Inheritance of a Chlorophyll Deficiency in Hazelnut

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Abstract. A chlorophyll deficiency expressed as yellowing of leaves was observed in hazelnut (*Corylus avellana* L.) progenies. Segregation ratios approximated 3 green : 1 yellow, indicating control by a single recessive gene designated *chlorophyll deficient* #1, for which the symbol *c*, is proposed. 'Barcelona', 'Butler', 'Compton', 'Lansing', 'Willamette', and the ornamental selection 'Redleaf #3' are heterozygous. Pedigree analysis strongly suggests that all heterozygotes inherited the recessive allele from 'Barcelona'. A cross of 'Barcelona' with the yellow-leafed ornamental *Corylus avellana* L. var. *aurea* Kirchn. produced no yellow-leafed seedlings, indicating that the chlorophyll deficiencies from these two sources are controlled by different loci. Progenies segregating simultaneously for this trait and the gene controlling presence of anthocyanin indicated that the two traits are inherited independently. Seedlings deficient in chlorophyll but with anthocyanin were able to survive under field conditions, while leaves of yellow-leafed seedlings lacking anthocyanin became scorched and the trees died.

Chlorophyll deficiencies commonly segregate in progenies of naturally cross-pollinated and clonally propagated plants and may be expressed as striped, variegated, albino,

yellow, yellow-green, or pale-green leaves. Chlorophyll deficiencies are often lethal or sublethal and are generally monogenic recessives. Many such mutants have been described in maize (Neuffer et al., 1968). Among the tree fruits, albinos have been reported in apple (Brown, 1975; Hall and Crane, 1933), peach (Bailey and French, 1941), and sweet cherry (Kerr, 1963). Klein et al. (1963) reported that 13 of 20 apple genotypes studied were heterozygous for a pale-green lethal. In this paper, we describe a monogenic recessive chlorophyll deficiency in seedlings of 'Barcelona' hazelnut and demonstrate that it is inherited independently of the presence

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Table 1. Segregation for green and yellow leaf color in hazelnut crosses.

Progeny code ^a	Parentage ^b	No. plants		χ^2 (3:1 ratio)	
		Green	Yellow	Value	P
77026	013.019 x Butler	58	31	4.59	0.03
77031	014.002 x Barcelona	11	4	0.02	0.9
77039	018.009 x Butler	66	17	0.90	0.3-0.4
77060	026.020 x 014.002	114	34	0.32	0.5-0.6
77067	Barcelona x 014.002	47	18	0.25	0.6
77068	Barcelona x Butler	105	23	3.38	0.05-0.1
86002	Barcelona x 017.068	31	10	0.01	0.9-0.95
89007	Willamette x self	43	11	0.62	0.4-0.5
89010	220.013 x Hend 3-70	33	8	0.66	0.4-0.5
89068	231.111 x 226.122	408	121	1.28	0.2-0.3
89071	244.001 x Hend 3-70	162	48	0.51	0.4-0.5
Pooled data		1078	325	2.52	0.1-0.2
Heterogeneity				10.02	0.2-0.3

The first two digits of the progeny code indicate the year of the cross and the last three digits, the number of the cross.

^aNumbered selections from the Oregon State Univ. breeding program are listed by location of the original seedling tree (row number.tree number).

of anthocyanin and not allelic to the chlorophyll deficiency found in *Corylus avellana* var. *aurea*.

The progenies studied were produced from controlled crosses as part of a hazelnut breeding program. Following stratification for 3 to 4 months at $\approx 4^\circ\text{C}$, seeds were planted in flats in the greenhouse. Progenies segregating for leaf color were noted and segregation ratios were scored 5 to 6 weeks after planting. Chi-square goodness-of-fit tests were performed for an expected ratio of 3 green : 1 yellow. For progenies segregating simultaneously for the chlorophyll deficiency and the presence of anthocyanin, ratios were tested separately for each trait, and a goodness-of-fit test to a combined 3 red : 3 green : 1 red-yellow : 1 yellow ratio was performed. A contingency chi-square test was used to detect deviations from expectations based on independent assortment.

Whereas 10 of the 11 progenies fit a 3 green : 1 yellow segregation expected for a single recessive gene, progeny 77026 had a surplus of yellow-leaved seedlings (Table 1). We propose the symbol c_l for this gene, designated *chlorophyll deficient #1* to indicate that it is the first such gene reported in hazelnut.

Pedigrees of parents segregating for yellow leaves were examined to determine if heterozygotes had a common ancestor (Table

2). 'Barcelona' is heterozygous ($C_l c_l$) and transmitted the c_l allele to many of its offspring. Other heterozygotes include 'Butler', 'Compton', and 'Lansing #1', grower selections that originated in Oregon, where 'Barcelona' is the leading cultivar and 'Daviana' the leading pollinizer. All three have long been suspected of being hybrids between 'Barcelona' and 'Daviana', as they are morphologically very similar to seedlings resulting from the controlled cross. Analysis of incompatibility alleles has shown that each has one allele in common with 'Barcelona' ($S_1 S_2$) and S_3 in common with 'Daviana' (Mehlenbacher and Thompson, 1988). It is very likely that the three grower selections inherited the yellow-leaf allele from 'Barcelona'. Twenty-one numbered selections and the new cultivar Willamette, a seedling from the cross 'Montebello' x 'Compton', are also heterozygous. In all cases, pedigrees indicate that heterozygotes inherited the chlorophyll-deficient allele either directly from 'Barcelona' or indirectly through one of the grower selections noted.

A cross of 'Barcelona' with *C. avellana* var. *aurea*, the yellow-leaved ornamental 'Gold-hasel' described by Goeschke (1887), produced 94 seedlings. All of them had green leaves, indicating that the two chlorophyll deficiencies are controlled by different loci. This result is consistent with the differences in chlo-

Table 2. Pedigrees of selections heterozygous at the *chlorophyll deficient #1* locus^a

Selection	Pedigree
013.019 ^a	Barcelona x Lansing #1
014.002	Barcelona x Butler
017.040	Barcelona x Tombul Ghiaghli
017.042	Barcelona x Tombul Ghiaghli
017.068	Barcelona x Tombul Ghiaghli
017.075	Barcelona x Tombul Ghiaghli
018.009	Barcelona x Lansing #1
023.024	Barcelona x Extra Ghiaghli (= Tombul)
026.020	Fitzgerald 20 x Lansing #1
040.032	Lansing #1 x Casina
041.119	Montebello x Compton
042.108	Montebello x Compton
067.026	014.019 x 017.068 014.019 = Barcelona x Butler
220.013	Negret x 023.024
226.122	Tonda Gentile delle Langhe x 067.026
231.111	Casina x Willamette
244.001	017.028 x Willamette 017.028 = Barcelona x Tombul Ghiaghli
246.128	033.113 x Willamette 033.113 = Lansing #1 o.p.
Hend 3-70	043.109 x Negret 043.109 = Montebello x Compton

^aGenotypes known to be heterozygous are in italics.

^bNumbered selections from the Oregon State Univ. breeding program are listed by location of the original seedling tree (row number.tree number).

rophyll content and spectra of intact leaves previously reported (Daley et al., 1986). The two mutants also differ in appearance. Yellow-leaved seedlings of 'Barcelona' are bright yellow but can be maintained in the greenhouse. Upon transplanting to the field, leaves become scorched and trees die. By contrast, trees of *C. avellana* var. *aurea* survive in the field and leaf color varies with position. Leaves at the top of the canopy, where they are exposed to the sun, are bright yellow. The leaves are yellowish-green 50 cm below the canopy surface, and inside the tree, leaves are nearly normal in color. The inheritance of the chlorophyll deficiency in *C. avellana* var. *aurea* still needs to be determined.

When the ornamental selection 'Redleaf #3' was crossed with three heterozygous ($C_l c_l$) green-leaved selections, simultaneous segregation for the presence of anthocyanin and chlorophyll deficiency was noted (Table

Table 3. Progenies segregating simultaneously for chlorophyll deficiency and presence of anthocyanin.

Progeny code ^a	Parentage ^b	No. plants				χ^2							
		Green		Yellow		3:1*		1:1*		3:3:1:1*		Indep. ^c	
		Red	Nonred	Red	Nonred	Value	P	Value	P	Value	P	Value	P
87072	040.032 x Redleaf #3	13	11	4	4	0.0	1.0	0.13	0.7-0.8	0.17	0.95-0.99	0.04	0.8-0.9
87071	017.075 x Redleaf #3	41	27	5	7	4.27	0.04	1.8	0.1-0.2	7.73	0.05-0.1	1.45	0.2-0.3
89102	017.075 x Redleaf #3	53	41	14	19	0.07	0.7-0.8	0.39	0.5-0.6	2.36	0.5	1.50	0.2-0.3
89103	Redleaf #3 x 017.075	48	42	8	13	2.19	0.3-0.4	0.01	0.5-0.6	3.53	0.3-0.4	1.42	0.2-0.3
89104	Redleaf #3 x 246.128	26	25	4	6	2.41	0.1-0.2	0.02	0.8-0.9	2.70	0.4-0.5	0.40	0.5-0.6
Pooled data		181	146	35	49	4.56	0.04	1.07	0.3	10.44	<0.005	1.22	0.2-0.3
Heterogeneity						4.38	0.3-0.4	1.28	0.8-0.9	6.05	0.1-0.2	3.59	0.4-0.5

^aThe first two digits of the progeny code indicate the year of the cross and the last three digits the number of the cross.

^bNumbered selections from the Oregon State Univ. breeding program are listed by location of the original seedling tree (row number.tree number).

*Expected ratio 3 green : 1 yellow.

*Expected ratio 1 red : nonred.

*Expected ratio 3 red : 3 green : 1 red-yellow : 1 yellow.

^cContingency test for independence.

2). All five progenies fit the ratio of 1 with anthocyanin : 1 without. This result is consistent with those of Thompson (1985), who demonstrated that in crosses of green-leafed cultivars with the red-leafed 'Rode Zeller' and *C. avellana* var. *fusco rubra* Dippel, the presence of anthocyanin is conferred by a single dominant gene. 'Redleaf #3', the parent of the progenies listed in Table 3, is an open-pollinated seedling of 'Barcelona', and morphological traits indicate that 'Rode Zeller' was the pollen parent. 'Redleaf #3', like 'Rode Zeller', is heterozygous for the dominant gene for leaf anthocyanin. Four of the five progenies fit the expected ratio of 3 green (or red-green) : 1 yellow (or red-yellow), but progeny 87071 had such a deficiency of yellow-leafed seedlings that it caused the pooled data from all five progenies to also show this deficiency. There is also a slight deficiency of yellow-leafed seedlings in the pooled data from crosses segregating only for this trait (Table 1), but it is not as striking as in Table 2. The five progenies also fit a combined segregation ratio of 3 red : 3 green : 1 red-yellow : 1 yellow, although the pooled data showed a significant deviation from the expected ratio due to deficiencies of green and red-yellow seedlings. Deficiencies of these two phenotypes were present in all progenies. Contingency chi squares showed independence of chlorophyll deficiency and presence of anthocyanin.

Seedlings that are homozygous c_1c_1 and have anthocyanin pigment were grown in pots in the greenhouse in Summer 1988 and transplanted to the field in the fall. Although the seedlings are smaller than their green- and red-leafed siblings, they are surviving. Apparently the anthocyanin pigment offers protection and prevents scorching of the leaves.

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