Incompatibility Alleles of Hazelnut Cultivars

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Abstract

Pollen-stigma incompatibility in hazelnut is sporophytic and under the control of a single locus with multiple alleles. To date, 33 alleles have been identified at the S-locus, and a designated pollen tester for each preserved in our collection. Hazelnut is diploid, and nearly all cultivars are heterozygous at the S-locus. Over the past 25 years, we have enlarged our collection by importing cultivars from several countries as scions. As the trees began to flower, we identified their S-alleles using florescence microscopy. In December, we bagged emasculated branches on trees growing in the field to protect the female inflorescences from wind-borne pollen. In January, we collected pollen from our tester trees. In February, females were collected from bagged branches and brought to the lab in petri dishes. The females were pollinated in the afternoon, one or two per tester pollen. The following day, the styles were squashed in aniline blue and observed under UV light. In compatible pollinations, pollen germination was excellent and tubes could be seen growing parallel down the style. In incompatible pollinations, germination was often reduced, pollen tubes were short and did not penetrate the stigmatic surface, and the tubes often ended in bulbs. Each pollination was scored as compatible or incompatible, and the testing of a tree required 1-3 years for completion. In this paper, we report the alleles of 170 cultivars for the first time, and summarize the alleles of 112 cultivars previously typed. Cultivars with different names often have identical microsatellite marker fingerprints and S-alleles. To reduce confusion, a list of cultivars with identical fingerprints is also included.

INTRODUCTION

Incompatibility in hazelnut is of the sporophytic type and under the control of a single S-locus with multiple alleles. European hazelnut (*Corylus avellana* L.) is diploid ($2n=2x=22$) and nearly all cultivars are heterozygous at the S-locus. The S-alleles of cultivars and selections are routinely determined by fluorescence microscopy. The S-alleles of many cultivars have been determined over the past 25 years, and in this paper we present summary lists. Both alleles are expressed by the stigmas. Underlined alleles are expressed in the pollen.

MATERIALS AND METHODS

Scions of hazelnut cultivars were imported from several countries and propagated by grafting. After two years in post-entry quarantine, the trees were planted in the field. When the trees began to flower in the 4th to 6th leaf, incompatibility testing was performed as described in detail by Mehlenbacher (1997). Two to four branches on each tree were marked, emasculated by clipping the catkins, and enclosed in two bags: an inner bag of Tyvekhouse wrap (DuPont, Wilmington, DE) and an outer bag of a cotton-polyester blend (Smith and Mehlenbacher, 1994). Pollen was collected from 33 tester trees and stored in the freezer (-18°C).

From mid-January to early March, when styles had emerged and were receptive, females were collected from bagged branches using forceps, and brought to the lab in petri dishes. Pollinations were performed in the laboratory the afternoon after collection

by holding the female with forceps, dipping the stigmatic styles into the vial of pollen, tapping the flower on the side of the vial to remove excess pollen, and placing the pollinated flower on a double layer of moist Whatman #1 filter paper. Unpollinated flowers were held in the refrigerator for a few days in petri dishes over moist filter paper for later use if the results of the first pollinations were unclear. The day following pollination, the styles were detached from the buds, squashed in aniline blue dye, and examined at 100× with a fluorescence microscope under UV light. Each pollination was scored as compatible or incompatible. In compatible pollinations, pollen germination was excellent and tubes could be seen growing parallel down the style. In incompatible pollinations, germination was often reduced, pollen tubes were short and did not penetrate the stigmatic surface, and the tubes often ended in bulbs. In most cases, the use of fresh, unpollinated female flowers and viable tester pollen made it easy and quick to distinguish the two reactions. When two of the 33 testers gave incompatible pollinations and the remaining 31 were compatible, the two alleles had been identified. As some pollinations gave inconclusive results, and the number of flowers on young trees was limited, testing of a cultivar required 1-3 years for completion.

RESULTS AND DISCUSSION

New Alleles and Testers

Mehlenbacher (1997) listed testers for 26 S-alleles. In this study we identified 7 new alleles and an improved tester for S_{13}.S_{27} is the dominant allele in Buttner's Zellernuss (S_{11} S_{27}). S_{28} is present in 'Cutleaf' (S_{20} S_{28}). Some offspring of 'Cutleaf' are self-compatible (Mehlenbacher and Smith, 2006). S_{29}, the dominant allele in OSU 930.081 (S_4 S_{29}), is from OSU 495.049 (S_{22} S_{29}) which originated from seeds sent from the former Soviet Union. S_{30}, an allele first detected in seedlings of 'The Shah' (S_{14} S_{30}), was later detected in seedlings from Azerbaijan. OSU 956.077 (S_4 S_{30}) and OSU 1116.049 (S_4 S_{30}) are the testers for S_{30}. S_{31} is the dominant allele in 'Ata Baba' (S_4 S_{31}), which is the leading cultivar in Azerbaijan. S_{32} is the dominant allele in the Serbian cultivar 'Reka #2'. S_{33} is a co-dominant allele in 'Ganja' (S_4 S_{33}) from Azerbaijan. S_{13}, previously identified in interspecific hybrid "Chinese Trazels", was found in 'Ashrafi' 1226.004 (S_{13} S_{31}) from Azerbaijan and OSU 1168.130 (S_4 S_{13}). The latter originated from seeds purchased in the village market in Holmskij near Krasnodar, Russia. Both are used as pollen testers, while the later-flowering 'Ashrafi' is the female tester for S_{13}.

S-Alleles in Cultivars

We report the alleles of 170 cultivars for the first time (Table 1), and summarize the alleles of 112 cultivars previously typed (Table 2).

Cultivars with Identical Fingerprints

Cultivars with different names often have identical microsatellite marker fingerprints and S-alleles (Boccacci et al., 2006; Gökirmak et al., 2009, Gürcan et al., 2010), which leads to confusion. A list of cultivars with identical fingerprints is included (Table 3), but only the preferred names appear in Tables 1 and 2.

Relationship of S-Alleles to Geographic Origin

Boccacci et al. (2006) and Gökirmak et al. (2009) assigned most hazelnut accessions to one of four groups: Northern European, English, Black Sea and Spanish-Italian. Old German cultivars belong to the northern European group. In this group, S_5, S_{15}, S_{20} and S_{25} are common. In the English cultivars, S_3, S_{10}, S_{11} and S_{14} are common. Cultivars from Turkey, Georgia, Azerbaijan and southern Russia belong to the Black Sea group (Gökirmak et al., 2009; Gürcan et al., 2010). In this group, S_4 is most common, but many other alleles are present. In the Spanish-Italian group, S_2 is most common, but many other alleles are present.

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4 Gruppen Herkünfte: 1) alte deutsche Sorten
2) englische Sorten
3) Türkei, Aserbaidschan, Georgien, südliches Russland
4) Spanien, Italien

CONCLUSIONS

In this paper we present tables of S-alleles of hazelnut cultivars. These tables should be useful to breeders in the planning of crosses, to germplasm curators, and to growers and nurseries as they choose cultivars and pollinizers when designing orchards.

ACKNOWLEDGEMENTS

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Tables

Table 1. Incompatibility alleles of hazelnut cultivars as determined by fluorescence microscopy.

Cultivar	S-alleles*		Cultivar	S-alleles	
Acorn Hazelnut	5	11	Crvenje	6	23
Albania 80	8	32	Cutleaf	20	28
Alli	9	20	Da Viega	10	21
Amarillo	2	6	Dal Rossa	5	18
Amarillo Tardio	2	2?	Dalian 83-81	3	19
Anakliuri	4	14	Dalian 84-349	5	6
Anglais	5	19	Dalian 84-75	3	7
Artellet	14	18	Danish Wild	8	23
Arzu	31	?	Dedoplistiti	8	14
Ashrafi 1090.011	16	31	Dnepr-1	15	21
Ashrafi 1226.004	13	31	Dowton Long (1-53)	9	10
Aslan Baba	4	15	Dowton Long (3-53)	3	14
Ata Baba	4	31	Ducalovici	1	9
Ata Ula	4	10	Durazno	1	2
Azeri	2	27	Early Long Zeller	20	25
B-4	10	17	Elbari	2	33
Bandnuss	10	11	Faroka	11	13
Barbakan	5	6	Farris 88BS	3	11
Barli	10	31	Finland COR 187	9	25
Barrettona	2	6	Firavan	4	31
Barr's Zellernuss	5	11	Francoli	17	22
Belle di Giubilino	1	10	Frango #2	5	5?
Bergeri	3	25	Frango #4	15	25
Bianca	2	2?	Frango #5	11	25
Bixby	20	23	Frizzled Filbert	9	10
Blumberger Zellernuss	4	20	Gakh Faresh	4	31
Bomba	2	33	Galib	4	16
Borovskoi	10	24	Ganja	4	33
Bosio	1	2	Garrofi	1	6
Buchanan	12	15	Gauna	1	1?
Bulgaria XI-8	4	12	Gironenc Vermellet	2	17
Burchardt's Zellernuss	2	7	Gizil Findiq	10	31
Buttner's Zellernuss	11	27	Gobekli	4	5
Catalan	10	25	Goc (mislabelled?)	6	15
Cherkesskii II	4	24	Grand Traverse	11	25
Chikivistava	4	10	Pioneer	2	4
Chines Trazel Gellatly #4	15	25	Pirosok	10	24
Chinese Trazel Gellatly #6	13	15	Planeta	1	2
Chinese Trazel Gellatly #11	13	15	Polli 3-10	2	27
Closca Molla	2	5	Potomac	5	12
Comun	10	10?	Princess Royal	11	14
Corabel	1	3	Prolific Closehead	5	11
Cozia	5	15	Punxenc	1	10

* Alleles expressed in the pollen are underlined. ? indicates an unknown allele, often because progeny testing has not been conducted to confirm homozygosity.

Table 1. Continued.

Cultivar	S-alleles*		Cultivar	S-alleles	
Grifoll	2	22	Qabala	4	6
Gubener Barcelloner	1	23	Ratllada	10	22
Hemplov Zellsky	12	20	Ratoli	2	10
Istarski Duguljasti	10	17	Red Fortrin	2	6
Jemtegaard 76	2	3	Reed	12	15
Jemtegaard 80	2	3	Reka #1	1	17
Kalinkara	4	21	Reka #2	2	32
Karol	11	15	Romavel	2	2?
Khachapura	3	18	Ruby	11	19
Kudryavchik 1226.003	4	10	Sachakhli	5	10
Kudryavchik 1226.041	4	24	San Benedetto	4	12
Lange Landsberger	15	20	Sant Joan	2	25
Lech	5	15	Shokoladnyi	4	11
Lenka #3	3	5	Shvelilskura Row 1190	4	14
Liegel's Zellernuss	12	20	Shveliskura	5	10
Little Poland	3	5	Siciliana Montebello	1	2
Louisen's Zellernuss	10	25	Sickler's Zellernuss	5	20
Lozovskoi Sharovidnyi	2	25	Sivri Ocak 5	8	10
Mar del Plata	16	23	Skorospelka	4	23
Maria	11	15	Sodlinger	6	11
Medium Long	11	12	Stepovy	2	5
Menoia	8	10	Suvodol	5	6
Mincane (Akcakoca)	4	10	Syrena	6	15
Molar	2	10	Tala	2	5
Napoletanedda	2	14	Tankoljuskasti	5	10
Nasimi	4	31	Tapparona di Mezzanego	5	25
Nemsa	1	4	Tapparona di S.C.C.	2	24
Pere Mas	9	10	The Shah	14	30
Pinyolenc #1	2	2?	Tokolyi Cosford	5	23
Pinyolenc #2	2	17	Tomasina	17	22
Tonda Bianca	1	23	Vistula	2	5
Tonda Rossa	8	23	Volle Zeller CC05.45	11	14
Tonnolella	2	24	Volle Zeller R639	3	14
Tonollo	1	2	Volski Round	5	11
Topkhara	2	10	Wallace Seedling	2	11
Trbusani	15	26	Warsaw Red	1	6
Trenet	2	15	Webb's Prize Cob	17	17?
Truchsess Zellernuss	5	25	White Filbert	5	10
Tskhenis Dzudzu	4	20	Whiteheart	2	10
Uebov	12	16	Yagli Findiq	4	4
Uzum Sakar	4	10	Yoder #5	10	23
Veleten	15	15?	Zaqatala-9	4	10
Verde	2	6	Zimmerman	1	3

* Alleles expressed in the pollen are underlined. ? indicates an unknown allele, often because progeny testing has not been conducted to confirm homozygosity.

? Wetcher

Table 2. S-alleles of hazelnut cultivars from publications.

Cultivar	S-alleles		Reference
Alcover	15	22	Mehlenbacher, 1997
Apolda	10	11	Mehlenbacher, 1997
Aurea	6	9	Mehlenbacher, 1997
Aveline d'Angleterre	5	16	Mehlenbacher, 1997
B-3	2	25	Mehlenbacher, 1997
Badem	2	5	Mehlenbacher and Thompson, 1988
Barcelloner Zellernuss	10	17	Mehlenbacher, 1997
Barcelona	1	2	Mehlenbacher and Thompson, 1988
Bearn	5	11	Mehlenbacher, 1997
Brixley's New	1	15	Mehlenbacher, 1997
Brixnut	1	14	Mehlenbacher and Thompson, 1988
Butler	2	3	Mehlenbacher and Thompson, 1988
Camponica	1	2	Mehlenbacher and Thompson, 1988
Casina	10	21	Mehlenbacher and Thompson, 1988
Clark (OSU 276.142)	3	8	Mehlenbacher et al., 2001
Comen	2	9	Mehlenbacher, 1997
Compton	2	3	Mehlenbacher and Thompson, 1988
Contorta	5	10	Mehlenbacher and Thompson, 1988
Cosford	3	11	Mehlenbacher, 1997
Creswell	2	10	Mehlenbacher and Thompson, 1988
Culpla	9	10	Mehlenbacher, 1997
Daria (104E)	2	3	Mehlenbacher, 1997
Daviana	3	11	Mehlenbacher and Thompson, 1988
Delta (OSU 510.041)	1	15	Mehlenbacher et al., 2004
DuChilly	10	14	Mehlenbacher, 1997
Early Long Zeller	4	20	Mehlenbacher, 1997
Ennis	1	11	Mehlenbacher and Thompson, 1988
Epsilon (OSU 699.073)	1	4	Mehlenbacher et al., 2004
Eta (OSU 984.075)	11	26	Mehlenbacher et al. (in press)
Fitzgerald 20	2	11	Mehlenbacher and Thompson, 1988
Freehusker	1	11	Mehlenbacher, 1997
Fusco Rubra	6	19	Mehlenbacher and Thompson, 1988
Gamma (OSU 589.028)	2	10	Mehlenbacher et al., 2004
Garibaldi	5	11	Mehlenbacher, 1997
Gasaway	3	26	Mehlenbacher, 1997
Gem	2	14	Mehlenbacher and Thompson, 1988
Ghirara	2	21	Mehlenbacher, 1997
Gironell (Grossal)	1	2	Mehlenbacher, 1997
Gunslebert	5	23	Mehlenbacher, 1997
Gustav's Zeller	15	20	Mehlenbacher, 1997
Hall's Giant	5	15	Mehlenbacher and Thompson, 1988
Henneman #3	6	10	Mehlenbacher and Thompson, 1988

Table 2. Continued.

Cultivar	S-alleles		Reference
Iannusa Racinante	1	8	Mehlenbacher, 1997
Imperatrice Eugenie	3	14	Mehlenbacher and Thompson, 1988
Imperiale de Trebizonde	2	10	Mehlenbacher and Thompson, 1988
Istarski Debeloplodna (640.004)	5	10	Mehlenbacher, 1997
Italian Red	15	20	Mehlenbacher and Thompson, 1988
Jean's	2	10	Mehlenbacher, 1997
Jefferson (OSU 703.007)	1	3	Mehlenbacher et al., 2011
Kadetten	20	25	Mehlenbacher, 1997
Kruse	1	2	Mehlenbacher and Thompson, 1988
Lansing #1	1	3	Mehlenbacher and Thompson, 1988
Lansing #2	3	10	Mehlenbacher and Thompson, 1988
Lewis (OSU 243.002)	3	8	Mehlenbacher et al., 2000
Lluenta	17	22	Mehlenbacher, 1997
Ludolph's Zeller	5	20	Mehlenbacher, 1997
Lyons	2	14	Mehlenbacher, 1997
Macrocarpa	1	2	Mehlenbacher, 1997
Martorella (COR 444)	17	22	Mehlenbacher, 1997
Montebello	1	2	Mehlenbacher and Thompson, 1988
Morell	1	2	Mehlenbacher and Thompson, 1988
Mortarella	2	17	Mehlenbacher and Thompson, 1988
Napoletana	1	23	Mehlenbacher, 1997
Negret	10	22	Mehlenbacher and Thompson, 1988
Negret Primerenc	10	22	Mehlenbacher, 1997
Neue Riesennuss	18	25	Mehlenbacher, 1997
Nixon	2	3	Mehlenbacher, 1997
Nocchiolino Sangrato	7	17	Mehlenbacher, 1997
Noce Lungha	10	17	Mehlenbacher, 1997
Nociara	1	3	Mehlenbacher, 1997
Nonpareil	1	3	Mehlenbacher and Thompson, 1988
Nooksack	6	14	Mehlenbacher and Thompson, 1988
Nottingham	8	10	Mehlenbacher and Thompson, 1988
Ordu	4	25	Mehlenbacher, 1997
Palaz	2	4	Mehlenbacher, 1997
Pallagrossa	5	25	Mehlenbacher, 1997
Pauetet	18	22	Mehlenbacher, 1997
Pellicule Rouge	5	10	Mehlenbacher, 1997
Pendula	3	9	Mehlenbacher, 1997
Red Lambert	5	10	Mehlenbacher and Thompson, 1988
Ribet	2	16	Mehlenbacher and Thompson, 1988
Riccia di Talanico	1	2	Mehlenbacher and Thompson, 1988
Riekchen's Zeller	5	25	Mehlenbacher, 1997
Rode Zeller (Rote Zellernuss)	6	11	Mehlenbacher, 1997

Table 2. Continued.

Cultivar	S-alleles		Reference
Romische Nuss	10	18	Mehlenbacher, 1997
Royal	1	3	Mehlenbacher and Thompson, 1988
Sacajawea (OSU 540.130)	1	22	Mehlenbacher et al., 2008
San Giovanni	2	8	Mehlenbacher, 1997
Sant Jaume	1	17	Mehlenbacher, 1997
Sant Pere	22	26	Mehlenbacher, 1997
Santiam (OSU 509.064)	3	15	Mehlenbacher et al., 2007
Segorbe	9	23	Mehlenbacher, 1997
Simon	6	22	Mehlenbacher, 1997
Sivri Ghiaghli	4	12	Mehlenbacher, 1997
Theta (OSU 1001.008)	5	15	Mehlenbacher et al. (in press)
Tombul Extra Ghiaghli	4	12	Mehlenbacher and Thompson, 1988
Tonda di Biglini	1	10	Mehlenbacher and Thompson, 1988
Tonda di Giffoni	2	23	Mehlenbacher, 1997
Tonda Gentile delle Langhe	2	7	Mehlenbacher and Thompson, 1988
Tonda Pacifica (OSU 228.084)	1	2	Mehlenbacher et al., 2011
Tonda Romana	10	20	Mehlenbacher and Thompson, 1988
Turk	1	2	Mehlenbacher, 1997
Ugbrooke	5	9	Mehlenbacher, 1997
VR 4-31	1	3	Mehlenbacher and Thompson, 1991
VR 11-27	1	3	Mehlenbacher and Thompson, 1991
VR 20-11	2	3	Mehlenbacher and Thompson, 1991
VR 23-18	1	3	Mehlenbacher and Thompson, 1991
White Aveline	5	10	Mehlenbacher and Thompson, 1988
Willamette	1	3	Mehlenbacher, 1997
Woodford	1	3	Mehlenbacher and Thompson, 1988
Yamhill (OSU 542.102)	8	26	Mehlenbacher et al., 2009
Zeta (OSU 670.095)	1	1	Mehlenbacher et al., 2004

Synonyme

Table 3. Hazelnut cultivars with identical SSR fingerprints. The S-alleles are listed in Tables 1 and 2 under the preferred name.

Cultivar name	Preferred name
A Pellicola Bianca	Bandnuss
Amandi	Casina
Apolda	Bandnuss
Atlas	Belle di Giubilino
Aveline Rouge	White Filbert
Avellana Speciale	Siciliana
Barbarella	White Filbert
Bard	Barr's Zellernuss
Bearn	Barr's Zellernuss
Carello	Siciliana
Ceret	Molar
Comun Aleva	Segorbe
Comune di Sicilia	Siciliana
D'Algers	Barcelona
Espinaredo	Casina
Fructo Albo	White Filbert
Fruttogrosso	Romische Nuss
Gironenc Coldejou	Segorbe
Grande	Barcelona
Heynick's Zellernuss	Gustav's Zellernuss
Istarski Debeloplodna	White Filbert
Istarski Okrogloplodna	Romische Nuss
Italian Red	Gustav's Zellernuss
Jeeve's Samling	Liegel's Zellernuss
Kadetten Zellernuss	Early Long Zellernuss
Karidaty	Imp. de Trebizonde
Kerasund Dlinnyi	Sivri Ocak 5
Korthaset Zellernuss	Du Chilly
Kruse	Macrocarpa
Kunzemuller's Zellernuss	Liegel's Zellernuss
Lenka #4	Maria
Locale di Piazza Armerina	Siciliana
Mansa	Siciliana
Minnolara	Siciliana
Mogulnuss	Riekchen's Zellernuss
Montebello	Siciliana
Multiflora	Cosford
Nocchione	Siciliana
Noce Lungha	Istrski Duguljasti
Nostrale	Siciliana

Table 3. Continued.

Cultivar name	Preferred name
Obrovsky Novy	Liegel's Zellernuss
Payrone	Romische Nuss
Pearson's Prolific	Nottingham
Pellicule Rouge	White Filbert
Petoka (not)	Cosford
Prolifique a Coque Serrée	Cosford
Pruhovany	Daviana
Purple Aveline	White Filbert
Purple Fortrin	White Filbert
Quiros	Casina
Racinante clone G	Siciliana
Red Filbert	Princess Royal
Restiello	Negret
Rimsky	Louisen's Zellernuss
Romai	RomischeNuss
Ros de la Selva	Pinyolenc #1
Rosetta	Barrettona
Rosset de Valls	Artellet
Tombul Ocak 1	Tombul Extra Ghiaghli
Turk	Macrocarpa
Vilcea 22	Imp. de Trebizonde
Wanliss Pride	Imp. de Trebizonde