Inheritance of the Blood-flesh Trait in Peach

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Abstract. Inheritance of the blood-flesh (red-violet mesocarp) trait in peach [*Prunus persica* (L.) Batsch.] was investigated in S₁, S₂, F₁, F₂, F₃, BC_{1P1}, and BC_{1P2} families derived from 'Harrow Blood', a clone showing anthocyanin accumulation in fruit about 45–50 days after anthesis. This trait invariably was associated with the red midrib leaf phenotype in 'Harrow Blood', an S₁ family from 'Harrow Blood', and in green leaf F₂ progeny derived from 'Harrow Blood' × 'Rutgers Red Leaf 2n'. A segregation ratio of about 3 blood-flesh : 1 wild-type was observed in the S₁ family, but F₁ progeny produced only wild-type fruit. Examination of F₂ progeny segregating for the blood-flesh and red leaf traits revealed no evidence of epistasis. Based on segregation ratios in F₁, F₂, F₃, BC_{1P1}, and BC_{1P2} families from this cross, the F₁ family from 'Contender' × ('Harrow Blood' × 'Rutgers Red Leaf 2n'), and six additional F₁ families from crosses between 'Harrow Blood' and green leaf clones with wild-type fruit, we propose that blood-flesh is controlled by one gene, designated *bf* (blood-flesh). The blood-flesh phenotype was associated with reduced tree height in S₁ and F₂ progeny derived from 'Harrow Blood'. Segregation for leaf blade color deviated significantly ($P = 0.05$) from the expected 3 red : 1 green ratio in six of the F₂ families derived from selfing seven F₁ trees from 'Harrow Blood' × 'Rutgers Red Leaf 2n'.

Wild-type peach fruit generally accumulate low to moderate quantities of anthocyanins late in development. Excessive anthocyanin accumulation in the mesocarp, giving it a red-violet color, is commonly called blood-flesh. Clones with this trait have existed for centuries and were grown in France as early as 1659 (Hedrick, 1917). Downing and Downing (1900) described three such cultivars: 'Blood-flesh Clingstone', 'French Blood-flesh Freestone', and 'Blood-flesh Freestone'. According to Fulton (1910), 'Blood-flesh Clingstone' was an American seedling of the French 'Sanguinolent à Chair Adhérente'. Conners (1922) proposed but did not confirm a relationship between the expression of blood-flesh and a red midrib color in leaves. Chaparro et al. (1995) reported that blood-flesh in both immature and mature fruit of 'Harrow Blood' was associated with a red midrib color on the

abaxial side of the leaf. Blake (1932) investigated the inheritance of the blood-flesh trait in F₁ families derived from crosses of 'Chinese Blood' and 'Japan Dwarf Blood' with 'J.H. Hale', and concluded that blood-flesh was dominant to wild-type. However, after further examination, Blake concluded (1937) that blood-flesh was associated with time of ripening and that its inheritance was more complex than reported originally. Bailey and French (1949) and Hesse (1975) stated that the inheritance of blood-flesh was unknown. Chaparro et al. (1995) reported that fruit of 'Harrow Blood' began accumulating anthocyanin in the mesocarp ≈45 to 50 d after anthesis, and that this early expression differed from that generally associated with the later stages of ripening in wild-type peach, providing a criterion for distinguishing blood-flesh cultivars.

The objectives of this study were to investigate the inheritance of the blood-flesh trait in 'Harrow Blood', and to determine if the red leaf gene interacted with the blood-flesh trait.

Data also are presented to document the relationship between the expressions of blood-flesh and red midrib. Additionally, because preliminary observations suggested a relationship between blood-flesh and plant vigor, studies were conducted to investigate this relationship.

Materials and Methods

To study the inheritance of blood-flesh and to determine if the red leaf trait (controlled by the *Gr* gene) interacts with it, 'Harrow Blood' S₁ and S₂ progeny were generated, and 'Harrow Blood' was crossed with 'Rutgers Red Leaf 2n' [a red leaf (*GrGr*) doubled haploid] to produce the following families: F₁, seven F₂, fifteen F₃, a BC_{1P1}, and a BC_{1P2}. The terms S₁ and S₂ refer to the first and second selfed generations derived from 'Harrow Blood'. Additionally, 'Contender' (a wild-type) was crossed with the F₁, and 'Harrow Blood' was crossed with six additional wild-type clones (Table 1). The 'Harrow Blood' clone used in this study was obtained from the virus-free fruit tree repository at Washington State Univ. as accession number 795-1. To generate S₁, S₂, F₂, and F₃ families by selfing, trees were covered before anthesis with netting to exclude pollinators. The 'Contender' × F₁, F₁, BC_{1P1}, and BC_{1P2} families were produced by hand emasculation and hand pollination. All seeds were harvested at maturity, stratified at 4 °C for 100 to 120 d, germinated in the greenhouse, grown there for ≈4 months, and then planted in the field at a spacing of ≈0.2 m, except for S₂ and F₃ families, which were scored for blood-flesh in the greenhouse based on the procedure described below.

The 'Contender' × F₁ cross, all crosses of 'Harrow Blood' with different wild-type clones, the 'Harrow Blood' S₁, all F₁, all F₂, the BC_{1P1}, and the BC_{1P2} families were characterized for blood-flesh by examining fruit ≈70 d after anthesis on 3- or 4-year-old field-grown trees. The 'Harrow Blood' S₂ families and the F₃ families were characterized for blood-flesh based on the presence or absence of a red midrib in 3-month-old seedlings, a trait invariably associated with blood-flesh and previously confirmed in the S₁ and F₂ families. To determine the relationship between blood-flesh and plant vigor, 1-year-old progeny from the

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Table 1. Crosses made and progeny number screened in a study of the inheritance of the blood-flesh trait in families derived from 'Harrow Blood' peach.

Cross	Families generated (progeny number) ²
'Harrow Blood' × self	S ₁ (440), S ₂
'Harrow Blood' × 'Rutgers Red Leaf 2n'	F ₁ (112), F ₂ , F ₃
('Harrow Blood' × 'Rutgers Red Leaf 2n') × 'Harrow Blood'	BC _{1P1} (98)
('Harrow Blood' × 'Rutgers Red Leaf 2n') × 'Rutgers Red leaf 2n'	BC _{1P2} (147)
'Harrow Blood' × PI 95501	F ₁ (6)
'Harrow Blood' × 'Pillar'	F ₁ (18)
'Harrow Blood' × 'White Glory'	F ₁ (4)
PI 65977 × 'Harrow Blood'	F ₁ (7)
'Davie II' × 'Harrow Blood'	F ₁ (82)
'Contender' × 'Harrow Blood'	F ₁ (33)
'Contender' × ('Harrow Blood' × 'Rutgers Red Leaf 2n')	F ₁ (65)

²Progeny number not shown in cases where multiple families were generated (S₂, F₂, and F₃). See text for details.

'Harrow Blood' S_1 family and from F_2 families 1, 2, and 3 of 'Harrow Blood' $\times$ 'Rutgers Red Leaf 2n' were assessed for vigor by measuring plant height to the nearest cm. In addition, all F_2 families were scored for red or green leaf color, which is controlled by the *Gr* locus. Because this trait is expressed in newly emerged seedlings, all F_2 plants were scored for leaf color in the greenhouse prior to transplanting in the field.

Ratios were calculated for the segregating families and tested using the Chi-square test for goodness of fit. The Chi-square test of independence was conducted to assess linkage between *Gr* and the blood-flesh trait. The *t* test was used to test 1-year-old trees for differences in vigor between blood-flesh and wild-type 'Harrow Blood' S_1 progeny and F_2 progeny from families 1, 2, and 3, as well as between red and green leaf progeny from the same F_2 families.

Results

No difficulty was experienced in discriminating blood-flesh from wild-type progeny at 70 d after anthesis. Blood-flesh and wild-type fruit were discernible $\approx$ 45 d after bloom, long before fruit maturity ($\approx$ 150 d postbloom). Anthocyanin accumulation began at the distal tip of the immature fruit, proceeded along the suture, and then spread throughout the mesocarp. Examination of fruit on segregating progeny confirmed that progeny expressing anthocyanin at 70 d after anthesis also showed expression at fruit maturity. Likewise, progeny lacking anthocyanin at 70 d lacked anthocyanin at fruit maturity. Blood-flesh progeny generally produced fruit with anthocyanin distributed throughout the mesocarp. Occasionally, some progeny bore fruit in which anthocyanin was localized in the outer mesocarp. These were also scored as blood-flesh.

Self-pollination of 'Harrow Blood' produced an S_1 family of 440 progeny that segregated for blood-flesh (311 blood-flesh : 129 wild-type), approximating a ratio of 3:1 ($P = 0.04$).

Selfing of blood-flesh 'Harrow Blood' S_1 progeny produced S_2 families that were predominantly blood-flesh (families 50, 80, 110, 120, and 130), with the exception of family 150, which contained 20% wild-type progeny (Table 2). Selfing of wild-type 'Harrow Blood' S_1 progeny produced S_2 families with predominantly wild-type seedlings (Table 2), but most families contained a significant number of blood-flesh progeny. However, segregation in these families was non-Mendelian.

The F_1 family from 'Harrow Blood' $\times$ 'Rutgers Red Leaf 2n' consisted of 112 progeny, all with wild-type flesh and red leaves. No blood-flesh progeny were found in the F_1 families from crosses of 'Harrow Blood' with the six other wild-type clones, and in the cross between 'Contender' $\times$ the F_1 (Table 1).

In contrast with the F_1 family (all wild-type), all seven F_2 families segregated for blood-flesh (Table 3). All seven F_2 families fit the 3 wild-type : 1 blood-flesh ratio that would be predicted from the segregation of one re-

cessive gene controlling blood-flesh. The Chi-square test of independence conducted for F_2 family 1 showed that red leaf and blood-flesh were not linked ($P > 0.95$). Individual progeny with both red leaves and blood-flesh fruit were observed in all seven F_2 families. The 'Harrow Blood' S_1 and the green leaf progeny in all F_2 families showed an invariate association between red midrib and blood-flesh fruit.

The BC_{1P1} family [from 'Harrow Blood' $\times$ ('Harrow Blood' $\times$ 'Rutgers Red Leaf 2n', F_1 tree 1)] segregated about 1 blood-flesh : 1 wild-type ($P = 0.77$) (Table 3). Most progeny in the BC_{1P2} family [from 'Rutgers Red Leaf 2n' $\times$ ('Harrow Blood' $\times$ 'Rutgers Red Leaf 2n', F_1 tree 1)] had red leaves and wild-type flesh (124), but 16 red leaf, blood-flesh progeny were recovered.

The F_3 families generated by selfing randomly chosen wild-type individuals in F_2 family 1 of 'Harrow Blood' $\times$ 'Rutgers Red Leaf 2n' either segregated for blood-flesh or produced all wild-type progeny (Table 4). All wild-type derived F_3 families that segregated for blood-flesh fit a 3 wild-type : 1 blood-flesh ratio. The F_3 families derived by self-pollination of randomly chosen blood-fleshed F_2 progeny were predominantly blood-fleshed.

Mean height of blood-flesh trees was reduced by 47% compared with their wild-type full sibs ($P < 0.001$) in the 'Harrow Blood' S_1 family and by 24%, 27%, and 20% ($P < 0.001$), respectively, in F_2 families 1, 2, and 3 of 'Harrow Blood' $\times$ 'Rutgers Red Leaf 2n' (Table 5). The observed ratio of red : green leaf progeny deviated from the expected 3:1 ratio in all seven families, with the excess of red leaf progeny being statistically significant in six of them (Table 6). The mean height of red leaf trees exceeded that of green leaf trees (Table

7) in those F_2 families (1, 2, and 3) that were measured.

Discussion

The approximate 3 blood-flesh : 1 wild-type ratio observed in the S_1 family suggests that 'Harrow Blood' is heterozygous for a dominant gene controlling expression of blood-flesh, consistent with Blake's (1932) initial contention that blood-flesh is dominant. Blake (1937) generated F_1 populations derived from crosses with 'Japan Dwarf Blood' that segregated for blood-flesh. However, he was unable to propose a genetic designator or inheritance model, possibly because, having scored progeny for blood-flesh expression at fruit maturity, he confused true blood-flesh individuals with those from wild-type individuals that accumulated excessive anthocyanin during ripening. However, the genetic mechanism controlling blood-flesh expression in 'Japan Dwarf Blood' may differ from that controlling its expression in 'Harrow Blood'.

In contrast with the S_1 data above, segregation of blood-flesh in F_1 , F_2 , F_3 , and BC families, in crosses between 'Harrow Blood' with six different wild-type clones, and in a cross between 'Contender' and the F_1 , was not consistent with the presence of a dominant gene for blood-flesh in 'Harrow Blood'. The lack of blood-flesh expression in any F_1 progeny, together with the 3 wild-type : 1 blood-flesh segregation ratio obtained in seven different F_2 families, suggests that blood-flesh is recessive and is controlled by a single gene. This is further supported by the F_3 data. Selfing of blood-flesh F_2 progeny yielded predominantly blood-flesh F_3 progeny; occasional wild-type progeny in families 7, 50, and 53 probably

Table 2. Segregation for blood-flesh in S_2 families derived from 'Harrow Blood' peach.

S_2 family	S_1 phenotype	Progeny phenotype		Expected S_2 segregation ^a
		Blood-flesh	Wild-type	
1	wild-type	19	64	see text
10	wild-type	16	82	see text
15	wild-type	12	60	see text
50	blood-flesh	126	2	all blood-flesh
80	blood-flesh	90	0	all blood-flesh
110	blood-flesh	209	1	all blood-flesh
120	blood-flesh	70	1	all blood-flesh
130	blood-flesh	74	3	all blood-flesh
150	blood-flesh	66	14	all blood-flesh

^aExpected segregation based on a one-gene model with blood-flesh recessive to wild-type.

Table 3. Segregation of the peach blood-flesh phenotype in seven F_2 families from 'Harrow Blood' $\times$ 'Rutgers Red Leaf 2n', and in BC_{1P1} and BC_{1P2} families generated from F_1 tree 1.

Family	Progeny flesh phenotype		Test ratio	χ^2 (1 df)	<i>P</i> value
	Wild-type	Blood-flesh			
F_2 #1	261	97	3:1	0.96	0.33
F_2 #2	187	48	3:1	2.74	0.10
F_2 #3	198	64	3:1	0.03	0.86
F_2 #4	210	62	3:1	0.71	0.40
F_2 #5	270	93	3:1	0.08	0.78
F_2 #6	290	102	3:1	0.22	0.64
F_2 #7	230	59	3:1	3.19	0.07
BC_{1P1} ^a	55	43	1:1	1.47	0.23
BC_{1P2} ^a	131	16	all wild-type		

^a BC_{1P1} = 'Harrow Blood' $\times$ F_1 tree 1 from ('Harrow Blood' $\times$ 'Rutgers Red Leaf 2n'). BC_{1P2} = 'Rutgers Red Leaf 2n' $\times$ F_1 tree 1 from ('Harrow Blood' $\times$ 'Rutgers Red Leaf 2n').

were the result of outcrossing. Selfing of wild-type F_2 progeny yielded F_3 families that were all wild-type or that segregated 3 wild-type : 1 blood-flesh. The 1 blood-flesh : 1 wild-type ratio obtained in the BC_{1P1} family and the lack of recovery of any blood-flesh progeny in crosses between 'Harrow Blood' and six other unrelated wild-type clones also is consistent with blood-flesh being recessive and under single gene control.

However, the segregation observed in the S_1 family derived from selfing 'Harrow Blood' and the segregations observed in the BC_{1P2} and the S_2 families derived from 'Harrow Blood' do not support a recessive gene model. All wild-type progeny were expected in the BC_{1P2} , but 16 blood-flesh progeny were recovered in the population of 140. As expected, S_2 families derived from selfing S_1 blood-flesh individuals (50, 80, 110, 120, 130, and 150) produced mainly blood-flesh progeny, but a few wild-type progeny were recovered, primarily in S_2 family 150.

We propose that blood-flesh is controlled by a single recessive gene, designated *bf*, that shows variable penetrance and/or instability in certain genetic backgrounds. We propose that 'Harrow Blood' has a genotype *bfbf*. Selfing of 'Harrow Blood' would be expected to yield only blood-flesh progeny. Recovery of wild-type progeny in the S_1 family may be caused by either variable penetrance or instability of *bf* in the 'Harrow Blood' background. We also propose that recovery of wild-type S_2 progeny from selfing blood-flesh S_1 progeny may result from either variable penetrance or instability of *bf* expression. We propose that 'Rutgers Red Leaf 2n' has genotype *BfBf* because it does not display the blood-flesh phenotype and F_1 progeny from its cross with 'Harrow Blood' are all wild-type. We conclude that the wild-type flesh, green leaf clones PI 65977, PI 95501, 'Contender', 'Davie II', 'Pillar', and 'White Glory' have genotype *BfBf* because neither they nor any F_1 offspring from crosses with 'Harrow Blood' had the blood-flesh phenotype.

Blood-flesh progeny were recovered at low frequency (20% to 25%) in all F_2 families, and none were found in the six F_1 families from crosses of 'Harrow Blood' with wild-type clones. These data support our conclusion that blood-flesh is recessive. Blake reported recovery (1932) of blood-flesh progeny in the F_1 of crosses between blood-flesh clones and 'J.H. Hale'. However, as previously stated, the ambiguity in his identification of true blood-flesh limits interpretation of his data. We repeated part of Blake's study by crossing blood-flesh cultivars Harrow Blood, Indian Blood, and Red English with 'J.H. Hale' and examined nine, seven, and six F_1 progeny, respectively. No blood-flesh progeny were recovered, confirming the recessive nature of the blood-flesh trait. We propose that the expression of blood-flesh conferred by *bf* as early as 45 d after anthesis clearly distinguishes the true blood-flesh trait from simple accumulation of anthocyanin during the later stages of ripening.

Segregation in BC_{1P1} supports the proposed

Table 4. Segregation for the blood-flesh phenotype in F_3 families of peach derived from the cross 'Harrow Blood' x 'Rutgers Red Leaf 2n'.

F_3 family ^a	F_2 phenotype	Progeny phenotype		Test ratio ^c	χ^2 (1 df)	P value
		Wild-type	Blood-flesh			
1	wild-type	20	0	all wt		
7	blood-flesh	2	88	all bf		
12	wild-type	130	45	3:1	0.05	0.82
15	wild-type	25	7	3:1	0.01	0.92
18	wild-type	50	18	3:1	0.08	0.77
23	blood-flesh	0	89	all bf		
29	wild-type	93	0	all wt		
41	wild-type	131	40	3:1	0.20	0.66
44	wild-type	119	0	all wt		
50	blood-flesh	3	189	all bf		
53	blood-flesh	2	152	all bf		
66	wild-type	54	12	3:1	1.63	0.20
79	wild-type	138	44	3:1	0.07	0.79
82	wild-type	39	0	all wt		
85	wild-type	136	0	all wt		

^aAll F_3 families were generated from green leaf F_2 progeny randomly selected from F_2 family 1 of 'Harrow Blood' x 'Rutgers Red Leaf 2n'. Blood-flesh was scored on 3- to 4-month-old greenhouse-grown seedlings. Blood flesh was scored by characterizing trees for the red midrib character associated with blood-flesh expression.

^cExpected segregation based on a one-gene model with blood-flesh (bf) recessive to wild-type (wt).

Table 5. Mean height of blood-flesh and wild-type peach progeny in S_1 and F_2 families derived from 'Harrow Blood'.

Family ^b	No. trees	Height (cm) ^c		P value ^a
		Blood-flesh	Wild-type	
S_1	384	157 ± 43	294 ± 35	<0.001
F_2 #1	357	106 ± 23	139 ± 23	<0.001
F_2 #2	226	95 ± 19	130 ± 19	<0.001
F_2 #3	254	104 ± 18	130 ± 21	<0.001

^aValue shown is mean ± SE.

^b S_1 = S_1 family derived from self-pollination of 'Harrow Blood'. F_2 #1, F_2 #2, and F_2 #3 are three full-sib families derived from a cross of 'Harrow Blood' x 'Rutgers Red Leaf 2n'.

^cSignificance of difference in height between blood-flesh and wild-type in *t* test.

Table 6. Segregation of leaf color in seven 'Harrow Blood' x 'Rutgers Red Leaf 2n' F_2 families of peach.^a

F_2 family	Progeny phenotype		Test ratio	χ^2 (1 df)	P value ^b
	Red leaf	Green leaf			
1	839	161	3:1	42.3	<0.01
2	222	44	3:1	9.8	<0.01
3	244	38	3:1	19.4	<0.01
4	348	69	3:1	15.7	<0.01
5	360	91	3:1	5.7	0.02
6	473	82	3:1	31.2	<0.01
7	296	81	3:1	2.4	0.12

^a F_2 family sizes shown in this table are larger than those in Table 2 showing blood-flesh segregation. Greater family sizes in this table represent additional seedlings that were grown and scored for leaf color in the greenhouse, but not transplanted to the field for scoring of blood-flesh data.

^bSignificance of χ^2 .

genotypes of the two parents and F_1 tree 1, as well as the proposed genetic model. The BC_{1P1} segregated 55 wild-type : 43 blood, approximating the expected 1:1 ratio ($P = 0.23$). The proposed genetic model predicts that all BC_{1P2} progeny should be wild-type. The recovery of 16 blood-flesh progeny in this backcross is inconsistent with our model, but could be the result of either self-contamination during crossing, or instability of expression of blood-flesh in this family. Our results essentially rule out the possibility of self-contamination during crossing. The F_1 was heterozygous for *Gr* and was used as the female parent, and self-contamination would have resulted in the presence of green leaf individuals in the BC_{1P1} progeny; however, no green leaf progeny were recovered.

Heights of individual blood-flesh progeny in the 'Harrow Blood' S_1 and three F_2 families from 'Harrow Blood' x 'Rutgers Red Leaf 2n' were reduced compared with their wild-type sibs. The reduced height may be due to linkage between the blood-flesh locus and loci influencing vigor, or to epistatic interactions between *bf* and other nonlinked segregating genes influencing vigor.

F_2 segregation at the red leaf locus (*Gr*) showed a significant deviation from the expected 3 red : 1 green ratio in six of seven families. All had more than the expected number of red leaf segregants. Interestingly, the average height of red leaf progeny exceeded that of green leaf progeny in the three F_2 families of 'Harrow Blood' x 'Rutgers Red Leaf 2n' that were measured. Possibly *Gr* is

associated with increased vigor in both the sporophyte and gametophyte. However, neither significant segregation distortion at the *Gr* locus nor increased vigor of red leaf trees has been reported previously in peach. In a recent study in peach (Chaparro et al., 1995), *Gr* segregated as expected in three wild-type flesh F_2 families. Thus *bf* may distort segregation at the *Gr* locus.

Of three additional blood-flesh cultivars examined at the U.S. Department of Agriculture peach germplasm collection at Byron, Ga., 'Red English' and 'Indian Blood' showed early expression of blood-flesh, associated reduction in vigor, and red midrib identical with those seen in 'Harrow Blood'. In contrast, J68-27 ('Indian Cling') showed intense anthocyanin accumulation only during the later stages of fruit development, with neither reduced vigor nor red midrib. This clone may have a different blood-flesh gene with different timing and lacking the effects on vigor and midrib color. The inheritance of this blood-flesh type is unknown.

Table 7. Mean height of red leaf and green leaf peach progeny in F_2 families 1, 2, and 3 from 'Harrow Blood' x 'Rutgers Red Leaf 2n'.

F_2 family	No. trees	Height (cm) ²		<i>P</i> value ³
		Red leaf	Green leaf	
1	385	130 ± 31	110 ± 26	<0.001
2	226	121 ± 25	99 ± 29	<0.001
3	263	124 ± 25	96 ± 14	<0.001

²Value shown is mean height ± SE.

³Significance of difference in height between red leaf and green leaf progenies by *t* test.

Budwood of germplasm described in this report can be obtained from D.J.W.

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