to be dominant to S_1 and 5 other alleles, and was believed to be dominant to S_3. The S_3 S_6 trees available at that time, however, produced poor quality pollen, and results on the dominance relationship in this pair were not conclusive. The recently tested selection OSU 514.080 ('Willamette' × OSU 26.072) produces pollen of excellent quality, and results clearly indicate that S_3 is dominant to S_6. Notes indicate that the misclassification of the other allele, S_9, was due to the use of old females of 'Segorbe' when testing pollen of an S_3 S_9 tree (selection H 143–6 from Bordeaux, France). The poor germination of H 143–6 pollen on 'Segorbe' females was interpreted to mean that the combination was incompatible. Subsequent studies have shown that 'Segorbe' females often give poor reactions, even when fresh; females of 456.005 and a few other seedlings that carry S_9 but which give sharply contrasting responses between compatible and incompatible pollinations are now used for this allele.

Improved testers are now available for several alleles, and pollen of each tester currently in use expresses a single allele. 'Tonda Gentile delle Langhe' sheds pollen very early in the season, and in some years the quantity and viability are low. OSU 278.095, which sheds slightly later and produces large quantities of excellent quality pollen, has replaced 'Tonda Gentile delle Langhe' as a tester for S_7. The early-shedding selection OSU 278.121 has replaced OSU 28.091 as the tester for S_{11}. Although OSU 28.091 produces large quantities of excellent pollen, it does not shed until the end of the testing season at which time females of early-flowering types are too old to be reliably used for testing. OSU 39.044 pollen expresses only S_{15} and has replaced 'Italian Red' and 'Hall's Giant', which express 2 alleles. Similarly, 'Kadetten' pollen expresses a single allele and has replaced 3 cultivars as a tester for S_{20}. Pollen of the 3 previously used testers for S_{20} ('Italian Red', 'Romisondo G-1', and 'Tonda Romana') expressed 2 codominant alleles. Unfortunately, 'Kadetten' pollen is shed late in the season and so must be stored in the freezer for 11 months for use on early-flowering genotypes. Selection OSU 485.010 replaces 'Ribet' as a tester for S_{16}. It sheds pollen of excellent quality, while 'Ribet' is nearly male-sterile. Similarly, selection OSU 452.026 which produces pollen of high quality replaces OSU 92.043 as a tester

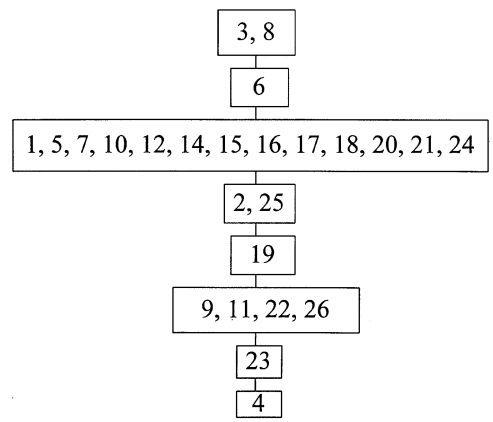

Fig. 1 Dominance hierarchy of S-alleles in hazelnut pollen. Alleles are dominant to alleles *below* them, and codominant with those at the *same level*

Table 2 Dominance relationships[a] between pairs of S-alleles. Blanks indicate pairs not observed

	1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	21	22
2.	1 > 2																				
3.	1 < 3	2 < 3																			
4.	1 > 4	2 > 4	3 > 4																		
5.	1 = 5	2 < 5	3 > 5	4 < 5																	
6.	1 < 6	2 < 6	3 > 6	4 < 6	5 < 6																
7.	1 = 7	2 < 7	3 > 7	4 < 7	5 = 7																
8.	1 < 8	2 < 8	3 = 8	4 < 8	5 < 8	6 < 8	7 < 8														
9.	1 > 9	2 > 9	3 > 9	4 < 9	5 > 9	6 > 9															
10.	1 = 10	2 < 10	3 > 10	4 < 10	5 = 10	6 > 10	7 = 10	8 > 10	9 < 10												
11.	1 > 11	2 > 11	3 > 11	4 < 11	5 > 11	6 > 11	7 > 11	8 > 11	9 = 11	10 > 11											
12.	1 = 12	2 < 12	3 > 12	4 < 12	5 = 12	6 > 12	7 = 12	8 > 12		10 = 12	11 < 12										
14.	1 = 14	2 < 14	3 > 14	4 < 14		6 > 14	7 = 14	8 > 14	9 < 14	10 = 14	11 < 14	12 = 14									
15.	1 = 15	2 < 15	3 > 15	4 < 15	5 = 15	6 > 15	7 = 15	8 > 15	9 < 15	10 = 15	11 < 15	12 = 15	14 = 15								
16.	1 = 16	2 < 16	3 > 16	4 < 16	5 = 16	6 > 16	7 = 16		9 < 16	10 = 16	11 < 16	12 = 16	14 = 16	15 = 16							
17.	1 = 17	2 < 17	3 > 17	4 < 17		6 > 17	7 = 17	8 > 17	9 < 17	10 = 17	11 < 17	12 = 17		15 = 17							
18.	1 = 18	2 < 18	3 > 18	4 < 18	5 = 18		7 = 18	8 > 18	9 < 18	10 = 18	11 < 18	12 = 18	14 = 18	15 = 18	16 = 18	17 = 18					
19.	1 > 19	2 > 19	3 > 19	4 < 19	5 > 19	6 > 19	7 > 19	8 > 19	9 < 19	10 > 19	11 < 19	12 > 19	14 > 19	15 > 19	16 > 19	17 > 19	18 > 19				
20.	1 = 20	2 < 20	3 > 20	4 < 20	5 = 20	6 > 20	7 = 20	8 > 20	9 < 20	10 = 20	11 < 20	12 = 20	14 = 20	15 = 20	16 = 20		18 = 20	19 < 20			
21.	1 = 21	2 < 21	3 > 21	4 < 21	5 = 21	6 > 21	7 = 21	8 > 21		10 = 21	11 < 21	12 = 21	14 = 21	15 = 21		17 = 21	18 = 21	19 < 21	20 = 21		
22.	1 > 22	2 > 22	3 > 22	4 < 22	5 > 22	6 > 22	7 > 22	8 > 22	9 = 22	10 > 22	11 = 22	12 > 22		15 > 22		17 > 22	18 > 22	19 > 22		21 > 22	
23.	1 > 23	2 > 23	3 > 23	4 < 23	5 > 23	6 > 23	7 > 23	8 > 23	9 > 23	10 > 23	11 > 23	12 > 23	14 > 23	15 > 23	16 > 23	17 > 23	18 > 23	19 > 23	20 > 23	21 > 23	22 < 23
24.	1 = 24		3 > 24	4 < 24																	
25.		2 = 25		4 < 25	5 > 25												18 > 25		20 > 25		
26.	1 > 26	2 > 26	3 > 26		5 > 26				9 = 26	10 > 26		12 > 26							20 > 26	21 > 26	22 = 26

$1 > 2$ indicates that S_1 is dominant to S_2; $1 < 3$ indicates that S_1 is recessive to S_3; and $1 = 5$ indicates that S_1 and S_5 are codominant in the pollen

Table 3 S-alleles of hazelnut cultivars and selections. Alleles expressed in the pollen are underlined

Cultivar	Source	S-alleles	
C. avellana var *aurea*	Morton Arboretum, Chicago, USA	6	9
C. avellana var *pendula*	Arnold Arboretum, Boston, USA	3	9
C. maxima Pellicule Rouge	Bordeaux, France	5	10
Alcover	Torino, Italy	15	22
Anglais (des Anglais)	Bordeaux, France	5	19
Apolda	Torino, Italy	10	11
Aveline d'Angleterre	Fruits Oubliés, France	5	16
B-3	Skopje, Macedonia	2	25
Barcelloner Zellernuss	Faversham, England	10	17
Bearn (DuBearn)	Rome, Italy	5	11
Brixley's New	Davis, California, USA	1	15
Comen	Torino, Italy	2	9
Cosford	Geneva, New York, USA	3	11
Culplá	Reus, Spain	9	10
DuChilly (Kentish Cob)	Newberg, Oregon, USA	10	14
Early Long Zeller	Wilhelminadorp, The Netherlands	4	20
Freehusker	Davis, California, USA	1	11
Garibaldi	Wilhelminadorp, The Netherlands	5	11
Gasaway	Washington, USA	3	26
Ghirara	Rome, Italy	2	21
Gironell (Grossal)	Bordeaux, France	1	2
Gunslebert	Bordeaux, France	5	23
Gustav's Zellernuss	Faversham, England	15	20
Iannusa Racinante	Torino, Italy	1	8
Istarski Debeloplodna	Ljubljana, Slovenia	5	10
Jean's	Rome, Italy	2	10
Kadetten	Faversham, England	20	25
Lluenta	Reus, Spain	17	22
Ludolph's Zellernuss	Faversham, England	5	20
Lyons	Davis, California, USA	2	14
Macrocarpa	Davis, California, USA	1	2
Martorella	Reus, Spain	17	22
Napoletana	Torino, Italy	1	23
Negret Primerenc	Reus, Spain	10	22
Neue Riesennuss	Wilhelminadorp, The Netherlands	18	25
Nixon	Davis, California, USA	2	3
Nocciolino Sangrato	Torino, Italy	7	17
Noce Lungha	Davis, California, USA	10	17
Nociara	Torino, Italy	1	3
Palaz	Greece	2	4
Pallagrossa	Torino, Italy	5	25
Pauetet	Reus, Spain	18	22
Riekchen's Zellernuss	Taastrup, Denmark	5	25
Rode Zeller (Rote Zellernuss)	The Netherlands	6	11
Römische Nuss[a]	Hermansverk, Norway	10	18
San Giovanni	Rome, Italy	2	8
Sant Jaume	Reus, Spain	1	17
Sant Pere	Reus, Spain	22	26
Segorbe	Bordeaux, France	9	23
Simón	Reus, Spain	6	22
Sivri Ghiaghli	Greece	4	12
Tonda di Giffoni	Rome, Italy	2	23
Turk	Davis, California, USA	1	2
Ugbrooke	New Zealand	5	9
Willamette	Corvallis, Oregon, USA	1	3
Selections from the University of Torino, Italy			
3L	(Tonda Gentile d. Langhe × Cosford)	2	3
101	"	3	7
104E	"	2	3
119	"	3	7
G-1	(listed as Payrone × Tonda Romana)	18	20

Table 3 Continued

Cultivar	Source	S-alleles	
Selections from Institut National de la Recherche Agronomique, Bordeaux, France			
GN 66(3)AF5	(Hall's Giant open pollinated)	11	15
H 88-14	(Cosford × Segorbe)	11	23
H 105-28	(T. G. d. Langhe × Daviana)	7	11
H 130-33	(Negret × Daviana)	3	10
H 140-4	(Gironell × Negret)	2	22
H 143-6	(Segorbe × Daviana)	3	9
H 168-9	(Gunslebert × Negret)	22	23
H 176-9	(Gironell × T. G. d. Langhe)	2	2?[b]
H 184-19	(Tonda di Giffoni × Segorbe)	9	23
H 317-5	(Hall's Giant × Tonda Romana)	10	15

[a] The following cultivars were also found to be S10 S18 and are morphologically indistinguishable from Römische Nuss: Istarski Okrogloplodna (from Slovenia), Romai and Payrone (from Torino, Italy), Fruttogrosso (from Slovenia)

[b] Believed to be homozygous for S_2. Neither S_1 nor S_7 are present. Progeny testing has not been performed to confirm this

for S_{19}. The latter produces limited quantities of poor quality pollen.

The availability of a tester for each of the 25 S-alleles has permitted identification of the alleles present in several cultivars (Table 3). The second alleles in 'Gasaway', 'Neue Riesennuss', 'Rode Zeller', 'Palaz', 'Segorbe', 'Sivri Ghiaghli', and 'Tonda di Giffoni' have been identified.

Discussion

As female inflorescences age, the incompatibility reactions are more difficult to classify. Only female testers whose pollinated flowers clearly distinguished between incompatible and compatible pollinations were considered to be reliable. Experience has shown that females of some genotypes (e.g. 'Segorbe') typically give poor reactions while those of others give excellent reactions. Other cultivars whose females give poor reactions include 'Heynick's Zellernuss', 'Kunzemuller's Zellernuss', 'Louisen's Zellernuss', 'Tonda Rossa', 'Ugbrooke', 'White Filbert', and selection B-4 from the former Yugoslavia. In many cases, these poor reactions have prevented identification of the S-alleles in these cultivars. The very dark color of the stigmatic styles of the red-leaved cultivar 'Rode Zeller' made it very difficult to identify its second allele. However, S_{11} was present in half the seedlings of OSU 23.024 (S_1 S_4) × 'Rode Zeller', and then its presence in the parent was confirmed. S_{11} is unusual in that pollen tends to germinate fairly well, and several long tubes are present in incompatible reactions, making it especially difficult to determine if a pollination is compatible or incompatible. This has also been observed to a lesser extent with S_2.

More than 2600 seedlings have been investigated to date, and in every case an allele from each parent has been expressed in the pistil. All genotypes exhibit codominance in the pistils, but exhibit dominance or codominance in the pollen and the dominance hierarchy is linear. This confirms the results of our earlier study (Mehlenbacher and Thompson 1988), although 2 alleles have been reassigned to lower levels in the dominance hierarchy in light of new information. Also, the dominance hierarchy now includes 4 new alleles as well as 3 that were previously unassigned to a level. It is interesting to note that 13 of the 25 alleles are on the same level in the dominance hierarchy. Knowledge of the dominance hierarchy allowed rapid isolation of new testers. Improved testers were identified for 6 alleles. Scions of all tester selections are available from the author.

S_{13} from Chinese Trazel Gellatly #4 was not included in this study. Although female inflorescences of USOR 98–83 are compatible with pollen of testers of all other alleles and germination is good, pollen tubes of this selection are abnormal on *C. avellana* flowers. The reason for this is unknown but may be due to the interspecific origin of the tester. An improved tester for this allele is being sought in backcrosses to *C. avellana*. S_{13} is known to be dominant to S_6 and S_{19} (Mehlenbacher and Thompson 1988).

The S-alleles of 55 cultivars have been identified (Table 3), and the list indicates great diversity at the S-locus. The alleles identified in 'DuChilly' (S_{10} S_{14}) did not agree with previous results. The alleles listed here for this cultivar were identified in three trees growing in three locations and confirmed by a second year of testing. The alleles in 'Negret Primerenc' were found to be the same as in 'Negret', which it resembles very closely. Likewise, the alleles in 'Belle di Giubilino' imported from Spain are identical to those in 'Tonda di Biglini' from Italy, which is consistent with the suspected synonymy of these 2 cultivars. The alleles of 'Römische Nuss' (S_{10} S_{18}) were also identified in

'Istarski Okrogloplodna' from Slovenia, 'Fruttogrosso' from Slovenia, 'Payrone' from Torino, Italy, and 'Romai' which are morphologically indistinguishable. 'Römische Nuss' was described by Goeschke (1887) and is a very old cultivar and could easily have been grown under different names in different regions.

The S-alleles in selections from the breeding programs at the University of Torino and the Institute National de la Recherche Agronomique in Bordeaux were also identified (Table 3). The alleles of these selections are consistent with expectations based on the alleles in their parents. However, the parents of selection G-1 from Torino are listed as 'Payrone' and 'Gentile di Viterbo' (syn. 'Tonda Romana'), which are cross-incompatible.

The sporophytic incompatibility system in hazelnut appears to be among the simplest of those studied. The alleles listed in Table 3 should be useful for breeders planning crosses and pomologists choosing pollenizers for new orchards.

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References

Goeschke F (1887) Die Haselnuss, ihre Arten und ihre Kultur. Paul Parey, Berlin

Hampson CR, Azarenko AN, Soeldner A (1993) Pollen-stigma interactions following compatible and incompatible pollinations in hazelnut. J Am Soc Hortic Sci 118 : 814–819

Imrie BC, Knowles PF (1971) Genetic studies of self-incompatibility in *Carthamus flavescens*. Crop Sci 11 : 6–9

Mehlenbacher SA, Thompson MM (1988) Dominance relationships among S-alleles in *Corylus avellana* L. Theor Appl Genet 76 : 669–672

Ockendon DJ (1974) Distribution of self-incompatibility alleles and breeding structure of open-pollinated cultivars of Brussel sprouts. Heredity 33 : 159–171

Richards RA, Thurling N (1973) The genetics of self-incompatibility in *Brassica campestris* L. ssp. *oleifera* Metzg. 1. Characteristics of the S-locus. Control of self-incompatibility. Genetica 44 : 428–438

Smith DC, Mehlenbacher SA (1994) Use of Tyvek housewrap for pollination bags in breeding hazelnut (*Corylus avellana* L.) HortScience 29 : 918

Stephens LC, Ascher PD, Widmer RE (1982) Genetics of self-incompatibility in diploid *Ageratum houstonianum* Mill. Theor Appl Genet 63 : 387–394

Thompson MM (1979a) Genetics of incompatibility in *Corylus avellana* L. Theor Appl Genet 54 : 113–116

Thompson MM (1979b) Incompatibility alleles in *Corylus avellana* cultivars. Theor Appl Genet 54 : 55 : 29–33

Thompson MM, Lagerstedt HB, Mehlenbacher SA (1996) Hazelnuts. In: Janick J, Moore JN (eds) Fruit breeding, vol. 3. Nuts. John Wiley & Sons, New York, pp 125–184