Inheritance of Style Color in Hazelnut

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Abstract. The style color of standard hazelnut (*Corylus avellana* L.) cultivars ranges from pink to dark purple. Styles with an unusual yellow color were first noted in seedlings of the progeny ‘Goodpasture’ x ‘Compton’, and the ratio was ≈3 red : 1 yellow. Controlled crosses were made to investigate the genetic control of style color. The same 3:1 ratio was observed in four additional crosses in which both parents had red styles. Two crosses of a red and a yellow parent gave ≈50% yellow styles, while a cross of two selections with yellow styles gave only seedlings with yellow color. These segregation ratios indicate control by a single locus, with yellow style color recessive to red. Seedlings with yellow styles have green buds and catkins and a more upright growth habit than their siblings with red styles. Inspection of the pedigrees of these progenies shows that ‘Daviana’, ‘Willamette’, ‘Butler’, ‘Compton’, ‘Goodpasture’, and ‘Lansing #1’ are heterozygous. ‘Daviana’ appears to be the original source of the allele for yellow styles, as it is a known or suspected parent or ancestor of the others. Ratios in a progeny segregating simultaneously for growth habit (normal vs. contorted) and style color indicated independence of the traits. However, in a progeny segregating simultaneously for leaf color (red vs. green) and style color, no redleaf seedlings had yellow styles. The S-alleles of eight genotypes with yellow styles were determined, and indicate a possible linkage between the yellow style locus and the S locus that controls pollen–stigma incompatibility. One explanation is that the yellow style trait is conferred by an allele (*a^{rs}*) at the anthocyanin (A) locus that controls leaf color. A second explanation is that there is a yellow style locus closely linked to the A locus. The A locus is known to be loosely linked to the S locus.

The European hazelnut (*Corylus avellana* L.) is a monoecious, wind-pollinated shrub that enforces cross-pollination through dichogamy and self-incompatibility. The style color of standard green-leaved hazelnut cultivars ranges from pink to dark purple. Only when branches are bagged to protect female inflorescences from wind-borne pollen do the styles continue to elongate and the color fades from red or pink to light yellow or white. In 1978, in the progeny ‘Goodpasture’ x ‘Compton’, styles with an unusual yellow color (Fig. 1) were noted in ≈25% of the seedlings. The yellow color was present when the styles first emerged and persisted as the flowers aged. We report here the results of an investigation of the genetic control of style color in hazelnut.

Materials and Methods

Controlled pollinations were performed over a period of several years as part of a hazelnut breeding program at Oregon State University using standard practices, including emasculation followed by bagging individual limbs or covering the entire tree with a wooden frame covered with white polyethylene (Thompson et al., 1996). Pollen was collected and stored in the freezer and compatibility of crosses was verified and S-alleles identified using fluorescence microscopy (Mehlenbacher, 1997). Selections with yellow styles were crossed with ‘Purple Aveline’, ‘Rode Zeller’, ‘Redleaf #3’, *C. a.*

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var. *aurea*, and the cutleaf hazelnut [*C. a. f. heterophylla* (Loud.) Rehder], all of which have red styles. Several additional crosses were made (Tables 1–4) among genotypes with various pedigrees (Table 2). Controlled pollinations were made in February and hybrid seeds were harvested in August. The seeds were stratified for 3 to 5 months and sprouted seeds were planted in flats in the greenhouse. When ≈20 cm tall the seedlings were transplanted to 3.8-L pots and grown in the greenhouse during the summer. The seedlings were moved outside in September and hardened for one month, then planted in the field in October. Style color was noted as the shrubs began to flower, generally 5 to 6 years after planting in the field.

Chi-square goodness-of-fit tests were performed for expected ratios of red : yellow styles of 3:1 or 1:1. A progeny segregating simultaneously for growth habit (normal vs. contorted) and style color was tested separately for each trait, and for a combined ratio of 9:3:3:1. A progeny segregating simultaneously for leaf anthocyanin (red vs. green color) and style color was also tested separately for each trait, and for a combined ratio of 2:1:1. Contingency chi-square tests were used to detect deviations from expectations based on independent assortment at two loci. The Yates correction factor was not used.

Results and Discussion

When selections with yellow styles were crossed with ‘Purple Aveline’, ‘Rode Zeller’, ‘Redleaf #3’, *C. a.* var. *aurea*, and the cutleaf hazelnut, all resulting seedlings had red styles (data not shown). In five progenies from crosses of parents with red styles, ≈25% of the seedlings had yellow styles (Table 1), indicating that the trait is recessive and that these parents

are heterozygous. Crosses in which one parent had red styles and the other yellow segregated ≈50% yellow, although progeny 97052 showed a deficiency of yellow styles. A cross of two selections with yellow styles gave only seedlings with yellow styles. These ratios indicate control by a single locus at which the allele for yellow style color is recessive.

Other phenotypic differences were seen. The leaf buds and catkins of seedlings with yellow styles are bright green, as they lack the traces of anthocyanin present on these plant parts in their siblings with red styles. Seedlings with yellow styles also have a more upright growth habit than their siblings with red styles.

Inspection of the pedigrees of these progenies (Table 2) shows that ‘Daviana’, ‘Willamette’, ‘Butler’, ‘Compton’, ‘Goodpasture’, and ‘Lansing #1’ are heterozygous. These last four cultivars were selected by hazelnut growers in Oregon and are believed to be hybrids between ‘Barcelona’, Oregon’s leading cultivar, and ‘Daviana’, its most common pollinizer. Seedlings with yellow styles were observed in the cross 525.085 x ‘Daviana’. As ‘Daviana’ is an ancestor of 525.085, and is believed to be a parent or ancestor of the other heterozygotes, it appears to be the original source of the allele for yellow styles.

Contorted growth habit is conferred by a recessive allele (*tw*) (Smith and Mehlenbacher, 1996). The progeny that segregated simultaneously for growth habit and style color (Table 3) fit a 9:3:3:1 ratio, and the contingency chi-square ($\chi^2 = 0.02$, $P = 0.89$) indicated independence of the two loci.

Thompson (1985) showed that crosses of the red-leaved cultivars ‘Rode Zeller’ and *C.*

Fig. 1. Hazelnut female inflorescences with red (left) and yellow (right) styles.

BREEDING, CULTIVARS, ROOTSTOCKS, AND GERMPLASM RESOURCES

Table 1. Segregation for style color in hazelnut progenies.

Progeny	Parents	Style color		χ^2	<i>P</i>
		Red	Yellow		
Progenies segregating 3:1					
72049	‘Goodpasture’ x ‘Compton’	113	34	0.27	0.60
81036	13.013 x 68.073	50	11	1.58	0.21
81062	33.113 x 67.026	15	5	0.00	1.00
81063	33.113 x ‘Willamette’	21	12	2.27	0.13
97055	525.085 x ‘Daviana’	47	13	0.36	0.55
	Pooled data (5 progenies)	246	75	0.46	0.50
	Heterogeneity			4.02	0.40
Progenies segregating 1:1					
88145	233.101 ^y x 234.025	12	18	1.20	0.27
97052	525.085 x 30.013 ^y	42	25	4.31	0.04
	Pooled data (2 progenies)	54	43	1.25	0.26
	Heterogeneity			4.26	0.04
Yellow x yellow					
94027	372.087 ^y x 246.128 ^y	0	10	---	---

^zSeedlings with no females were excluded(43 seedlings in progeny 72049, 2 in 88145, and 1 each in 81036, 81062, and 81063).

^ySelection with yellow styles.

a. fusco-rubra with green-leaved selections segregated 1 red : 1 green, indicating control by a single leaf anthocyanin locus which she designated A. She also proposed a second locus for leaf color (C) linked to the A and S loci in interspecific crosses, but a single locus was sufficient to explain segregation in crosses within *C. avellana*. In the progeny that segregated simultaneously for leaf color and style color (Table 4), no seedlings with red leaves and yellow styles were recovered, for which we offer two explanations. The first hypothesis is that there are three alleles at the anthocyanin locus (A, a, and a^{ys}) which show a dominance hierarchy (A > a > a^{ys}). Trees that carry the A allele have much anthocyanin in styles, leaves, and catkins. Trees that are homozygous a^{ys} a^{ys} have green leaves and yellow styles, and trees homozygous (a a) or heterozygous (a a^{ys}) for the wild-type allele (a) have red styles and traces of anthocyanin in leaves and catkins. The red-leaved parent trees 452.109 and 452.120 would be heterozygous (A a^{ys}), as their female parent has yellow styles. From crosses of these two selections with 525.085 (a a^{ys}), a phenotypic segregation ratio of 2 red leaves and red styles (A a and A a^{ys}) : 1 green leaves and red styles (a a^{ys}) : 1 green leaves and yellow styles (a^{ys} a^{ys})

would be expected. An alternate hypothesis is that there are two closely linked loci, A that controls leaf color and Ys that controls style color, and that we failed to recover seedlings with red leaves and yellow styles because of the small population size. Recovery of seedlings with red leaves and yellow styles in a larger population would rule out the first hypothesis.

The incompatibility alleles of 8 selections with yellow styles (OSU 233.101, 233.106, 234.019, 246.128, 246.148, 372.087, 732.109, and 732.114) were identified using fluorescence microscopy. OSU 372.087 was S₁ S₁₁, 732.109 was S₃ S₁₁, and 732.114 was S₁ S₁, while the other five were S₁ S₃. 'Daviana' is S₃ S₁₁ (Thompson, 1979). The small number of alleles (three) in these selections is partly a function of the inbreeding needed to recover recessive homozygotes, but also suggests a possible loose linkage between the ys and incompatibility (S) loci. Thompson (1985) presented evidence that the anthocyanin locus (A) and the incompatibility locus (S) were linked. If the presence of anthocyanin in leaves and styles is the result of action of different alleles at a single locus, or two closely linked loci, then linkage to the S locus would be expected. The identification of S-alleles in seedlings in a progeny segregating

Table 2. Pedigrees of selections. Selections with yellow styles are indicated in bold. Heterozygous selections are indicated in italics.

Selection	Parents
13.013	Barcelona x Lansing
26.122	Goodpasture x Compton
26.126	Goodpasture x Compton
30.009	Goodpasture x Compton
30.013	Goodpasture x Compton
33.113	Lansing o.p.
67.026	14.019 x 17.068
	14.019 = Barcelona x Butler
	17.068 = Barcelona x Tombul Ghiagli
68.073	14.019 x 17.068
233.007	13.013 x Henneman #3
233.101	13.013 x 68.073
233.106	13.013 x 68.073
234.019	13.013 x 68.073
234.025	13.013 x 68.073
246.128	33.113 x Willamette
246.148	33.113 x Willamette
372.087	26.122 x 26.126
452.109	30.013 x Rode Zeller
452.120	30.013 x Rode Zeller
486.060	246.128 x Contorta
486.062	246.128 x Contorta
525.085	233.007 x 246.128
732.109	372.087 x 246.128
732.114	372.087 x 246.128
899.010	525.085 x 452.120
899.036	525.085 x Daviana
900.010	525.085 x 30.013

for style color would confirm the existence of separate but linked ys and S loci.

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Table 3. Simultaneous segregation for growth habit and style color.^z

Progeny	Parents	Growth habit									
		Style color				3:1 Style		3:1 Growth		9:3:3:1	
		Red	Yellow	Red	Yellow	Value	P	Value	P	Value	P
97051	486.060 x 486.062	36	12	10	3	0.01	0.92	0.44	0.51	0.46	0.93

^zSeedlings with no female inflorescences (four with normal and seven with contorted growth habit) were excluded in the calculation of chi-square test statistics. If these are included, the test statistic for fit to a 3:1 ratio for growth habit is 0.005 and 0.9 < P < 0.95.

Table 4. Simultaneous segregation for leaf color and style color.

		χ^2					
		Leaf color					
		Red		Green			
		Style color				χ^2 (2:1:1 ^z)	
Progeny	Parents	Red	Yellow	Red	Yellow	Value	<i>P</i>
97053	525.085 (<i>a a^{ys}</i>) x 452.109 (<i>A a^{ys}</i>)	41	0	20	14	1.61	0.45
97054	525.085 (<i>a a^{ys}</i>) x 452.120 (<i>A a^{ys}</i>)	17	0	8	6	0.55	0.76
Pooled data		58	0	28	20	2.15	0.34
Heterogeneity						0.01	0.995

^zRatio expected if red leaves and red styles are controlled by different alleles (A, a, and a^{ys}) at a single anthocyanin locus. Control by two tightly linked loci (A and Ys) would give the same expected ratio.