

Geographic Distribution of Incompatibility Alleles in Cultivars and Selections of European Hazelnut

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ABSTRACT. The European hazelnut (*Corylus avellana* L.) is native to most of Europe and nearby areas in Asia Minor and the Caucasus Mountains. Cross-pollination is enforced by sporophytic incompatibility under the control of a single locus with multiple alleles (haplotypes). Fluorescence microscopy is routinely used to determine if a pollination is compatible or incompatible, and use of an array of known testers allows identification of the alleles of cultivars and selections. Both alleles are expressed in the stigmas, but often only one is expressed in the pollen because of dominance. Cultivars are highly heterozygous diploids ($2n = 2x = 22$) and clonally propagated. Most of the world's leading cultivars were selected from local wild populations near where they are now planted on a commercial scale. Genetic improvement efforts are recent and, although tremendous genetic variability is available, such efforts have had little impact outside of Oregon and France. Studies of genetic diversity using simple sequence repeat markers have placed most cultivars in one of the four main groups: Spanish-Italian, Central European, English, or Black Sea. This study presents 17 years of data on incompatibility in hazelnut, including the discovery of six new S-alleles and determination of the dominance relationships among 105 new pairs of alleles. The total number of alleles now stands at 33. The S-alleles of 284 cultivars, 13 interspecific hybrids, and 522 selections of diverse origin are presented. The S-alleles identified in hazelnut cultivars is information that should be useful to breeders in the planning of crosses, to curators of germplasm collections, and to growers and nurseries as they choose cultivars and pollenizers when designing orchards. Differences in S-allele frequency seen in the cultivars and selections are related to geographic origin. The most common alleles of cultivars in the major geographical groups are S_2 in the Spanish-Italian group, S_5 in the Central European group, S_3 in the English group, and S_4 in the Black Sea group. Most selections belonged to the Black Sea group, and S_4 was by far the most common allele. Differences in allele frequency were also observed among seed lots within a country.

European hazelnut, a member of the Betulaceae, is monoecious, dichogamous, and wind-pollinated. Hazelnuts thrive in maritime climates where temperatures are moderate in winter and summer. The major world producers of hazelnuts are Turkey and Italy with additional production in Azerbaijan, the United States, Georgia, Spain, Iran, China, and France (Food and Agriculture Organization of the United Nations, 2011). Hazelnuts were cultivated in the Roman Empire and much earlier near the Black Sea in Turkey and the Caucasus. Most of the world's production is based on selections from local wild populations with different cultivars grown in each zone. Most cultivars are single clones, although some, including a few leading Turkish types (e.g., Tombul), appear to be groups of clones with similar phenotypes. Cultivars are traditionally propagated from suckers or by layerage, although grafting and in vitro culture are also possible. The local origin of important cultivars, and their limited movement from one production zone to another, contrasts sharply with the situation with the major food crops.

Pollen–stigma incompatibility in hazelnut is of the sporophytic type and controlled by a single locus, designated the

S-locus, with multiple alleles (haplotypes), and the stigmatic surface is the site of the incompatibility reaction (Thompson, 1979a). Thompson (1979b) listed the alleles of several cultivars. Additional early work on S-allele identification was reviewed by Germain (1994). Hampson et al. (1993) used electron microscopy to study compatible and incompatible pollinations in detail. Hazelnuts are diploid ($2n = 2x = 22$), and most cultivars are heterozygous at the S-locus. Fluorescence microscopy is used routinely to determine if a pollination is compatible or incompatible and to identify the S-alleles in cultivars and selections (Mehlenbacher, 1997a). Mehlenbacher (1997b) reported 25 S-alleles and for each allele identified a tester genotype whose pollen expresses that allele. Mehlenbacher (1997b) updated the results of Mehlenbacher and Thompson (1988) and presented dominance relationships based on 233 pairs of alleles. In all pairs, both alleles were expressed in the stigmas, but often only one was expressed by the pollen because of dominance. The dominance hierarchy is linear with eight levels (Mehlenbacher, 1997b). By convention, the allele(s) expressed in the pollen are underlined. Recently, Martins et al. (2012) investigated the S-alleles of Portuguese landraces, and Mehlenbacher (2013) listed the S-alleles of 282 cultivars. The linkage map of Mehlenbacher et al. (2006), constructed using random amplified polymorphic DNA and simple sequence repeat (SSR) markers, placed the S-locus on linkage group 5 (LG5).

Self-pollination of most cultivars results in very low nut set. Mehlenbacher and Smith (1991) identified partial self-compatibility in 'Montebello', 'Tombul', and a few offspring of 'Montebello'. In this material, self-pollination unfortunately

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resulted in low nut set and a high frequency of blanks. More recently, Mehlenbacher and Smith (2006) identified self-compatible seedlings of the cutleaf hazelnut [*Corylus avellana* f. *heterophylla* (Loud.) Rehder]. In these seedlings, self-pollination results in good nut set and few blanks. The cutleaf hazelnut has alleles S₂₀ and S₂₈. The latter gives self-compatibility when combined with a second allele low in the dominance hierarchy.

In this study, I identified six new S-alleles and determined the dominance relationships for 105 new pairs of alleles. I determined the alleles of 522 selections originating from nuts imported from many locations and examined the data for cultivars and selections for geographic patterns in the distribution of S-alleles.

Materials and Methods

The hazelnut breeding program at Oregon State University (OSU), in cooperation with the U.S. Department of Agriculture, Agriculture Research Service, National Clonal Germplasm Repository (USDA-ARS-NCGR) in Corvallis, OR, imported scions of cultivars from Georgia, Azerbaijan, and several European countries. The scions were grafted to rooted layers, held in post-entry quarantine for two growing seasons, and then planted in the field. When the trees began to flower, generally the fourth year after planting, incompatibility testing was performed as described by Mehlenbacher (1997a). Two to four branches on each tree were marked, emasculated by clipping the catkins, and enclosed in two bags: an inner bag of Tyvek housewrap (DuPont, Wilmington, DE) and an outer bag of a cotton-polyester blend (Smith and Mehlenbacher, 1994). Pollen was collected from tester trees (Table 1) and stored in the freezer at -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 laboratory in petri dishes. Pollinations were performed in the laboratory the afternoon after collection by holding the female with forceps, dipping the 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 P5 filter paper (Fisher Scientific, Pittsburgh, PA). Unpollinated flowers were held in the refrigerator for a few days in petri dishes over moist filter paper to allow repetition of the pollinations if the first results were unclear. The day after pollination, styles were detached from the buds, squashed in aniline blue dye, and examined at 100× with a fluorescence microscope under ultraviolet 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 testers gave incompatible pollinations and all others were compatible, the two alleles in the female parent had been identified. Some pollinations gave inconclusive results, and the number of flowers on young trees was limited, so testing an introduced cultivar required 1 to 3 years for completion.

The OSU hazelnut breeding program collected germplasm as seeds from several countries, including Turkey, Georgia, Azerbaijan, Armenia, Russia, Ukraine, and Iran (Table 2).

Table 1. Pollen testers for incompatibility alleles in hazelnut.

Allele no.	Tester ^z	Alleles in tester (no.) ^y	
1	'Barcelona'	<u>1</u>	<u>2</u>
2	OSU 20.058 ^x	<u>2</u>	<u>2</u>
3	'Nonpareil'	<u>1</u>	<u>3</u>
4	OSU 194.001	<u>4</u>	<u>4</u>
5	'Badem'	<u>2</u>	<u>5</u>
6	'Henneman #3'	<u>6</u>	<u>10</u>
7	OSU 278.095	<u>4</u>	<u>7</u>
8	'San Giovanni'	<u>2</u>	<u>8</u>
9	'Segorbe'	<u>9</u>	<u>23</u>
10	'Kargalak'	<u>2</u>	<u>10</u>
	'Gamma'	<u>2</u>	<u>10</u>
11	OSU 278.121	<u>4</u>	<u>11</u>
12	OSU 55.077	<u>2</u>	<u>12</u>
13	'Ashrafi' 1226.004	<u>13</u>	<u>31</u>
14	'Gem'	<u>2</u>	<u>14</u>
15	GN66(3)AF5	<u>11</u>	<u>15</u>
16	OSU 485.015	<u>11</u>	<u>16</u>
17	'Mortarella'	<u>2</u>	<u>17</u>
18	'Neue Riesen'	<u>18</u>	<u>25</u>
19	OSU 452.026	<u>4</u>	<u>19</u>
20	OSU 1038.084	<u>2</u>	<u>20</u>
21	OSU 168.026	<u>2</u>	<u>21</u>
22	OSU 937.069	<u>4</u>	<u>22</u>
23	OSU 385.006	<u>4</u>	<u>23</u>
24	OSU 54.041	<u>2</u>	<u>24</u>
	OSU 1092.108	<u>4</u>	<u>24</u>
25	'Ordu'	<u>4</u>	<u>25</u>
26	OSU 447.015	<u>26</u>	<u>26</u>
27	'Buttner's Zeller'	<u>11</u>	<u>27</u>
	OSU 962.014	<u>4</u>	<u>27</u>
28	OSU 562.031	<u>26</u>	<u>28</u>
29	OSU 930.081	<u>4</u>	<u>29</u>
30	OSU 1116.049	<u>4</u>	<u>30</u>
31	'Ata Baba'	<u>4</u>	<u>31</u>
32	'Reka #2'	<u>2</u>	<u>32</u>
33	'Ganja'	<u>4</u>	<u>33</u>

^zTwo testers are used for some S-alleles.

^yAlleles expressed by the pollen are underlined.

^xOSU = Oregon State University.

These countries represent the eastern part of the distribution of *C. avellana*. The seeds were stratified and planted in the greenhouse as root tips emerged 3 to 5 months later. Seedlings were grown in 3.8-L containers in a glasshouse the first summer and transplanted into the field in October. The S-alleles in the selections were identified using the same procedures as for the cultivars. Their flowering generally begins in the fourth year in the field. Before identification of their S-alleles, seedlings were selected for precocity, round nut shape, few defects, and few buds blasted by mites (primarily *Phytoptus avellanae* Nal.).

When a cultivar or selection representing a new pair of S-alleles was identified, its pollen was placed on female inflorescences of two different cultivars or selections. Each expressed one of the two alleles in the new pair, 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

Table 2. Origin of hazelnut seed lots by country, year and collection location, and the number of selections from each lot whose S-alleles were identified.

Country	Lot no.	Yr	No. Selections	Location	Description ^z	Other comments
Turkey	1	1975	11	Giresun	Orchard	
	2	1990	12	Istanbul	Market	
	3	1991	24	Unknown	Market	
	4	1993	30	Akcakoca	Orchard	
	5	1993	17	Giresun and Ordu	Orchards	
	6	1993	31	Trabzon	Orchard	
	7	1997	18	Samsun	Orchard and market	
	8	2004	114	Giresun	Hazelnut Research Institute	
Georgia	1	2001	8	Kakheti	Orchards	
	2	2001	10	Zugdidi	Orchards	Large, round nuts
	3	2001	11	Zugdidi	Orchards	Small, round nuts
	4	2001	3	Zugdidi	Orchards	Oblate nuts
	5	2001	6	Zugdidi	Orchards	Dark-shelled nuts
	6	2003	5	Vani and Abasha	Orchards	
Azerbaijan	1	2001	26	Zaqatala	Orchards	
	2	2001	8	Qabala	Orchards	
	3	2001	15	Xacmaz	Orchards	
Armenia	—	2002	26	Various	Markets, six vendors	
Russia	1	2002	8	Sochi	Institute cultivar collection	
	2	2002	18	Sochi	Market	Seven vendors
	3	2002	18	Holmskij	Market	Five vendors
	4	2002	10	Krasnodar	Market	Three vendors
	5	2002	13	Central Asia	Cultivar collection	'Panahei' seeds
	6	2002	3	Maikop	VIR cultivar collection	
	7	1989	6	Leningrad	VIR collection, southern Russia	
	8	1992	18	Moscow	Wild	
Ukraine	—	2002	24	Alushka-Simferopol	Vendors (4), Nikita Gardens	
Iran	—	2003	9	Near Caspian Sea	Orchard and roadside vendor	
Other	1	1992	13	Piemonte	Wild	
	2	2005	3	Latvia	Cultivar collection	
	3	2005	1	Lithuania	Cultivar collection	
	4	2000	1	Estonia	Wild	
	5	1987	1	Univ. of Minnesota	Seedlings	

^zVIR = N.I. Vavilov Research Institute of Plant Industry.

other allele in the cultivar or selection being tested. If both pollinations were incompatible, the two alleles in the cultivar or selection were considered to be codominant in its pollen. Females of a third genotype expressing different alleles were pollinated to verify that the selection's pollen was viable.

If two of the testers gave incompatible pollinations and all others were compatible, the two alleles had been identified. A single incompatible reaction and 24 compatible reactions indicated either the presence of one known and one unknown allele or homozygosity. If pollen of a cultivar or selection was compatible on all known alleles, it was considered a potential tester for a novel S-allele. Testers that express the novel allele in their pollen and produce large quantities of pollen early in the season are preferred.

S₂₈ from the cutleaf hazelnut, which gives self-compatible seedlings on some combinations (Mehlenbacher and Smith,

2006), was excluded from this study, because its presence cannot be detected by standard procedures.

Based on SSR markers, Boccacci et al. (2006) and Gökirmak et al. (2009) assigned most hazelnut accessions to one of four groups: Spanish-Italian, Central European, English, and Black Sea. SSR markers were used by Boccacci et al. (2008) to investigate cultivars in northeastern Spain and by Gürçan et al. (2010) to investigate cultivars in the Black Sea group. Cultivars previously fingerprinted with SSR markers (Boccacci et al., 2006, 2008; Gökirmak et al., 2009; Gürçan et al., 2010; S.A. Mehlenbacher, unpublished data) are listed by their assigned group. Other previously fingerprinted very diverse accessions that were not placed in one of the four main groups are presented as a group labeled "other." Accessions that had not yet been fingerprinted were placed in the most suitable group based on their geographic origin with consideration of morphological

Table 3. Dominance relationships among pairs of S-alleles in hazelnut.^z

Allele no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
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	6 > 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	7 > 9	8 > 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	9 < 12	10 = 12	11 < 12																
13	1 > 13	2 > 13	3 > 13	4 < 13							11 > 13	12 > 13															
14	1 = 14	2 < 14	3 > 14	4 < 14	5 = 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	15 > 13	14 = 15													
16	1 = 16	2 < 16	3 > 16	4 < 16	5 = 16	6 > 16	7 = 16	8 > 16	9 < 16	10 = 16	11 < 16	12 = 16		14 = 16	15 = 16												
17	1 = 17	2 < 17	3 > 17	4 < 17	5 = 17	6 > 17	7 = 17	8 > 17	9 < 17	10 = 17	11 < 17	12 = 17		14 = 17	15 = 17	16 = 17											
18	1 = 18	2 < 18	3 > 18	4 < 18	5 = 18	6 > 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	17 = 20	18 = 20	19 < 20								
21	1 = 21	2 < 21	3 > 21	4 < 21	5 = 21	6 > 21	7 = 21	8 > 21	9 < 21	10 = 21	11 < 21	12 = 21		14 = 21	15 = 21	16 = 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	13 < 22	14 > 22	15 > 22	16 > 22	17 > 22	18 > 22	19 > 22	20 > 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	2 < 24	3 > 24	4 < 24	5 = 24	6 > 24	7 = 24		9 < 24	10 = 24		12 = 24		14 > 24	15 > 24	16 = 24	17 = 24	18 = 24	19 < 24	20 > 24	21 > 24	22 < 24	23 < 24				
25		2 = 25		4 < 25	5 > 25					10 > 25		12 > 25			15 > 25			18 > 25	19 < 25	20 > 25		22 < 25	23 < 25				
26	1 > 26	2 > 26	3 > 26	4 < 26	5 > 26	6 > 26	7 > 26	8 > 26	9 = 26	10 > 26	11 = 26	12 > 26			15 > 26	17 > 26		18 > 26	19 > 26	20 > 26	21 > 26	22 = 26	23 < 26	24 > 26	25 > 26		
27	1 > 27	2 = 27	3 > 27	4 < 27			8 > 27			10 > 27	11 < 27				15 > 27					20 > 27		22 > 27	23 < 27	24 > 27			
29	1 > 29	2 > 29		4 < 29						10 > 29					15 > 29							22 > 29					
30		2 < 30	3 > 30	4 < 30		6 > 30				10 = 30		12 = 30		14 = 30				18 = 30		20 = 30		22 < 30		24 = 30	26 < 30		
31	1 > 31	2 > 31	3 > 31	4 < 31				8 > 32	9 > 31	10 > 31	11 > 31		13 > 31		15 > 31	16 > 31	18 > 31				21 > 31				26 > 31	27 > 31	
32	1 = 32	2 < 32				6 > 32						12 = 32															
33	1 > 33	2 > 33		4 < 33			8 > 33					12 > 33													24 = 32		

^zPairs of S-alleles not reported previously are shown in bold. S₂₈ from the cutleaf hazelnut gives self-compatibility in some pairs. S₂₈ was not included in this study. 1 > 2 indicates that S₁ is dominant to S₂; 1 < 3 indicates that S₁ is recessive to S₃; and 1 = 5 indicates that S₁ and S₅ are codominant in the pollen.

traits. Boccacci et al. (2006), Gökirmak et al. (2009), and Gürcan et al. (2010) identified the presumed parentage of several cultivars based on microsatellite markers.

Cultivars and selections were grouped by SSR marker profiles and geographic origin, and the most common alleles in each group were identified. The data were examined for differences in S-allele frequency associated with geographic origin. Variability in S-allele frequency among seed lots from the same country was also examined.

Results

NEW ALLELES AND TESTERS. Mehlenbacher (1997b) listed testers for 26 S-alleles, including S_{13} from the interspecific hybrids called “Chinese Trazels.” In this study we identified six new alleles and a *C. avellana* tester for S_{13} (Table 1). S_{27} is the dominant allele in ‘Buttner’s Zellernuss’ (S_{11} S_{27}). S_{28} is present in ‘Cutleaf’ (S_{20} S_{28}), as mentioned previously but was excluded from this study. S_{29} , the dominant allele in tester OSU 930.081 (S_4 S_{29}), was inherited from Russian selection OSU 495.049 (S_{22} S_{29}). The latter originated from seeds sent from the headquarters of the N.I. Vavilov Research Institute of Plant Industry in the city then called Leningrad. Most of the hazelnuts in Russia are grown in the south, from the Black Sea coast through the Caucasus Mountains to Krasnodar. We believe that the seeds sent to us originated in this region of southern Russia. S_{30} was first detected in seedlings of ‘The Shah’ (S_{14} S_{30}), which had been imported as scions from the United Kingdom. S_{30} was later detected in selections from Azerbaijan and Turkey. OSU 1116.049 (S_4 S_{30}), a selection from Azerbaijan, is the pollen tester 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 ‘Reka #2’ (S_2 S_{32}) from Serbia. The most recent new allele, S_{33} , is a codominant allele in ‘Ganja’ (S_4 S_{33}) from Azerbaijan. A tester that expresses only S_{33} in its pollen has not yet been identified. ‘Ata Baba,’ ‘Reka #2,’ and ‘Ganja’ are the pollen testers for S_{31} , S_{32} , and S_{33} , respectively. S_{13} , previously identified in “Chinese Trazels,” was found in the ‘Ashrafi’ clone 1226.004 (S_{13} S_{31}) from Azerbaijan. It was also detected in selection OSU 1168.130 (S_4 S_{13}), which originated from seeds purchased in the market in Holmskij, a village near Krasnodar, Russia, and in selection OSU 1090.042, which originated in a seed lot from Georgia. ‘Ashrafi’ and OSU 1168.130 are used as pollen testers, whereas the later-flowering ‘Ashrafi’ is also the female tester for S_{13} .

DOMINANCE RELATIONSHIPS. Mehlenbacher (1997b) presented dominance relationships based on 233 pairs of alleles. We identified 105 new pairs of alleles (Table 3) and in this article show the relationships for 338 of the possible 496 pairs of alleles. The number of pairs was limited for the most recently identified alleles. In all pairs, both alleles were expressed in the stigmas, but often only one was expressed in the pollen because of dominance. A revised dominance hierarchy was drawn based on new data for pairs of alleles (Fig. 1). The dominance hierarchy is linear with eight levels (Mehlenbacher, 1997b). The relationships among four alleles (S_{13} , S_{23} , S_{29} , and S_{31}) are unknown, so they are shown as adjacent boxes. All four are dominant to S_4 and recessive to one or more of the alleles at the next higher level (S_9 , S_{11} , S_{22} , and S_{26}).

S-ALLELES IN CULTIVARS. Mehlenbacher (2013) reported the alleles of 282 unique cultivars, including 112 from previous reports (Table 3). Cultivars with different names often have

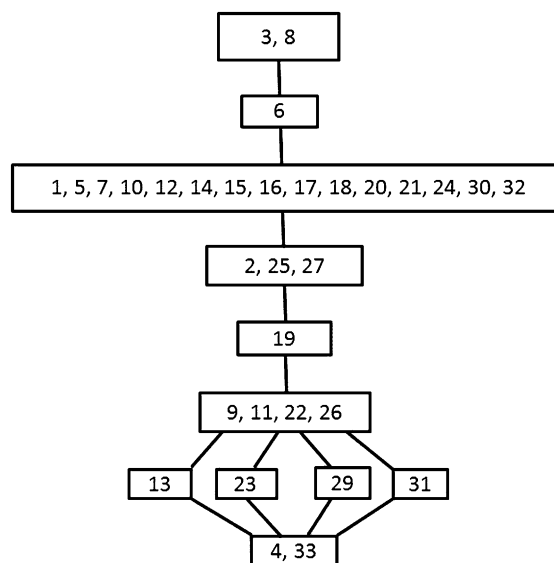


Fig. 1. Dominance hierarchy of S-alleles in hazelnut pollen. Alleles are dominant to alleles below them and codominant with those at the same level.

identical microsatellite marker fingerprints and S-alleles (Boccacci et al., 2006; Gökirmak et al., 2009; Gürcan et al., 2010), which leads to confusion. As a result, the number of unique genotypes in collections is often less than the number of names. Mehlenbacher (2013) listed cultivars with identical fingerprints and gave the preferred name for each. The S-alleles of 13 interspecific hybrids are also listed.

RELATIONSHIP OF S-ALLELES TO GEOGRAPHIC ORIGIN IN HAZELNUT CULTIVARS. Boccacci et al. (2006) and Gökirmak et al. (2009) assigned most hazelnut accessions to one of four groups: Spanish-Italian, Central European, English, and Black Sea. Other very diverse accessions that were not placed in one of the four main groups are presented as a group labeled “other” (Tables 4 and 5). Cultivars that have been fingerprinted with SSR markers (Boccacci et al., 2006; Gökirmak et al., 2009; S.A. Mehlenbacher, unpublished data) are listed as members of their assigned group. Accessions that have not yet been fingerprinted were placed in the most suitable group based on their geographic origin with consideration of morphological traits. The presumed parentage of several cultivars, based on microsatellite markers (Boccacci et al., 2006, 2008; Gökirmak et al., 2009; Gürcan et al., 2010), is listed (Table 4). The most frequent alleles in the 284 hazelnut cultivars (excluding interspecific hybrids) are: S_2 (13.9%), S_1 (9.3%), S_{10} (8.5%), S_5 (7.2%), S_3 (6.2%), S_4 (6.0%), and S_6 (5.3%). Percentages for all other alleles were less than 5.0%. Half of the alleles had frequencies below 2%. Allele frequencies differed among the cultivar groups. In the following paragraphs, alleles with frequencies greater than 4% are called common, alleles with frequencies between 2% and 4% are called rare, and alleles with frequencies less than 2% are called very rare.

The Spanish-Italian group contains 71 cultivars. The common alleles and their frequencies are: S_2 (30.3%), S_1 (14.1%), S_{10} (9.2%), S_{22} (7.8%), S_{17} (6.3%), and S_{23} (4.9%). The common alleles reflect the importance of ‘Barcelona’ (S_1 S_2), ‘Siciliana’ (syn. ‘Montebello’) (S_1 S_2), ‘Negret’ (S_{10} S_{22}), ‘Segorbe’ (S_9 S_{23}), and ‘Tonda di Giffoni’ (S_2 S_{23}) in this group.

Table 4. S-alleles and origins of hazelnut cultivars by group.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
Spanish-Italian	Alcover	Spain	<u>15</u>	22	
Spanish-Italian	Amarillo	Chile	<u>2</u>	<u>6</u>	
Spanish-Italian	Amarillo Tardio	Chile	<u>2</u>	<u>2</u>	
Spanish-Italian	B-3	Macedonia	<u>2</u>	<u>25</u>	
Spanish-Italian	Badem	Turkey	2	<u>5</u>	
Spanish-Italian	Barcelona	Spain	<u>1</u>	<u>2</u>	
Spanish-Italian	Barrettona	Italy	2	<u>6</u>	
Spanish-Italian	Belle di Giubilino	Italy	<u>1</u>	<u>10</u>	
Spanish-Italian	Bianca	Italy	<u>2</u>	<u>2</u>	
Spanish-Italian	Camponica	Italy	<u>1</u>	<u>2</u>	
Spanish-Italian	Casina	Spain	<u>10</u>	<u>21</u>	
Spanish-Italian	Closca Molla	Spain	2	<u>5</u>	
Spanish-Italian	Comen	Piemonte, Italy	<u>2</u>	9	
Spanish-Italian	Comun	Portugal	<u>10</u>	Unknown	
Spanish-Italian	Culpla	Spain	9	<u>10</u>	Negret × unknown ^y
Spanish-Italian	Da Viega	Portugal	<u>10</u>	<u>21</u>	
Spanish-Italian	Daria (104E)	Italy	2	<u>3</u>	TGdL × Cosford ^x
Spanish-Italian	Durazno	Chile	<u>1</u>	<u>2</u>	
Spanish-Italian	Fitzgerald 20	Oregon, U.S.	<u>2</u>	11	
Spanish-Italian	Francoli	Spain	<u>17</u>	22	Negret × Tomasina ^y
Spanish-Italian	Garrofi	Spain	1	<u>6</u>	
Spanish-Italian	Ghirara	Italy	2	<u>21</u>	
Spanish-Italian	Gironell (Grossal)	Spain	<u>1</u>	<u>2</u>	
Spanish-Italian	Gironenc Vermellet	Spain	2	<u>17</u>	
Spanish-Italian	Grifoll	Spain	2	22	Negret × Morell ^y
Spanish-Italian	Gubener Barcelloner	Germany	<u>1</u>	23	
Spanish-Italian	Iannusa Racinante	Italy	1	<u>8</u>	
Spanish-Italian	Lluenta	Spain	<u>17</u>	22	Negret × Gironenc Vermellet ^y
Spanish-Italian	Lozovskoi Sharovidnyi	Ukraine	<u>2</u>	<u>25</u>	
Spanish-Italian	Macrocarpa	United Kingdom	<u>1</u>	<u>2</u>	San Giovanni × Tonda Bianca ^y
Spanish-Italian	Martorella (COR 444)	Spain	<u>17</u>	22	
Spanish-Italian	Molar	Portugal	2	<u>10</u>	
Spanish-Italian	Morell	Spain	<u>1</u>	<u>2</u>	
Spanish-Italian	Mortarella	Italy	2	<u>17</u>	
Spanish-Italian	Napoletana	Italy	<u>1</u>	23	
Spanish-Italian	Napoletanecda	Italy	2	<u>14</u>	
Spanish-Italian	Negret	Spain	<u>10</u>	22	
Spanish-Italian	Nocchiolino Sangrato	Italy	<u>7</u>	<u>17</u>	
Spanish-Italian	Nociara	Italy	1	<u>3</u>	
Spanish-Italian	Pauetet	Spain	<u>18</u>	22	Negret × Artellet ^y
Spanish-Italian	Pere Mas	Spain	9	<u>10</u>	
Spanish-Italian	Pinyolenc #1	Spain	<u>2</u>	<u>2</u>	
Spanish-Italian	Pinyolenc #2	Spain	2	<u>17</u>	
Spanish-Italian	Planeta	Spain	<u>1</u>	<u>2</u>	
Spanish-Italian	Punxenc	Spain	<u>1</u>	<u>10</u>	Negret × unknown ^w
Spanish-Italian	Ratlada	Spain	<u>10</u>	22	
Spanish-Italian	Ratoli	Spain	2	<u>10</u>	
Spanish-Italian	Ribet	Spain	2	<u>16</u>	
Spanish-Italian	Riccia di Talanico	Italy	<u>1</u>	<u>2</u>	
Spanish-Italian	Römische Nuss	Italy (?)	<u>10</u>	<u>18</u>	
Spanish-Italian	San Giovanni	Italy	2	<u>8</u>	
Spanish-Italian	Sant Jaume	Spain	<u>1</u>	<u>17</u>	Barcelona × Pinyolenc #2 ^y
Spanish-Italian	Sant Joan	Spain	<u>2</u>	<u>25</u>	
Spanish-Italian	Sant Pere	Spain	<u>22</u>	<u>26</u>	Negret × unknown ^y
Spanish-Italian	Segorbe	Spain	9	23	
Spanish-Italian	Siciliana Montebello	Italy	<u>1</u>	<u>2</u>	
Spanish-Italian	Simon	Spain	<u>6</u>	22	Negret × Garrofi ^y
Spanish-Italian	Tapparona di Mezzanego	Italy	<u>5</u>	25	

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Table 4. Continued.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
Spanish-Italian	Tapparona di S.C.C. ¹	Italy	2	<u>24</u>	
Spanish-Italian	Tokolyi Cosford	Australia	<u>5</u>	<u>23</u>	
Spanish-Italian	Tomasina	Spain	<u>17</u>	<u>22</u>	
Spanish-Italian	Tonda Bianca	Italy	<u>1</u>	<u>23</u>	
Spanish-Italian	Tonda di Giffoni	Italy	<u>2</u>	<u>23</u>	
Spanish-Italian	Tonda Gentile delle Langhe	Italy	<u>2</u>	<u>7</u>	
Spanish-Italian	Tonda Romana	Italy	<u>10</u>	<u>20</u>	
Spanish-Italian	Tonda Rossa	Italy	<u>8</u>	<u>23</u>	
Spanish-Italian	Tonnolella	Italy	<u>2</u>	<u>24</u>	
Spanish-Italian	Tonollo	Australia	<u>1</u>	<u>2</u>	
Spanish-Italian	Trenet	Spain	<u>2</u>	<u>15</u>	
Spanish-Italian	Turk	Oregon, U.S.	<u>1</u>	<u>2</u>	
Spanish-Italian	Verde	Chile	<u>2</u>	<u>6</u>	
Central European	Acorn Hazelnut	Poland	<u>5</u>	<u>11</u>	Cosford × unknown ^y
Central European	Alli	Estonia	<u>9</u>	<u>20</u>	
Central European	Anglais	France	<u>5</u>	<u>19</u>	
Central European	Aveline d'Angleterre	France	<u>5</u>	<u>16</u>	
Central European	Barr's Zellernuss	United Kingdom	<u>5</u>	<u>11</u>	
Central European	Bergeri	France	<u>3</u>	<u>25</u>	
Central European	Blumberger Zellernuss	Germany/Poland	<u>4</u>	<u>20</u>	
Central European	Borovskoi	Ukraine	<u>10</u>	<u>24</u>	
Central European	Catalan	Poland	<u>10</u>	<u>25</u>	
Central European	Early Long Zeller	Wertheim, U.K.	<u>20</u>	<u>25</u>	
Central European	Frango #2	Poland	<u>5</u>	Unknown	Cosford × Pallagrossa ^y
Central European	Frango #4	Poland	<u>15</u>	<u>25</u>	
Central European	Frango #5	Poland	<u>11</u>	<u>25</u>	Cosford × Pallagrossa ^y
Central European	Goc	Poland	<u>6</u>	<u>15</u>	
Central European	Gunslebert	Germany	<u>5</u>	<u>23</u>	
Central European	Gustav's Zeller	Germany	<u>15</u>	<u>20</u>	
Central European	Hall's Giant	Germany	<u>5</u>	<u>15</u>	
Central European	Hemplov Zellsky	Germany	<u>12</u>	<u>20</u>	
Central European	Karol	Poland	<u>11</u>	<u>15</u>	
Central European	Lange Landsberger	Germany	<u>15</u>	<u>20</u>	Hall's Giant × Early Long Zeller ^y
Central European	Lech	Poland	<u>5</u>	<u>15</u>	
Central European	Lenka #3	Poland	<u>3</u>	<u>5</u>	Cosford × unknown ^y
Central European	Liegel's Zellernuss	Germany	<u>12</u>	<u>20</u>	
Central European	Louisen's Zellernuss	Germany	<u>10</u>	<u>25</u>	
Central European	Ludolph's Zeller	Germany	<u>5</u>	<u>20</u>	Hall's Giant × Early Long Zeller ^y
Central European	Maria	Poland	<u>11</u>	<u>15</u>	Cosford × unknown ^y
Central European	Neue Riesennuss	Germany	<u>18</u>	<u>25</u>	
Central European	Pallagrossa	Piemonte, Italy	<u>5</u>	<u>25</u>	
Central European	Pirosok	Ukraine	<u>10</u>	<u>24</u>	
Central European	Red Fortrin	Washington, U.S.	<u>2</u>	<u>6</u>	Barcelona × Rode Zeller ^y
Central European	Rode Zeller (Rote Zellernuss)	Netherlands/Germany	<u>6</u>	<u>11</u>	
Central European	Riekchen's Zeller	Germany	<u>5</u>	<u>25</u>	Hall's Giant × Early Long Zeller ^y
Central European	Sickler's Zellernuss	Germany	<u>5</u>	<u>20</u>	Hall's Giant × Early Long Zeller ^y
Central European	Syrena	Poland	<u>6</u>	<u>15</u>	
Central European	Truchsess Zellernuss	Germany	<u>5</u>	<u>25</u>	
Central European	Veleten	Ukraine	<u>15</u>	<u>15</u>	
Central European	Vistula	Poland	<u>2</u>	<u>5</u>	
Central European	Volski Round	Poland	<u>5</u>	<u>11</u>	Hall's Giant × Cosford ^y
English	Artellet	Spain	<u>14</u>	<u>18</u>	
English	Bandnuss	United Kingdom	<u>10</u>	<u>11</u>	

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Table 4. Continued.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
English	Brixley's New	Oregon, U.S.	<u>1</u>	<u>15</u>	
English	Brixnut	Oregon, U.S.	<u>1</u>	<u>14</u>	Barcelona × DuChilly ^y
English	Butler	Oregon, U.S.	<u>2</u>	<u>3</u>	Barcelona × Daviana ^{y,v}
English	Buttner's Zellernuss	Germany	11	<u>27</u>	
English	Compton	Oregon, U.S.	<u>2</u>	<u>3</u>	Barcelona × Daviana (?)
English	Contorta	United Kingdom	<u>5</u>	<u>10</u>	
English	Corabel	France	<u>1</u>	<u>3</u>	Barcelona × Cosford ^{y,v}
English	Frizzled Filbert	United Kingdom	<u>9</u>	<u>10</u>	
English	Cosford	United Kingdom	<u>3</u>	<u>11</u>	
English	Creswell	Oregon, U.S.	<u>2</u>	<u>10</u>	
English	Daviana	United Kingdom	<u>3</u>	<u>11</u>	
English	Downton Long #1	United Kingdom	<u>3</u>	<u>14</u>	
English	Downton Long #2	United Kingdom	<u>9</u>	<u>10</u>	
English	DuChilly	United Kingdom	<u>10</u>	<u>14</u>	
English	Empress Eugenie	United Kingdom	<u>3</u>	<u>14</u>	DuChilly × Cosford ^{y,v}
English	Ennis	Washington, U.S.	<u>1</u>	<u>11</u>	Barcelona × Daviana ^{y,v}
English	Fitzgerald	Washington, U.S.	<u>2</u>	<u>3</u>	Barcelona × Daviana ^y
English	Fitzgerald #20	Washington, U.S.	<u>2</u>	<u>11</u>	Barcelona × Daviana (?)
English	Freehusker	Oregon, U.S.	<u>1</u>	<u>11</u>	Barcelona × Cosford ^y
English	Garibaldi	United Kingdom	<u>5</u>	<u>11</u>	
English	Gauna	Argentina	<u>1</u>	<u>1</u>	
English	Gem	Oregon, U.S.	<u>2</u>	<u>14</u>	Barcelona × DuChilly ^y
English	Henneman #3	Unknown	<u>6</u>	<u>10</u>	
English	Jemtegaard 76	Oregon, U.S.	<u>2</u>	<u>3</u>	
English	Jemtegaard 80	Oregon, U.S.	<u>2</u>	<u>3</u>	
English	Lansing #1	Oregon, U.S.	<u>1</u>	<u>3</u>	Barcelona × Daviana (?)
English	Lansing #2	Oregon, U.S.	<u>3</u>	<u>10</u>	
English	Little Poland	Poland	<u>3</u>	<u>5</u>	Cosford × unknown ^y
English	Lyons	Oregon, U.S.	<u>2</u>	<u>14</u>	Barcelona × DuChilly ^y
English	March del Plata	Argentina	<u>16</u>	<u>23</u>	
English	Medium Long	New York, U.S.	<u>11</u>	<u>12</u>	
English	Moscow N35	Moscow Forestry Institute, Russia	<u>5</u>	<u>6</u>	
English	Nixon	Oregon, U.S.	<u>2</u>	<u>3</u>	Barcelona × Cosford ^y
English	Nonpareil	Oregon, U.S.	<u>1</u>	<u>3</u>	Barcelona × Daviana ^y
English	Nooksack	Washington, U.S.	<u>6</u>	<u>14</u>	DuChilly × unknown ^y
English	Nottingham	United Kingdom	<u>8</u>	<u>10</u>	
English	Princess Royal	United Kingdom	<u>11</u>	<u>14</u>	
English	Prolific Closehead	United Kingdom	<u>5</u>	<u>11</u>	
English	Royal	Oregon, U.S.	<u>1</u>	<u>3</u>	Barcelona × Cosford ^{y,w}
English	The Shah	United Kingdom	<u>14</u>	<u>30</u>	
English	Wallace Seedling	Oregon, U.S.	<u>2</u>	<u>11</u>	Barcelona × Daviana (?)
English	Warsaw Red	Poland	<u>1</u>	<u>6</u>	Barcelona × Henneman #3 ^y
English	Woodford	Oregon, U.S.	<u>1</u>	<u>3</u>	Barcelona × Daviana ^y
English	Volle Zeller CC05.45	Germany	<u>11</u>	<u>14</u>	
English	Volle Zeller R639	Germany	<u>3</u>	<u>14</u>	
Black Sea	Anakliuri	Georgia	<u>4</u>	<u>14</u>	
Black Sea	Arzu	Azerbaijan	<u>31</u>	<u>31</u>	
Black Sea	Ashrafi 1090.011	Azerbaijan	<u>16</u>	<u>31</u>	
Black Sea	Ashrafi 1226.004	Azerbaijan	<u>13</u>	<u>31</u>	
Black Sea	Aslan Baba	Azerbaijan	<u>4</u>	<u>15</u>	
Black Sea	Ata Baba	Azerbaijan	<u>4</u>	<u>31</u>	
Black Sea	Ata Ula	Azerbaijan	<u>4</u>	<u>10</u>	
Black Sea	Azeri	Azerbaijan	<u>2</u>	<u>27</u>	
Black Sea	B-4	Macedonia	<u>10</u>	<u>17</u>	
Black Sea	Barli	Azerbaijan	<u>10</u>	<u>31</u>	

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Table 4. Continued.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
Black Sea	Bomba	Azerbaijan	<u>2</u>	33	
Black Sea	Bulgaria XI-8	Bulgaria	<u>4</u>	<u>12</u>	
Black Sea	Cherkesskii II	Russia	4	<u>24</u>	
Black Sea	Chikivistava	Georgia	4	<u>10</u>	
Black Sea	Cozia	Romania	<u>5</u>	<u>15</u>	
Black Sea	Dal Rossa	Italy	<u>5</u>	<u>18</u>	
Black Sea	Dedoplistiti	Georgia	<u>8</u>	14	
Black Sea	Elbari	Azerbaijan	<u>2</u>	33	
Black Sea	Firavan	Azerbaijan	4	<u>31</u>	
Black Sea	Galib	Azerbaijan	4	<u>16</u>	
Black Sea	Ganja	Azerbaijan	<u>4</u>	<u>33</u>	
Black Sea	Georgian OSU 759.010	Georgia	4	<u>20</u>	
Black Sea	Gizil Findiq	Azerbaijan	<u>10</u>	31	
Black Sea	Gobekli	Azerbaijan	4	<u>5</u>	
Black Sea	Imperiale de Trebizonde	Turkey	2	<u>10</u>	
Black Sea	Istarski Duguljasti	Slovenia	<u>10</u>	<u>17</u>	
Black Sea	Ordu	Turkey	4	<u>25</u>	
Black Sea	Kalinkara	Turkey	4	<u>21</u>	Incekara × Palaz or Kan ^u
Black Sea	Khachapura	Georgia	<u>3</u>	18	
Black Sea	Kudryavchik 1226.003	Georgia	4	<u>10</u>	
Black Sea	Kudryavchik 1226.041	Georgia	4	<u>24</u>	
Black Sea	Mincane (Akcakoca)	Turkey	4	<u>10</u>	
Black Sea	Nasimi	Azerbaijan	4	<u>31</u>	
Black Sea	Nemsa	Georgia	<u>1</u>	4	
Black Sea	Palaz	Turkey	<u>2</u>	4	
Black Sea	Pellicule Rouge	France (?)	<u>5</u>	<u>10</u>	
Black Sea	Pioneer	Ukraine	<u>2</u>	4	
Black Sea	Qabala	Azerbaijan	4	<u>6</u>	
Black Sea	Red Lambert	United Kingdom (in 1600s)	<u>5</u>	<u>10</u>	
Black Sea	Romavel	Romania	<u>2</u>	Unknown	
Black Sea	Sachakhli	Azerbaijan	<u>5</u>	<u>10</u>	
Black Sea	Ordu	Turkey	4	<u>25</u>	
Black Sea	San Benedetto	Italy	4	<u>12</u>	
Black Sea	Shokoladnyi	Ukraine	4	<u>11</u>	
Black Sea	Shveliskura	Georgia	<u>5</u>	<u>10</u>	
Black Sea	Shveliskura Row 1190	Georgia	4	<u>14</u>	
Black Sea	Skorospelka	Georgia	4	<u>23</u>	
Black Sea	Sivri Ghiaghli	Greece	4	<u>12</u>	
Black Sea	Sivri Ocak 5	Turkey	<u>8</u>	10	
Black Sea	Tala	Azerbaijan	<u>2</u>	<u>5</u>	
Black Sea	Tombul (syn. Extra Ghiaghli)	Turkey	4	<u>12</u>	
Black Sea	Tombul Ghiaghli	Greece/Turkey	4	<u>8</u>	
Black Sea	Topkhara	Azerbaijan	2	<u>10</u>	
Black Sea	White Filbert	Southern Europe (?)	<u>5</u>	<u>10</u>	White Filbert × unknown ^y
Black Sea	Whiteheart	New Zealand	2	<u>10</u>	
Black Sea	Ugbrooke	New Zealand	<u>5</u>	9	
Black Sea	Uzum Sakar	Azerbaijan	4	<u>10</u>	
Black Sea	Webb's Prize Cob	United Kingdom	<u>17</u>	<u>17</u>	
Black Sea	Yagli Findiq	Azerbaijan	<u>4</u>	<u>4</u>	
Other	Albania 80	Albania	<u>8</u>	32	
Other	Aurea	France	<u>6</u>	9	
Other	Barbakan	Unknown?	<u>5</u>	6	
Other	Barcelloner Zellernuss	Spain	<u>10</u>	<u>17</u>	
Other	Bosio	Italy	<u>1</u>	2	
Other	Burchardt's Zellernuss	Germany	2	<u>7</u>	

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Table 4. Continued.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
Other	Crvenje	Serbia	<u>6</u>	23	
Other	Cutleaf	United Kingdom	<u>20</u>	<u>28</u>	
Other	Danish Wild	Denmark	<u>8</u>	23	
Other	Dnepr-1	Ukraine	<u>15</u>	<u>21</u>	
Other	Ducalovici	Serbia	<u>1</u>	9	
Other	Finland COR 187	Finland	9	<u>25</u>	
Other	Fusco Rubra	Breslau, Germany	<u>6</u>	19	
Other	Gasaway	Washington, U.S.	<u>3</u>	26	
Other	Jean's	Italy (?)	2	<u>10</u>	
Other	Menoia	Italy	<u>8</u>	<u>10</u>	
Other	Moscow N01	Moscow Forestry Institute, Russia	<u>21</u>	23	
Other	Moscow N01.06	Moscow Forestry Institute, Russia	<u>6</u>	20	
Other	Moscow N01.07	Moscow Forestry Institute, Russia	<u>6</u>	20	
Other	Moscow N02	Moscow Forestry Institute, Russia	<u>6</u>	20	
Other	Moscow N06	Moscow Forestry Institute, Russia	2	<u>20</u>	
Other	Moscow N08	Moscow Forestry Institute, Russia	<u>5</u>	26	
Other	Moscow N11	Moscow Forestry Institute, Russia	<u>6</u>	20	
Other	Moscow N12	Moscow Forestry Institute, Russia	<u>6</u>	20	
Other	Moscow N23	Moscow Forestry Institute, Russia	<u>6</u>	30	
Other	Moscow N26	Moscow Forestry Institute, Russia	<u>1</u>	29	
Other	Moscow N27	Moscow Forestry Institute, Russia	<u>19</u>	23	
Other	Moscow N28	Moscow Forestry Institute, Russia	<u>2</u>	26	
Other	Moscow N30	Moscow Forestry Institute, Russia	26	<u>30</u>	
Other	Moscow N31	Moscow Forestry Institute, Russia	26	Unknown	
Other	Moscow N33	Moscow Forestry Institute, Russia	<u>5</u>	19	
Other	Moscow N34	Moscow Forestry Institute, Russia	9	<u>20</u>	
Other	Moscow N36	Moscow Forestry Institute, Russia	<u>1</u>	<u>20</u>	
Other	Moscow N37	Moscow Forestry Institute, Russia	1	<u>6</u>	
Other	Moscow N38	Moscow Forestry Institute, Russia	<u>20</u>	<u>30</u>	
Other	Moscow N43	Moscow Forestry Institute, Russia	<u>6</u>	32	
Other	Moscow N45	Moscow Forestry Institute, Russia	<u>6</u>	32	
Other	Pendula	France	<u>3</u>	9	
Other	Polli 3-10	Estonia	<u>2</u>	<u>27</u>	
Other	Reka #1	Serbia	<u>1</u>	<u>17</u>	
Other	Reka #2	Serbia	2	<u>32</u>	
Other	Sodlinger	Serbia (Slovenia)	<u>6</u>	11	

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Table 4. Continued.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
Other	Stepovy	Not in USDA database	2	<u>5</u>	
Other	Suvodol	Ukraine	5	<u>6</u>	
Other	Trbusani	Serbia	<u>15</u>	26	
Other	Uebov	Serbia	<u>12</u>	<u>16</u>	
Other	Zimmerman	Oregon, U.S.	1	<u>3</u>	Barcelona × Gasaway ^y
OSU ^s	Clark (OSU 276.142)	Oregon, U.S.	<u>3</u>	<u>8</u>	Tombul Ghiaghli × Willamette ^x
OSU	Delta (OSU 510.041)	Oregon, U.S.	<u>1</u>	<u>15</u>	OSU 249.159 × VR 17-15 ^x
OSU	Dorris (OSU 876.041)	Oregon, U.S.	<u>1</u>	<u>12</u>	OSU 309.074 × Delta ^x
OSU	Epsilon (OSU 699.073)	Oregon, U.S.	<u>1</u>	<u>4</u>	(T. Romana × T. Ghiaghli) × Zimmerman ^x
OSU	Eta (OSU 984.075)	Oregon, U.S.	<u>11</u>	<u>26</u>	OSU 581.039 × OSU 553.090 ^x
OSU	Felix (OSU 941.016)	Oregon, U.S.	<u>15</u>	<u>21</u>	OSU 384.095 × Delta ^x
OSU	Gamma (OSU 589.028)	Oregon, U.S.	2	<u>10</u>	Casina × (R. di Talanico × Gasaway) ^x
OSU	Jefferson (OSU 703.007)	Oregon, U.S.	1	<u>3</u>	OSU 252.146 × OSU 414.062 ^x
OSU	Lewis (OSU 243.002)	Oregon, U.S.	<u>3</u>	<u>8</u>	(Barc. × Tombul Ghiaghli) × Willamette ^x
OSU	Red Dragon	Oregon, U.S.	<u>6</u>	26	OSU 487.055 × OSU 367.039 ^x
OSU	Sacajawea (OSU 540.130)	Oregon, U.S.	<u>1</u>	22	OSU 43.091 × Sant Pere ^x
OSU	Santiam (OSU 509.064)	Oregon, U.S.	<u>3</u>	15	OSU 249.159 × VR 17-15 ^x
OSU	Theta (OSU 1001.008)	Oregon, U.S.	<u>5</u>	<u>15</u>	OSU 561.184 × Delta ^x
OSU	Tonda Pacifica (OSU 228.084)	Oregon, U.S.	<u>1</u>	<u>2</u>	TGdL × (Barc. × Extra Ghiaghli) ^x
OSU	VR 11-27	Oregon, U.S.	1	<u>3</u>	Montebello × Gasaway ^x
OSU	VR 20-11	Oregon, U.S.	2	<u>3</u>	(Barc. × Compton) × Gasaway ^x
OSU	VR 23-18	Oregon, U.S.	1	<u>3</u>	(Barc. × Lansing) × Gasaway ^x
OSU	VR 4-31	Oregon, U.S.	1	<u>3</u>	Montebello × Gasaway ^x
OSU	Wepster (OSU 894.030)	Oregon, U.S.	<u>1</u>	<u>2</u>	T. Pacifica × OSU 440.005 ^x
OSU	Willamette (OSU 43.058)	Oregon, U.S.	1	<u>3</u>	Montebello × unknown ^x
OSU	Yamhill (OSU 542.102)	Oregon, U.S.	<u>8</u>	26	OSU 296.082 × (Montebello × Gasaway) ^x
OSU	York (OSU 878.048)	Oregon, U.S.	2	<u>21</u>	OSU 479.027 × OSU 504.065 ^x
OSU	Zeta (OSU 670.095)	Oregon, U.S.	<u>1</u>	<u>1</u>	OSU 342.019 × Zimmerman ^x
Interspecific hybrids	Bixby	U.S.	<u>20</u>	23	Rush × Italian Red ^x
Interspecific hybrids	Buchanan	U.S.	<u>12</u>	<u>15</u>	
Interspecific hybrids	Chinese Trazel Gellatly #4	British Columbia, Canada	<u>15</u>	25	
Interspecific hybrids	Chinese Trazel Gellatly #11	British Columbia, Canada	13	<u>15</u>	
Interspecific hybrids	Chinese Trazel Gellatly #6	British Columbia, Canada	13	<u>15</u>	
Interspecific hybrids	Dalian 83–81	China	<u>3</u>	19	
Interspecific hybrids	Dawei (Dalian 84-329)	China	5	<u>6</u>	
Interspecific hybrids	Dalian 84-75	China	<u>3</u>	7	
Interspecific hybrids	Faroka	Michigan, U.S.	<u>11</u>	13	
Interspecific hybrids	Farris 88BS	Michigan, U.S.	<u>3</u>	11	
Interspecific hybrids	Grand Traverse	Michigan, U.S.	11	<u>25</u>	Faroka × unknown ^x

Continued next page

Table 4. Continued.

Group ^z	Cultivar	Origin	S-alleles (no.)		Parentage
Interspecific hybrids	Potomac	U.S.	<u>5</u>	<u>12</u>	Rush × DuChilly ^x
Interspecific hybrids	Reed	U.S.	<u>12</u>	<u>15</u>	Rush × Hall's Giant ^x

^zCultivars assigned to groups based primarily on simple sequence repeat analysis (Boccacci et al., 2006; Gökirmak et al., 2009; Mehlenbacher, unpublished data) with consideration of morphology and geographic origin.

^yParentage based on simple sequence repeat markers (Gökirmak et al., 2009).

^xParentage based on publications and/or breeder records.

^wParentage based on simple sequence repeat markers (Boccacci et al., 2008).

^vParentage based on simple sequence repeat markers (Boccacci et al., 2006).

^uParentage based on simple sequence repeat markers (Gürcan et al., 2010).

^tTapparona di San Colombano Cortemoli.

^sOSU = Oregon State University breeding program.

The Central European group contains 38 cultivars. The most common alleles are S_5 (21.1%), S_{15} (14.5%), S_{25} (13.2%), S_{20} (11.8%), S_{11} (9.2%), S_6 (5.3%), and S_{10} (5.3%). The common alleles reflect the importance of 'Hall's Giant' (S_5 S_{15}) and 'Early Long Zeller' (S_{20} S_{25}) in this group, which also includes hybrids with the English cultivars Daviana (S_3 S_{11}) and Cosford (S_3 S_{11}).

The English group contains 57 cultivars. The most common alleles are S_3 (19.2%), S_{11} (13.8%), S_{14} (12.8%), S_2 (11.7%), S_{10} (9.6%), and S_5 (5.3%). The common alleles reflect the importance of English cultivars Daviana (S_3 S_{11}), Cosford (S_3 S_{11}), and DuChilly (S_{10} S_{14}). The group includes several hybrids between these three English cultivars and 'Barcelona' (S_1 S_2).

The Black Sea group contains 58 cultivars. The most common alleles and their frequencies are: S_4 (27.6%), S_{10} (15.5%), S_2 (8.6%), S_5 (8.6%), and S_{31} (7.8%). The first four alleles had been reported earlier in Turkish cultivars (Erdoğan et al., 2005; Mehlenbacher, 1997b), whereas S_{31} is common in cultivars from Azerbaijan.

To simplify discussion, all 47 other accessions were placed in a single very diverse group called "other." The most frequent alleles in this group were S_6 (16.0%), S_{20} (10.6%), S_2 (8.5%), S_1 (7.5%), S_{26} (6.4%), S_5 (5.3%), and S_9 (5.3%). This group includes the ornamentals 'Fusco Rubra', 'Aurea', 'Pendula', 'Cutleaf', and 21 selections from the Russian Research Institute of Forestry and Mechanization (Pushkino, Russian Federation). Half of the Moscow selections from Pushkino have red leaves. S_{20} is common in the cold-hardy Central European types with large nuts [e.g., 'Early Long Zeller' (S_{20} S_{25})] that were probably used as parents in Moscow. The high frequency of S_{26} in this group is surprising, because its frequency is only 1.76% of the total in the 284 cultivars. S_{26} may be common in the parents of the Moscow selections. To survive in Moscow, the parents and selections must be cold-hardy.

In the 23 cultivars and pollenizers released by the OSU breeding program, the most common alleles are S_1 (28.3%), S_3 (19.6%), S_2 (10.9%), S_{15} (8.7%), S_8 (6.5%), and S_{26} (6.5%), which reflects the contributions of 'Barcelona' (S_1 S_2), 'Montebello' (S_1 S_2), 'Daviana' (S_3 S_{11}), 'Tonda Gentile delle Langhe' (S_2 S_7), 'Hall's Giant' (S_5 S_{15}), 'Tombul Ghiaghli' (S_4 S_8), and 'Gasaway' (S_3 S_{26}).

INTERSPECIFIC HYBRIDS. The 13 interspecific hybrids include four *C. americana* Marsh. × *C. avellana* hybrids ('Bixby', 'Buchanan', 'Potomac', and 'Reed'), three *C. heterophylla*

Fisch. × *C. avellana* hybrids from Dalian, China, and six hybrids with *C. colurna* L. and *C. avellana* in their pedigrees. S_{15} was present in all three Chinese Trazels.

S-ALLELES IN SELECTIONS. The S-alleles of 522 selections of diverse origin were determined and are presented by geographic origin (Table 6). The origin of the seed lots is listed (Table 2).

TURKISH SELECTIONS. The S-alleles were determined for 258 selections in eight groups of Turkish origin (Table 7). Of these, 114 originated as seeds harvested in the collection block at the Hazelnut Research Institute in Giresun and the remainder from various orchards and markets. In the Turkish selections, S_4 was by far the most common allele, representing 30.2% of the total. S_4 was present in high frequency in all eight groups of Turkish selections. The second most common allele was S_{12} , which represented 10.7% of the total and was also present in all eight groups. The next most common alleles were S_8 (9.9%), S_{10} (9.9%), S_2 (7.8%), and S_{16} (4.3%), which were present in eight, six, seven, and four groups, respectively. Rare alleles detected at frequencies of 2% to 4% include S_{14} , S_3 , S_5 , S_9 , and S_{25} , which were present in four, four, five, five, and six groups, respectively. Of the 33 alleles so far identified, only three (S_{23} , S_{29} , and S_{31}) were absent in the Turkish selections; 18 others were present at frequencies less than 2%. The most common alleles in the selections are also present in Turkish cultivars, but the selections include a very large number of additional alleles present at low frequency.

GEORGIAN SELECTIONS. Nuts were collected in orchards in the Republic of Georgia (Table 8). Selections in Groups 1 through 5 were from nuts collected in 2001 and selections in Group 6 were from nuts collected in 2003. Eight selections (Group 1) were from nuts collected in orchards in the inland area of Kakheti at the base of the Caucasus Mountains near the border with Azerbaijan. The other five groups were collected in orchards near the Black Sea coast; Groups 2 to 5 were collected near Zugdidi. In the 43 selections, the most frequent allele was S_4 (22.1%) followed by S_2 (11.6%), S_{10} (9.3%), and S_{20} (8.1%). Four additional alleles (S_{31} , S_1 , S_{19} , and S_{27}) were present at frequencies of 4% to 6%. Eight alleles were rare and present at frequencies of 2% to 4% (S_8 , S_{14} , S_3 , S_5 , S_6 , S_{11} , S_{18} , and S_{30}). Seven alleles were present at frequencies less than 2% and nine were absent. S_4 is present in 'Anakliuri', which is the most widely planted in Georgia.

AZERBAIJAN SELECTIONS. Nuts were collected in orchards in three locations: Zaqatala, Qabala, and Xaçmaz. The cultivars

Table 5. Frequency of S-alleles in hazelnut cultivars by group.

Allele	Group							
	Spanish-Italian		Central European		English		Black Sea	
	(no.)	(%)	(no.)	(%)	(no.)	(%)	(no.)	(%)
1	20	14.08	0	0.00	12	12.77	1	0.86
2	43	30.28	2	2.63	11	11.70	10	8.62
3	2	1.41	2	2.63	18	19.15	1	0.86
4	0	0.00	1	1.32	0	0.00	32	27.59
5	4	2.82	16	21.05	5	5.32	10	8.62
6	5	3.52	4	5.26	4	4.26	1	0.86
7	2	1.41	0	0.00	0	0.00	0	0.00
8	3	2.11	0	0.00	1	1.06	3	2.59
9	4	2.82	1	1.32	2	2.13	1	0.86
10	13	9.15	4	5.26	9	9.57	18	15.52
11	1	0.70	7	9.21	13	13.83	1	0.86
12	0	0.00	2	2.63	1	1.06	4	3.45
13	0	0.00	0	0.00	0	0.00	1	0.86
14	1	0.70	0	0.00	12	12.77	3	2.59
15	2	1.41	11	14.47	1	1.06	2	1.72
16	1	0.70	1	1.32	1	1.06	2	1.72
17	9	6.34	0	0.00	0	0.00	4	3.45
18	2	1.41	1	1.32	1	1.06	2	1.72
19	0	0.00	1	1.32	0	0.00	0	0.00
20	1	0.70	9	11.84	0	0.00	1	0.86
21	3	2.11	0	0.00	0	0.00	1	0.86
22	11	7.75	0	0.00	0	0.00	0	0.00
23	7	4.93	1	1.32	1	1.06	1	0.86
24	2	1.41	2	2.63	0	0.00	2	1.72
25	4	2.82	10	13.16	0	0.00	1	0.86
26	1	0.70	0	0.00	0	0.00	0	0.00
27	0	0.00	0	0.00	1	1.06	1	0.86
28	0	0.00	0	0.00	0	0.00	0	0.00
29	0	0.00	0	0.00	0	0.00	0	0.00
30	0	0.00	0	0.00	1	1.06	0	0.00
31	0	0.00	0	0.00	0	0.00	9	7.76
32	0	0.00	0	0.00	0	0.00	0	0.00
33	0	0.00	0	0.00	0	0.00	3	2.59
Unknown	1	0.70	1	1.32	0	0.00	1	0.86
Total	142	100.00	76	100.00	94	100.00	116	100.00

Allele	Group					
	Other		OSU releases ^z		Total	
	(no.)	(%)	(no.)	(%)	(no.)	(%)
1	7	7.45	13	28.26	53	9.33
2	8	8.51	5	10.87	79	13.91
3	3	3.19	9	19.57	35	6.16
4	0	0.00	1	2.17	34	5.99
5	5	5.32	1	2.17	41	7.22
6	15	15.96	1	2.17	30	5.28
7	1	1.06	0	0.00	3	0.53
8	3	3.19	3	6.52	13	2.29
9	5	5.32	0	0.00	13	2.29
10	3	3.19	1	2.17	48	8.45
11	1	1.06	1	2.17	24	4.23
12	1	1.06	1	2.17	9	1.58
13	0	0.00	0	0.00	1	0.18
14	0	0.00	0	0.00	16	2.82
15	2	2.13	4	8.70	21	3.70
16	1	1.06	0	0.00	6	1.06
17	2	2.13	0	0.00	15	2.64

Continued next page

Table 5. Continued.

Allele	Group				Total	
	Other		OSU releases ^z			
	(no.)	(%)	(no.)	(%)	(no.)	(%)
18	0	0.00	0	0.00	6	1.06
19	3	3.19	0	0.00	4	0.70
20	10	10.64	0	0.00	21	3.70
21	2	2.13	2	4.35	7	1.23
22	0	0.00	1	2.17	12	2.11
23	4	4.26	0	0.00	14	2.46
24	0	0.00	0	0.00	6	1.06
25	1	1.06	0	0.00	16	2.82
26	6	6.38	3	6.52	10	1.76
27	1	1.06	0	0.00	3	0.53
28	1	1.06	0	0.00	1	0.18
29	1	1.06	0	0.00	1	0.18
30	3	3.19	0	0.00	4	0.70
31	0	0.00	0	0.00	9	1.58
32	4	4.26	0	0.00	4	0.70
33	0	0.00	0	0.00	3	0.53
Unknown	1	1.06	0	0.00	4	0.70
Total	94	100.00	46	100.00	568	100.00

^zOSU = Oregon State University.

grown in each location are different. The most common alleles in the selections were S_4 (29.6%), S_{31} (18.4%), S_{10} (14.3%), S_{18} (7.1%), S_2 (6.1%), and S_{24} (4.1%) (Table 9). Rare alleles present in frequencies of 2% to 4% included S_3 , S_7 , S_{12} , S_{14} , and S_{19} . Eight additional alleles were present at frequencies less than 2% and 12 were absent. The high frequency of S_4 and S_{31} reflects the importance of ‘Ata Baba’ (S_4 S_{31}) in the country. Fewer alleles were detected in selections from Azerbaijan than in selections from Turkey, Russia, and Georgia.

ARMENIAN SELECTIONS. The S-alleles were identified in 26 selections (Table 6) that originated from seeds purchased in markets in 2002 by J. Postman of USDA-ARS-NCGR. The most common alleles were S_4 (17.3%), S_2 and S_{31} (11.5% each), S_3 (7.7%), and S_9 and S_{26} (5.8% each). Rare alleles present at frequencies of 2% to 4% were S_7 , S_{16} , S_{18} , S_{20} , S_{25} , S_{27} , and S_{30} . Six alleles were very rare and only detected in one selection each, whereas 12 alleles were absent. The most common alleles (S_4 and S_{31}) are those of the most important cultivar in Azerbaijan, ‘Ata Baba’.

RUSSIAN SELECTIONS. The most common alleles in the eight groups of Russian selections were S_4 (21.3%), S_{24} (10.6%), S_{10} (8.5%), S_5 (7.4%), and S_{14} (4.3%), which were found in five, five, six, three, and two of the eight groups, respectively (Table 10). Groups 1 to 5 could be considered cultivated Russian types, whereas Groups 6 and 7 originated in germplasm collection blocks, and Group 8 represents selections grown from nuts collected in the wild near Moscow. S_4 , S_{24} , and S_{10} were very common in the cultivated Russian groups, reflecting the importance of ‘Cherkesskii II’ (S_4 S_{24}). Twelve rare alleles present at frequencies of 2% to 4% were S_2 , S_6 , S_{15} , S_{17} , S_{19} , S_3 , S_8 , S_{11} , S_{18} , S_{26} , S_{20} , and S_{31} . Only S_{27} and S_{33} were absent in the Russian selections, which overall were a very diverse population.

UKRAINIAN SELECTIONS. Nuts collected in the Crimea in 2002 gave 24 selections (Table 6). Of these, 21 were from nuts purchased from roadside vendors between Alushta and Simferopol, and

three originated from seeds collected at the Nikita Botanical Garden in Yalta. Most of the nuts purchased from vendors were very small and may have been collected from the wild. The most common alleles in the Crimean selections were S_{10} (22.9%), S_2 (12.5%), S_{25} (8.3%), S_9 (8.3%), S_3 and S_{14} (6.3% each), S_{16} , S_{21} , S_{22} , and S_{24} (4.2% each). Eight rare alleles were present at frequencies of 2% to 4%, and 13 alleles were not detected.

IRANIAN SELECTIONS. Seeds were collected from a small orchard in a valley in the foothills of the Elburz Mountains south of the Caspian Sea in 2003. Additional seeds were purchased from a roadside vendor along the main highway in the Talesh Mountains west of Astara. These seed lots gave six and three selections, respectively. Only four alleles were detected in the nine selections (Table 6): S_2 (55.6%), S_{33} (27.8%), S_8 (11.1%), and S_4 (5.6%).

OTHER SELECTIONS. Of the 19 selections in the miscellaneous group labeled “other” (Table 6), 13 were from seeds collected in the wild in 1990 or 1992 in northern Italy. Three were from nuts collected in Latvia, one from Lithuania, and one from Estonia. Nuts from the University of Minnesota, likely of Scandinavian origin, gave rise to selection OSU 408.040. The most common alleles in this miscellaneous group were S_9 (15.9%), S_5 and S_6 (10.5% each), and S_{10} and S_{15} (7.9% each). Rare alleles detected once or twice were: S_2 , S_4 , S_7 , S_{12} , S_{14} , S_{16} , S_{18} , S_{19} , S_{23} , S_{24} , S_{27} , and S_{30} . Twelve alleles were not detected.

Differences were noted in allele frequency between cultivars and selections (Table 11). S_4 was much more common in the selections than in the cultivars, whereas S_1 and S_2 were more common in the cultivars than in the selections.

Discussion

RELATIONSHIP OF S-ALLELES TO GEOGRAPHIC ORIGIN IN HAZELNUT CULTIVARS. Boccacci et al. (2006), Gökirmak et al. (2009), and Gürçan et al. (2010) assigned most hazelnut

Table 6. S-alleles in hazelnut selections originating from seeds collected in several countries.^z

Allele no.	Country								Total		Countries in which present (no.)
	Turkey	Georgia	Azerbaijan	Armenia	Russia	Ukraine	Iran	Other	(no.)	(%)	
1	8	4	0	1	3	0	0	0	16	1.53	4
2	40	10	6	6	7	6	10	1	86	8.24	8
3	16	2	2	4	5	3	0	0	32	3.07	6
4	156	19	29	9	40	1	1	1	256	24.52	8
5	12	2	1	0	14	1	0	4	34	3.26	6
6	4	2	1	1	7	1	0	4	20	1.92	7
7	2	1	3	2	2	0	0	1	11	1.05	6
8	51	3	1	1	5	1	2	0	64	6.13	7
9	11	1	1	3	3	4	0	6	29	2.78	7
10	51	8	14	0	16	11	0	3	103	9.87	6
11	1	2	0	0	5	1	0	0	9	0.86	4
12	55	0	2	1	1	0	0	1	60	5.75	5
13	1	1	0	0	1	0	0	0	3	0.29	3
14	18	3	2	0	8	3	0	1	35	3.35	6
15	1	0	0	1	6	0	0	3	11	1.05	4
16	22	0	1	2	2	2	0	1	30	2.87	6
17	3	1	0	0	6	1	0	0	11	1.05	4
18	3	2	7	2	5	0	0	1	20	1.92	6
19	5	4	3	0	6	1	0	1	20	1.92	6
20	2	7	0	2	4	0	0	0	15	1.44	4
21	9	1	0	1	1	2	0	2	16	1.53	6
22	7	0	1	0	2	2	0	2	14	1.34	5
23	0	0	0	0	3	1	0	1	5	0.48	3
24	2	1	4	1	20	2	0	1	31	2.97	7
25	11	1	1	2	2	4	0	2	23	2.20	7
26	5	0	0	3	5	0	0	0	13	1.25	3
27	2	4	0	2	0	0	0	1	9	0.86	4
28	0	0	0	0	0	0	0	0	0	0.00	0
29	0	0	0	0	1	0	0	0	1	0.10	1
30	9	2	1	2	1	0	0	1	16	1.53	6
31	0	5	18	6	4	0	0	0	33	3.16	4
32	3	0	0	0	2	0	0	0	5	0.48	2
33	1	0	0	0	0	0	5	0	6	0.57	2
Unknown	5	0	0	0	1	1	0	0	7	0.67	3
Sum	516	86	98	52	188	48	18	38	1044	100.00	

^zShown for each S-allele are the counts of the number of seedlings with that allele.

accessions to one of four groups based on microsatellite marker fingerprints: Spanish-Italian, Central European, English, and Black Sea. We present the S-alleles of cultivars and selections by group. Accessions that had not yet been fingerprinted were placed in the most suitable group based on their geographic origin with consideration of morphological traits. Other very diverse accessions that were not placed in one of the four main groups are presented as a group labeled “other.” The most frequent alleles in the 284 hazelnut cultivars (excluding interspecific hybrids) are S_2 , S_1 , S_{10} , S_5 , S_3 , and S_4 . Percentages for all other alleles were less than 6.0%. Many alleles were detected but at low frequency; half of the alleles had frequencies below 2%. There were striking differences in S-allele frequencies among the cultivar groups (Table 5).

In the Spanish-Italian group, the most common alleles are S_2 , S_1 , S_{10} , S_{22} , and S_{17} . The first four reflect the importance of ‘Barcelona’ ($S_1 S_2$), ‘Siciliana’ [syn. ‘Montebello’ ($S_1 S_2$)], and ‘Negret’ ($S_{10} S_{22}$) in this group. In the Central European group, the most common alleles are S_5 , S_{15} , S_{25} , S_{20} , and S_{11} . This

reflects the importance of ‘Hall’s Giant’ ($S_5 S_{15}$), ‘Early Long Zeller’ ($S_{20} S_{25}$), and ‘Pallagrossa’ ($S_5 S_{25}$). The German group includes several hybrids between German cultivars with the English cultivars Daviana ($S_3 S_{11}$) and Cosford ($S_3 S_{11}$), which accounts for the high frequency of S_{11} . Three Polish cultivars in this group (Frango #2, Frango #5, and Volski Round) were determined by Gökirmak et al. (2009) to be seedlings of ‘Cosford’. In the English group, the most common alleles are S_3 , S_{11} , S_1 , S_{14} , S_2 , and S_{10} . The common alleles reflect the importance of the English cultivars Daviana, Cosford, and DuChilly ($S_{10} S_{14}$). Several cultivars in this group are hybrids between English cultivars and ‘Barcelona’ ($S_1 S_2$), which accounts for the high frequencies of S_1 and S_2 . Several cultivars selected by growers in the Pacific Northwestern United States appear to be hybrids of ‘Barcelona’ and ‘Daviana’ (‘Butler’, ‘Ennis’, ‘Fitzgerald’, ‘Nonpareil’, and ‘Woodford’ and probably also ‘Compton’, ‘Fitzgerald #20’, ‘Lansing #1’, and ‘Wallace Seedling’). An additional three grower selections (‘Freehusker’, ‘Nixon’, and ‘Royal’) and the French cultivar Corabel are hybrids between ‘Barcelona’ and ‘Cosford’,

Table 7. Frequency of S-alleles in hazelnut selections originating in eight seed lots collected in Turkey.

Allele no.	Turkish selection group no.								Total		Groups present (no.)
	1	2	3	4	5	6	7	8	(no.)	(%)	
1	1	1	0	1	1	0	0	4	8	1.55	5
2	1	0	17	3	1	1	5	12	40	7.75	7
3	0	0	1	2	0	1	0	12	16	3.10	4
4	9	5	15	16	12	26	8	65	156	30.23	8
5	2	0	1	1	1	0	0	7	12	2.33	5
6	0	0	1	0	0	0	1	2	4	0.78	3
7	0	0	0	0	0	0	1	1	2	0.39	2
8	4	9	3	11	1	14	2	7	51	9.88	8
9	1	1	0	0	0	1	2	6	11	2.13	5
10	2	0	1	11	4	0	8	25	51	9.88	6
11	0	0	0	0	0	0	0	1	1	0.19	1
12	1	1	2	6	7	1	1	36	55	10.66	8
13	0	0	0	0	0	0	0	1	1	0.19	1
14	0	1	0	1	2	14	0	0	18	3.49	4
15	0	1	0	0	0	0	0	0	1	0.19	1
16	0	0	2	4	0	0	2	14	22	4.26	4
17	0	1	0	0	0	0	0	2	3	0.58	2
18	0	1	0	1	0	0	0	1	3	0.58	3
19	0	0	1	0	0	3	0	1	5	0.97	3
20	0	0	1	0	1	0	0	0	2	0.39	2
21	0	0	2	2	0	0	1	4	9	1.74	4
22	0	1	0	0	0	0	2	4	7	1.36	3
23	0	0	0	0	0	0	0	0	0	0.00	0
24	1	0	0	1	0	0	0	0	2	0.39	2
25	0	1	1	1	4	0	1	3	11	2.13	6
26	0	0	0	1	0	0	2	2	5	0.97	3
27	0	0	0	0	0	0	0	2	2	0.39	1
28	0	0	0	0	0	0	0	0	0	0.00	0
29	0	0	0	0	0	0	0	0	0	0.00	0
30	0	0	0	0	0	0	0	9	9	1.74	1
31	0	0	0	0	0	0	0	0	0	0.00	0
32	0	0	0	0	0	0	0	3	3	0.58	1
33	0	0	0	0	0	0	0	1	1	0.19	1
Unknown	0	1	0	0	0	1	0	3	5	0.97	3
Sum	22	24	48	60	34	62	36	228	516	100.00	

whereas three grower selections ('Brixnut', 'Gem', and 'Lyons') are hybrids between 'Barcelona' and 'DuChilly'. These grower selections were placed in the English group because of their English parents. In the Black Sea group, the most common alleles in cultivars are S_4 , S_{10} , S_2 , S_5 , and S_{31} . The first four of these alleles had been reported earlier in Turkish cultivars (Erdoğan et al., 2005; Mehlenbacher, 1997b), including 'Tombul' ($S_4 S_{12}$), 'Sivri' ($S_8 S_{10}$), 'Mincane' ($S_4 S_8$), 'Palaz' ($S_2 S_4$), 'Kargalak' ($S_2 S_{10}$), and 'Yassi Badem' ($S_2 S_5$). Erdoğan et al. (2005) reported S-alleles expressed in pollen of Turkish cultivars. S_4 , which is at the bottom of the dominance hierarchy (Fig. 1), is likely the second allele in several Turkish cultivars but is not expressed in their pollen. S_{31} is present in 'Ata Baba' ($S_4 S_{31}$) and is common in other cultivars from Azerbaijan. In the other 45 accessions, the most frequent alleles were S_6 , S_{20} , S_1 , S_2 , and S_{26} . This group includes several ornamentals and 21 selections from a forestry institute near Moscow, Russia. Half of the Moscow selections have red leaves. In breeding, two sources of red leaves have been used: 'Fusco Rubra' ($S_6 S_{19}$) and 'Rode Zeller' ($S_6 S_{11}$). In *C. avellana*, red leaf color is conferred by a dominant allele at the anthocyanin

locus, which is linked to the S-locus (Thompson, 1985). Given the presence of S_6 in both redleaf parents and the linkage of S_6 with the allele for leaf anthocyanin, the high frequency of S_6 is not surprising. S_{20} is common in the cold-hardy Central European types with large nuts [e.g., 'Early Long Zeller' ($S_{20} S_{25}$)] that were probably used as parents in Moscow. The high frequency of S_{26} in this "other" group is surprising, because its overall frequency in the 284 cultivars is only 1.8%.

S-ALLELES IN TURKISH SELECTIONS. Large differences in S-allele frequency were seen among the groups as well as among seed lots within a group. In the Turkish selections, S_4 was by far the most common allele, representing 30.2% of the total. It was present in high frequency in all eight groups of selections. The second most common allele, S_{12} , represented 10.7% of the total. S_{12} is present in 'Extra Ghiaghli' ($S_4 S_{12}$), which is a clone of the important cultivar Tombul. The next most common alleles were S_8 , S_{10} , S_2 , and S_{16} . Of the six most common alleles, five had been reported in Turkish cultivars, whereas the high frequency of S_{16} was unexpected. Four rare alleles detected at frequencies of 2% to 4% (S_{14} , S_3 , S_9 , and S_{25}) had not been previously reported for Turkish cultivars, whereas S_5 is present in 'Yassi

Table 8. Frequency of S-alleles in hazelnut selections originating in six seed lots collected in Georgia.

Allele no.	Georgian selection group no.						Total		Groups present (no.)
	1	2	3	4	5	6	(no.)	(%)	
1	0	2	0	0	2	0	4	4.65	2
2	3	3	2	1	1	0	10	11.63	5
3	0	0	1	1	0	0	2	2.33	2
4	3	6	5	0	2	3	19	22.09	5
5	0	0	1	0	1	0	2	2.33	2
6	2	0	0	0	0	0	2	2.33	1
7	0	0	0	0	1	0	1	1.16	1
8	0	0	1	0	2	0	3	3.49	2
9	1	0	0	0	0	0	1	1.16	1
10	3	0	3	0	0	2	8	9.30	3
11	0	1	0	1	0	0	2	2.33	2
12	0	0	0	0	0	0	0	0.00	0
13	0	1	0	0	0	0	1	1.16	1
14	0	1	2	0	0	0	3	3.49	2
15	0	0	0	0	0	0	0	0.00	0
16	0	0	0	0	0	0	0	0.00	0
17	0	0	0	0	0	1	1	1.16	1
18	0	0	0	2	0	0	2	2.33	1
19	1	0	2	0	0	1	4	4.65	3
20	1	1	1	1	2	1	7	8.14	6
21	0	0	1	0	0	0	1	1.16	1
22	0	0	0	0	0	0	0	0.00	0
23	0	0	0	0	0	0	0	0.00	0
24	0	0	0	0	0	1	1	1.16	1
25	0	1	0	0	0	0	1	1.16	1
26	0	0	0	0	0	0	0	0.00	0
27	0	2	0	0	1	1	4	4.65	3
28	0	0	0	0	0	0	0	0.00	0
29	0	0	0	0	0	0	0	0.00	0
30	1	1	0	0	0	0	2	2.33	2
31	1	1	3	0	0	0	5	5.81	3
32	0	0	0	0	0	0	0	0.00	0
33	0	0	0	0	0	0	0	0.00	0
Unknown	0	0	0	0	0	0	0	0.00	0
Sum	16	20	22	6	12	10	86	100.00	

Badem'. Three alleles (S_{23} , S_{29} , and S_{31}) were absent in the Turkish selections, and 18 others were present at frequencies less than 2%. 'Ata Baba' (S_4 S_{31}), the leading cultivar in Azerbaijan, has more vigorous and upright growth than the leading Turkish cultivars, but its nuts, husks, and kernels are very similar. Given the common ethnic origin of the people in the two countries and extensive trade over many centuries, it was surprising to find S_{31} absent in the Turkish selections. Differences in allele frequency among the eight Turkish seed lots were apparent. S_8 was very common in Group 4 from Akçakoca and Group 6 from Trabzon. S_{10} was common in Group 4. S_{14} was common in Group 6 but in no other Turkish group. S_{16} and S_{25} were especially common in Group 8 from the Hazelnut Research Institute. Alleles S_{27} to S_{33} are recorded as absent in Groups 1 to 7 of the Turkish selections (Table 7). However, we note that testers for these alleles were not available at the time that selections in Groups 1 to 7 were typed, and few selections from these groups have been preserved in our permanent collection. New alleles low in the dominance hierarchy (S_{27} , S_{29} , S_{31} , and S_{33}) may indeed be present in selections in Groups 1 to 7 but not detected because

they were not expressed in the pollen. However, S_{30} and S_{32} are high in the dominance hierarchy. Their presence would have been detected in selections in Groups 1 to 7 because only one other allele would have been identified, and their pollen would have been compatible on females expressing all other alleles. New testers would have been identified if S_{30} or S_{32} had been present in Turkish selections Groups 1 to 7. In summary, the Turkish selections showed great diversity with respect to their S-alleles and differences in S-allele frequency among groups.

SELECTIONS FROM THE CAUCASUS. In the 43 selections from Georgia, the most frequent alleles were S_4 , S_2 , S_{10} , S_{20} , and S_{31} . Three of these alleles are present in the Georgian cultivars (Table 8), but not S_2 . It is likely that S_{31} was contributed by 'Ata Baba' (S_4 S_{31}) from neighboring Azerbaijan. An additional 18 alleles were detected at frequencies of 1% to 5%, indicating great diversity in the alleles present, whereas nine were absent. S_4 is present in four Georgian cultivars, including Anakliuri (S_4 S_{14}), which is the most widely planted. Of three selected seedlings of 'Khachapura' (S_3 S_{18}), which has oblate nuts, two had S_{18} and the other had S_3 . In selections from Azerbaijan,

Table 9. Frequency of S-alleles in hazelnut selections originating in three seed lots collected in Azerbaijan.

Allele no.	Azerbaijan group no.			Total	
	1	2	3	(no.)	(%)
1	0	0	0	0	0.00
2	1	0	5	6	6.12
3	1	1	0	2	2.04
4	15	6	8	29	29.59
5	0	0	1	1	1.02
6	0	0	1	1	1.02
7	1	1	1	3	3.06
8	1	0	0	1	1.02
9	1	0	0	1	1.02
10	4	3	7	14	14.29
11	0	0	0	0	0.00
12	0	1	1	2	2.04
13	0	0	0	0	0.00
14	1	1	0	2	2.04
15	0	0	0	0	0.00
16	1	0	0	1	1.02
17	0	0	0	0	0.00
18	7	0	0	7	7.14
19	0	2	1	3	3.06
20	0	0	0	0	0.00
21	0	0	0	0	0.00
22	1	0	0	1	1.02
23	0	0	0	0	0.00
24	2	0	2	4	4.08
25	1	0	0	1	1.02
26	0	0	0	0	0.00
27	0	0	0	0	0.00
28	0	0	0	0	0.00
29	0	0	0	0	0.00
30	0	0	1	1	1.02
31	15	1	2	18	18.37
32	0	0	0	0	0.00
33	0	0	0	0	0.00
Unknown	0	0	0	0	0.00
Sum	52	16	30	98	100.00

the most common alleles, S_4 and S_{31} , were present in all three locations (Zaqatala, Qabala, and Xaçmaz). Zaqatala, located at the base of the Caucasus Mountains not far from the Georgian border, is the most important production zone. There, 'Ata Baba' ($S_4 S_{31}$) is the most important cultivar. The third common allele (S_{10}) is present in several cultivars from Azerbaijan. An additional 17 alleles were present at frequencies of 1% to 7%, and 12 were absent. Twenty S-alleles were found in the Azeri selections, which is fewer than in selections from Turkey, Russia, and Georgia. Hazelnut orchards were established during the Soviet era on state and collective farms. All aspects of production, including the choice of cultivars and pollenizers, were chosen by government officials. Most of the nuts from Azerbaijan were collected in such orchards. The most common alleles in the Armenian selections, all from nuts purchased in markets, were S_4 , S_2 , S_{31} , S_3 , S_9 , and S_{26} . The common alleles S_4 and S_{31} are those of 'Ata Baba', the most important cultivar in Azerbaijan. The presence of rare allele S_{31} in high frequency in all three former Soviet republics in the Caucasus indicates probable sharing of plant material. The level of diversity in

Armenian selections is similar to that observed in selections from Azerbaijan.

RUSSIA AND UKRAINE. Taken as a whole, the Russian selections were very diverse. The most common alleles in the eight groups of Russian selections were S_4 , S_{24} , S_{10} , and S_5 . The first two alleles are present in 'Cherkesskii II' ($S_4 S_{24}$), which is the most important cultivar in the north Caucasus. In the Crimea (Ukraine), hazelnut is cultivated to a very limited extent in the protected, mild climate on the south coast of the peninsula. Most of the nuts purchased from vendors were very small and may have been collected from the wild. The six most common alleles in the 24 Crimean selections were S_{10} , S_2 , S_{25} , S_9 , S_3 , and S_{14} . Twelve rare alleles were present at frequencies of 2% to 5%, and 13 alleles were not detected. The Crimean selections showed fewer S-alleles than the Russian, Georgian, and Turkish selections.

IRAN. Only four alleles were detected in the Iranian selections: S_2 , S_{33} , S_8 , and S_4 . The number of alleles was strikingly less than in selections from other countries. S_{33} is a very rare allele present in 'Ganja' ($S_4 S_{33}$) from Azerbaijan and very few selections, so it was surprising that S_{33} accounted for 27.8% of the alleles in the Iranian selections. In visits by the author to orchards near the Caspian Sea, little phenotypic diversity was seen and nut yields were low, which is consistent with a narrow genetic base. It is unclear if *C. avellana* is native to Iran, and it seems likely that the species was introduced. In all other countries from which seeds were collected, hazelnut bushes could be seen growing in roadsides and hedgerows. Such seedlings were not seen in Iran. In fact, even a large hazelnut planting visited in the Talesh Mountains had been established by planting seedlings.

OTHER SELECTIONS. Of the selections in the miscellaneous group, 13 originated in northern Italy, three originated in Latvia, and one from Lithuania. The nuts received from Latvia and Lithuania were large and presumably from a collection of cold-hardy cultivars with large nuts. The most common alleles in this miscellaneous group were S_9 , S_5 , S_6 , S_{10} , and S_{15} .

DIFFERENCES BETWEEN CULTIVARS AND SELECTIONS. Differences in allele frequencies (Table 11) between cultivars and selections reflect their geographic origin. The most common S-alleles in cultivars and selections in each group are presented in Table 12. Most of the cultivars were from western Europe, whereas most of the selections belonged to the Black Sea group and originated in the eastern part of the distribution of *C. avellana*. S_4 was very common in selections from Turkey, Georgia, Azerbaijan, Armenia, and Russia. S_8 and S_{12} were common in Turkish selections. These three alleles were much more common in the selections than in the cultivars. On the other hand, some alleles were more common in the cultivars than in the selections. S_1 and S_2 were common in the Spanish-Italian cultivars and S_3 and S_{11} were common in the English cultivars. S_5 was common in the Central European cultivars, whereas S_6 was present in the Spanish-Italian and other cultivars. All six of these alleles were present in the selections but at lower frequency than in the cultivars.

THE SPREAD OF HAZELNUT AND ORIGIN OF CULTIVARS. *Corylus avellana* is found throughout Europe, the Caucasus, and Asia Minor where it is generally found as an understory shrub in mixed deciduous forests. Palme and Vendramin (2002) used four polymorphic chloroplast microsatellite markers to investigate diversity in 248 individuals representing 26 natural

Table 10. Frequency of S-alleles in hazelnut selections originating in eight seed lots collected in Russia.

Allele no.	Russian selection group no.								Total		Groups present (no.)
	1	2	3	4	5	6	7	8	(no.)	(%)	
1	1	0	0	0	0	0	0	2	3	1.60	2
2	2	0	4	1	0	0	0	0	7	3.72	3
3	0	1	2	0	0	1	1	0	5	2.66	4
4	3	13	11	4	9	0	0	0	40	21.28	5
5	0	0	0	0	4	0	1	9	14	7.45	3
6	1	1	2	0	0	0	1	2	7	3.72	5
7	1	0	0	1	0	0	0	0	2	1.06	2
8	0	1	1	1	0	0	0	2	5	2.66	4
9	0	0	2	1	0	0	0	0	3	1.60	2
10	4	3	1	5	0	0	2	1	16	8.51	6
11	1	0	1	0	0	2	1	0	5	2.66	4
12	0	0	1	0	0	0	0	0	1	0.53	1
13	0	0	1	0	0	0	0	0	1	0.53	1
14	0	3	0	0	0	0	0	5	8	4.26	2
15	1	0	0	0	0	0	1	4	6	3.19	3
16	0	1	0	0	0	0	0	1	2	1.06	2
17	0	0	0	0	0	0	0	6	6	3.19	1
18	0	1	0	4	0	0	0	0	5	2.66	2
19	0	3	1	0	0	0	1	1	6	3.19	4
20	0	2	0	1	0	0	0	1	4	2.13	3
21	0	0	0	0	0	1	0	0	1	0.53	1
22	0	1	0	0	0	0	1	0	2	1.06	2
23	0	2	1	0	0	0	0	0	3	1.60	2
24	1	2	6	2	9	0	0	0	20	10.64	5
25	0	1	0	0	0	0	0	1	2	1.06	2
26	0	1	2	0	2	0	0	0	5	2.66	3
27	0	0	0	0	0	0	0	0	0	0.00	0
28	0	0	0	0	0	0	0	0	0	0.00	0
29	0	0	0	0	0	0	1	0	1	0.53	1
30	0	0	0	0	0	0	1	0	1	0.53	1
31	1	0	0	0	0	2	1	0	4	2.13	3
32	0	0	0	0	2	0	0	0	2	1.06	1
33	0	0	0	0	0	0	0	0	0	0.00	0
Unknown	0	0	0	0	0	0	0	1	1	0.53	1
Sum	16	36	36	20	26	6	12	36	188	100	

populations across Europe but did not include samples from Turkey, the Caucasus, or Iran. Boccacci and Botta (2009) used the same markers to investigate diversity in 75 cultivars, including a few from Turkey and Iran but none from the Caucasus republics or southern Russia. Both studies give insight into the spread of the hazelnut and its domestication. The chloroplast is generally inherited maternally in angiosperms and thus only dispersed by seeds. The present-day distribution of *C. avellana* was established $\approx 7,000$ BP as a result of postglacial recolonization that had started $\approx 11,000$ years earlier (Huntley and Birks, 1983). Between 10,000 and 9,000 BP, there was a sharp increase in the amount of *Corylus* L. pollen found across Europe (Huntley and Birks, 1983). Nut dispersal during the postglacial recolonization was caused by small mammals, birds, and human migration. Archaeologists have repeatedly found nuts, kernels, and shell remains from many archaeological sites all over Europe. Hazelnuts are easy to store and transport, and kernels have a high energy value; thus, it is likely that Mesolithic tribes aided the spread of hazelnut and undoubtedly selected for productivity.

Palme and Vendramin (2002) found a clear geographical structure of chloroplast haplotypes that divides Europe into two parts. Chlorotype A, which represented 76% of the sampled wild individuals, and chlorotype B, which represented 4%, were well distributed across western and northern Europe. Chlorotypes C, D, E, and F were restricted to southern and central Italy, Croatia, Romania, and Greece. These results indicate that recolonization of most of Europe was from one or more refugia in southwestern France by the Bay of Biscay. Expansion in Italy and the Balkans, where almost all chlorotype diversity was observed, was local.

Where and when the domestication of *C. avellana* was started is not yet clear, although it was cultivated by the Romans, especially in the southern Italian region of Campania. According to Trotter (1921), cultivars were selected from local wild populations. Many cultivars have unclear origins. Chloroplast marker data for 75 hazelnut cultivars (Boccacci and Botta, 2009) suggested considerable exchange of germplasm between Italy and Spain, probably by the Romans, and thus a common genetic base of cultivars in the two countries. Boccacci and Botta (2009) propose separate domestication of hazelnut in

Table 11. Differences in the frequency of S-alleles in hazelnut cultivars and selections.^z

Allele no.	Frequency of S-alleles (%)		Difference	Comment
	Cultivars (n = 284)	Selections (n = 522)		
4	5.99	24.52	-18.54	Black Sea selections
12	1.58	5.75	-4.16	Turkish selections
8	2.29	6.13	-3.84	Turkish selections
24	1.06	2.97	-1.91	Russian selections
16	1.06	2.87	-1.82	Turkish selections
31	1.58	3.16	-1.58	
10	8.45	9.87	-1.42	
19	0.70	1.92	-1.21	
18	1.06	1.92	-0.86	
30	0.70	1.53	-0.83	
14	2.82	3.35	-0.54	
7	0.53	1.05	-0.53	
9	2.29	2.78	-0.49	
27	0.53	0.86	-0.33	
21	1.23	1.53	-0.30	
13	0.18	0.29	-0.11	
33	0.53	0.57	-0.05	
Unknown	0.70	0.67	0.03	
29	0.18	0.10	0.08	
28	0.18	0.00	0.18	
32	0.70	0.48	0.23	
26	1.76	1.25	0.52	
25	2.82	2.20	0.61	
22	2.11	1.34	0.77	
17	2.64	1.05	1.59	
23	2.46	0.48	1.99	
20	3.70	1.44	2.26	Other and Central European cultivars
15	3.70	1.05	2.64	Central European cultivars
3	6.16	3.07	3.10	English cultivars
11	4.23	0.86	3.36	English cultivars
6	5.28	1.92	3.37	Other and Spanish-Italian cultivars
5	7.22	3.26	3.96	Central European cultivars
2	13.91	8.24	5.67	Spanish-Italian cultivars
1	9.33	1.53	7.80	Spanish-Italian cultivars

^zAlleles are ranked from largest negative to largest positive difference.

three areas: the Mediterranean (Spain and Italy), Turkey, and Iran. Boccacci and Botta (2009) detected little gene flow from east to west. The presence of chlorotype A in all cultivar groups may be the result of spread of hazelnut throughout the empire by the Romans. Further studies of chlorotypes of germplasm from the Caucasus republics (Georgia, Armenia, and Azerbaijan) and southern Russia will be enlightening.

According to Erfatpour et al. (2011), hazelnut is native to the Talesh Mountains in northwestern Iran (Tandehbin and Makesh regions of Guilan Province). The nuclear microsatellite data of Erfatpour et al. (2011) and Ghanbari et al. (2005) show considerable variation among Iranian hazelnut cultivars in contrast to our observations during orchard visits. The people of Azerbaijan are Turkic. Treaties signed by Russia and Persia in 1813 and 1828 divided Azerbaijan. Today, the northern third is the republic of Azerbaijan and the southern two-thirds remain part of Iran. Some exchange of plant materials among farmers and gardeners would be expected. The ancient Silk Road passed through Iran, and it seems likely that hazelnut were disseminated along the route.

Although the origins of many hazelnut cultivars are unknown, humans undoubtedly played a role in their selection and

spread through clonal or seed propagation. Like with other fruit and nut crops, superior cultivars are propagated and sold by nurseries, farmers, and gardeners often sharing scions, rooted suckers, and seeds. Goeschke (1887) described many old cultivars. In England, the major cultivar is DuChilly (syn. 'Kentish Cob'). Richard Webb of Reading is credited as the source of 'Cosford', 'Daviana', 'Garibaldi', 'Empress Eugenia', and 'Princess Royal'. In Germany, at least five people are credited with developing locally adapted types with large nuts. S.D.L. Henne of Gunsleben is the originator of 'Gunslebener Zeller'. Jacob Mackoy et Cie in Luttich is the originator of 'Berger's Zeller'. C.R. Peicker of Hertwigswalde is the originator of 'Louisen's Zeller' and 'Neue Riesen'. C.G. Buttner of Halle is the originator of 'Hall's Giant' (syn. 'Halle'sche Riesennuss') and 'Volle Zeller'. Justizrat Burchardt of Landsberg is credited as the originator of no less than 12 cultivars, including 'Buttner's Zeller', 'Gubener Zeller', 'Gustav's Zeller', 'Riekchen's Zeller', and 'Truchsess Zeller'. Some of these German cultivars were the parents of others. As noted earlier, cultivars selected by growers in the Pacific Northwestern United States and placed in the English group have been identified as hybrids between

Table 12. Most common S-alleles in hazelnut cultivars and selections by group.

Cultivar group ^z	Allele ^y	Frequency (%)	Seedling group ^x	Allele ^x	Frequency (%)
Spanish-Italian (n = 71)	2	30.28	Turkey (n = 258)	4	30.23
	1	14.08		12	10.66
	10	9.15		8	9.88
	22	7.75		10	9.88
	17	6.34		2	7.75
Central European (n = 38)	5	21.05	Georgia (n = 43)	4	22.09
	15	14.47		2	11.63
	25	13.16		10	9.30
	20	11.84		20	8.14
	11	9.21		31	5.81
English (n = 47)	3	19.15	Azerbaijan (n = 49)	4	29.59
	11	13.83		31	18.37
	1	12.77		10	14.29
	14	12.77		18	7.14
	2	11.70		2	6.12
	10	9.57	Armenia (n = 26)	4	17.31
Black Sea (n = 60)	4	26.67		2	11.54
	10	15.83		31	11.54
	2	10.00		3	7.69
	5	8.33		9	5.77
	31	7.50		26	5.77
OSU releases ^w (n = 22)	1	29.55	Russia (n = 94)	4	21.28
	3	20.45		24	10.64
	2	11.36		10	8.51
	8	6.82		5	7.45
	15	6.82	Ukraine (n = 24)	10	22.92
	26	6.82		2	12.50
Other (n = 45)	6	16.67		9	8.33
	20	11.11		25	8.33
	1	7.78		3	6.25
	2	6.67		14	6.25
	26	6.67			
Total (n = 283)	2	13.96	Iran (n = 9)	2	55.56
	1	9.36		33	27.78
	10	8.48		8	11.11
	5	7.24		4	5.56
	3	6.18	Other (n = 19)	9	15.79
				5	10.53
	4	6.01		6	10.53
				10	7.89
				15	7.89
			Total (n = 522)	4	24.66
				10	10.07
				2	7.94
				8	5.46
				12	5.29

^zNumber of cultivars or seedlings in each group (n) is shown.^yAlleles in cultivars with frequencies greater than 6%.^xAlleles in seedlings with frequencies greater than 5%.^wOSU = Oregon State University.

‘Barcelona’ and three other cultivars: Daviana, Cosford, and DuChilly.

Conclusions

Hazelnut cultivars and selections are self-incompatible. Fluorescence microscopy is routinely used to determine if a pollination is compatible or incompatible, and use of an array of known testers allows identification of the alleles of cultivars and selections. Both alleles are expressed in the stigmas, but often only one is expressed in the pollen because of dominance. This study reports six new S-alleles, an improved tester for S_{13} , and the dominance relationships for 105 new pairs of alleles. The S-alleles of 284 cultivars, 13 interspecific hybrids, and 522 selections of diverse origin are summarized and presented. Most of the world’s leading cultivars were selected from the local vegetation near where they are now planted on a commercial scale. Tremendous genetic variability is available in cultivated and wild hazelnuts, but genetic improvement efforts have only recently led to improved cultivars. Based on SSR markers and geographic origin, most hazelnut cultivars have been assigned to one of the four main groups (Spanish-Italian, English, Central European, or Black Sea), yet many accessions lie outside these main clusters. Differences in S-allele frequency related to geographic origin were seen in the cultivars and selections. The S-alleles identified in hazelnut cultivars and selections is information that should be useful to breeders in the planning of crosses, to germplasm curators, and to growers and nurseries as they choose cultivars and pollenizers when designing orchards.

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