The Inheritance of Three Major Fruit Colors in Grapes[1]

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Abstract. In the grape, 3 major fruit color phenotypes occur: white, red, and black. Segregation for fruit color is reported for 43 crosses involving 27 parent varieties. Evidence is presented which supports a 2-gene hypothesis for the inheritance of fruit color. A gene for black fruit color ($B---$) was dominant and epistatic to that for red and white fruit with red fruit ($bbR-$) dominant to white ($bbrr$). Fruit color genotypes are presented for 27 grape varieties.

Introduction

MANY grape breeders have reported segregation for fruit color in their grape progenies, but none has proposed a satisfactory scheme for the inheritance of fruit color. Crossing 2 white-fruited varieties (1, 2, 5) and selfing white-fruited varieties (4, 6, 7) have resulted in only white-fruited progeny. These observations have led to the suggestion that white fruit color is homozygous (2, 3) and recessive to colored fruit (2, 6, 7). Selfed red-fruited varieties and crosses between red-fruited varieties have produced only white- and red-fruited progeny (4, 5, 6). Crosses between white- and red-fruited varieties also produced only white- and red-fruited progeny (5, 6, 7).

Snyder and Harmon (4) reported white- and black-fruited seedlings from selfed black-fruited varieties. Crosses involving at least one black-fruited parent have usually produced white, red- and black-fruited seedlings (2, 3, 5, 7).

This paper presents a simple genetic hypothesis for the inheritance of these fruit colors in the grape.

Materials and Methods

The seedlings of 43 crosses involving 27 parent varieties and selections were classified with respect to fruit color in 3 categories: white, red and black. The distinction was clear-cut with the exception of a very few reddish black types. Subclasses in the white fruit category were green, yellowish green, yellow and golden-yellow (amber); in the red fruit category pink, light red, bright red, and brick red; and in the black fruit category purple, reddish black and bluish black.

All the crosses reported are part of the grape breeding project of the New York State Agricultural Experiment Station at Geneva. Many of the segregation ratios were obtained by the authors from present field plantings while others were obtained from seedling descriptions made by earlier workers.

The parent varieties are predominantly *Vitis labrusca* types but many have *V. vinifera* and *V. aestivalis* ancestry. Several parent varieties are *V. labrusca* × *V. vinifera* hybrids ('Golden Muscat', 'Himrod', 'Interlaken Seedless', and 'Schuyler') and three parents are seedless *V. vinifera* varieties ('Black Corinth', 'Black Monukka', and 'Thompson Seedless').

Chi-square tests were used to determine the agreement of observed and theoretical fruit color ratios.

Results

The segregation ratios for fruit color are presented in Tables 1 and 2; in the crosses in Table 1 a distinction was made between white-, red-, and black-fruited seedlings, while in the crosses in Table 2 a distinction between red- and black-fruited seedlings was not made, resulting in only 2 categories, white and colored.

Seedlings with colored fruit, red or black, were not found in crosses when both parents were white-fruited (Table 1), suggesting that white fruit color was homozygous. In crosses involving one white- and one red-fruited parent, white- and red-fruited seedlings occurred in a ratio of 1:1, typical of monohybrid inheritance. If one gene were involved in red color inheritance, it would be heterozygous in the red-fruited parents studied.

Crosses involving one white- and one black-fruited parent produced 2 distinct segregation patterns: a white

Table 1. Frequency distributions for fruit color in grapes and chi-square values based on expected ratios determined from hypothesized genotypes.

Parents	Expected ratio			Observed frequency				Chi-square
	White	Red	Black	White	Red	Black	Total	
White × White								
Golden Muscat × Thompson Seedless	1	0	0	34	0	0	34	—
Niagara × N.Y. 36806	1	0	0	146	0	0	146	—
Ontario × Thompson Seedless	1	0	0	38	0	0	38	—
Ontario × N.Y. 36806	1	0	0	90	0	0	90	—
White × Red								
Niagara × N.Y. 45910	1	1	0	62	51	3	116	1.08
Red × White								
Delaware × N.Y. 33873	1	1	0	41	39	4	84	0.05
Iona × N.Y. 36806	1	1	0	19	14	0	33	0.76
Yates × N.Y. 36806	1	1	0	15	16	0	31	0.03
Yates × N.Y. 33873	1	1	0	9	12	0	21	0.42
White × Black								
Golden Muscat × Black Corinth	1	0	1	52	1	50	103	0.04
Ontario × Black Corinth	1	0	1	21	0	23	44	0.10
Ontario × Black Monukka	1	0	1	33	5	31	69	0.40
Ontario × N.Y. 46101	1	0	1	41	2	31	74	1.38
Black × White								
Van Buren × N.Y. 36806	1	0	1	48	1	61	110	1.55
Athens × N.Y. 33873	1	0	1	20	0	20	40	0
Schuyler × Himrod	1	0	1	8	1	4	13	1.32
Concord × N.Y.15305	1	0	1	11	1	5	17	2.26
Bath × N.Y. 36806	0	1	1	0	23	16	39	1.26
Bath × N.Y. 33873	0	1	1	0	6	4	10	0.40
Steuben × Interlaken Seedless	0	1	1	0	8	5	13	0.72
Buffalo × Interlaken Seedless	0	1	1	0	7	5	12	0.34
Buffalo × N.Y. 36806	0	1	1	0	18	9	27	3.00
Red × Black								
Iona × N.Y. 46101	1	1	2	14	17	37	68	0.80
Yates × N.Y. 46101	1	1	2	12	14	15	41	3.15
Black × Red								
Van Buren × N.Y. 33905	1	1	2	8	5	16	29	0.93
Van Buren × N.Y. 45910	1	1	2	20	25	58	103	2.41
Athens × N.Y. 33905	1	1	2	6	10	20	36	1.33
Concord × N.Y. 21553	1	1	2	10	17	21	48	2.79
Bath × N.Y. 21553	0	1	1	0	18	17	35	0.04
Black × Black								
Van Buren × Concord	1	0	3	7	0	19	26	0.05
Schuyler × N.Y. 21552	1	0	3	6	0	15	21	0.15
Concord × Van Buren	1	0	3	7	6	31	44	0.88
Concord × N.Y. 21552	1	0	3	13	2	36	51	0.06
Athens × Van Buren	1	0	3	14	2	27	43	1.83
Bath × N.Y. 21552	0	1	3	0	9	24	33	0.09
Bath × N.Y. 46101	0	1	3	1	26	90	117	0.41
Steuben × N.Y. 46101	0	1	3	1	6	71	78	12.61*
Buffalo × N.Y. 46101	0	1	3	0	11	24	35	0.77
Fredonia × Black Monukka	0	1	3	0	7	24	31	0.10

*Significantly different from expected ratio (P = .05).

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Table 2. Frequency distributions of white versus colored fruit in grapes and chi-square values based on expected ratios determined from hypothesized genotypes.

Parents	Expected ratio White : Colored			Observed frequency White : Colored			Chi-square
	White	:	Colored	White	Colored	Total	
Red × Black							
Yates × N.Y. 46101	1	:	3	8	25	33	0.10
Iona × N.Y. 46101	1	:	3	12	42	54	0.23
Delaware × N.Y. 46101	1	:	3	23	49	[illegible]	5.33*
Black × Red							
Schuyler × N.Y. 21553	1	:	3	2	20	22	2.98

*Significantly different from expected ratio (P = .05).

to black ratio of 1:1 and a red to black ratio of 1:1 (Table 1). One gene could not account for these ratios.

In many of the crosses in which both parents were black-fruited a white to black seedling ratio of 1:3 was obtained (Table 1). This would suggest that black fruit color was dominant to white and that the parents were heterozygous. In a second group of black-fruited × black-fruited crosses, a red to black seedling ratio of 1:3 was obtained (Table 1). This would also suggest that black fruit color was dominant over red and that the parents were heterozygous. A single gene hypothesis with complete or incomplete dominance could not explain these results.

These ratios would be possible if 2 genes were responsible, one for black fruit color (*B*), and a second for red fruit color (*R*). White fruit color would result if only recessive alleles were present for both genes (*bbrr*). Since black seedlings did not result from red-fruited × white-fruited crosses, the gene for black color in both parents must be homozygous recessive (*bb – –*). A white to red fruit ratio of 1:1 occurred in such crosses, indicating that the red color gene was heterozygous (*bbRr*) in the red-fruited parents ('Delaware', 'Iona', 'Yates', and N.Y. 45910).

In many of the black-fruited × white-fruited crosses, for example 'Athens' × N.Y. 33873; no red-fruited seedlings occurred, suggesting that the gene for red fruit color was homozygous recessive in the black parents. The occurrence of white-fruited seedlings indicated that in the black parent the gene for black color was heterozygous. Thus the genotype of the black-fruited parents in these crosses, 'Van Buren', 'Athens', 'Schuyler', and 'Concord' would be *Bbrr*.

In a second group of black-fruited × white-fruited crosses, for example 'Bath' × N.Y. 33873, no white-fruited seedlings occurred, only red and black in a ratio of 1:1. This would occur if the black-fruited parents, 'Bath', 'Buffalo', and 'Steuben', were heterozygous for the black gene and homozygous dominant for the red gene (*BbRR*). In these varieties the black color produced by the dominant allele at the black locus must mask the red color produced by the dominant alleles at the red color locus. Thus a variety or seedling with at least one dominant allele at the black locus (*B – – –*) would have black fruit.

In one group of black-fruited × black-fruited crosses, for example 'Van Buren' × 'Concord', seedlings occurred in a white to black ratio of 1:3. To obtain white seedlings each black parent must have been heterozygous for the black gene. Since red seedlings did not occur in these crosses, the red gene must have been homozygous recessive in each parent (*Bbrr*). In a second group of black-fruited × black-fruited crosses, for example 'Bath' × N.Y. 46101, segregation ratios of one red- to three black-fruited seedlings occurred. This ratio could result if both parents were heterozygous at the black color locus and if one parent were homozygous dominant for the red locus ('Bath', *BbRR*), and if the other were homozygous recessive for the red color locus (N.Y. 46101, *Bbrr*).

Working from observed white:red: black ratios, color genotypes were proposed on the basis of a 2-gene hypothesis for the 27 parent varieties studied (Table 3). Expected ratios determined from hypothesized genotypes were compared with the observed frequencies (Tables 1 and 2), and in only 2 of 43 crosses did a Chi-square test (P = .05) indicate a poor fit. These 2 exceptions, 'Steuben' × N.Y. 46101 (Table 1) and 'Delaware' × N.Y. 46101 (Table 2) were probably chance variations.

In the cross 'Niagara' (*bbrr*) × N.Y. 45910 (*bbRr*) black-fruited seedlings should not be found, according to the hypothesis, but 3 were recorded (Table 1). Discrepencies of this type were infrequent, 28 in over 2000 seedlings, and were probably the result of errors in labeling and recording, contamination from foreign pollen, and probably of considerable importance, from the misclassification of reddish black-fruited seedlings.

Only one reciprocal cross was reported, involving 'Van Buren' and 'Concord' and it would appear that the direction of the cross did not alter the fruit color ratio.

Table 3. Twenty-seven grape varieties and selections with their parentage, fruit color and proposed genotype.

Variety	Parentage	Fruit color	Proposed genotype
Athens	Hubbard × Portland	black	*Bbrr*
Bath	Fredonia × N.Y. 10805 (Chasselas Rose-Violet × Mills)	black	*BbRR*
Black Monukka	unknown	black	*Bbrr*
Black Corinth	unknown	black	*Bbrr*
Buffalo	Herbert × Watkins	black	*BbRR*
Concord	open pollinated *V. labrusca*	black	*Bbrr*
Delaware	unknown	red	*bbRr*
Fredonia	Champion × Lucile	black	*BbRR*
Golden Muscat	Muscat Hamburg × Hubbard	white	*bbrr*
Himrod	Ontario × Thompson Seedless	white	*bbrr*
Interlaken Seedless	Ontario × Thompson Seedless	white	*bbrr*
Iona	open pollinated Diana	red	*bbRr*
Niagara	Concord × Cassady	white	*bbrr*
Ontario	Winchell × Diamond	white	*bbrr*
Schuyler	Zinfandel × Ontario	black	*Bbrr*
Steuben	Wayne × Sheridan	black	*BbRR*
Thompson Seedless	unknown	white	*bbrr*
Van Buren	Fredonia × Worden	black	*Bbrr*
Yates	Mills × Ontario	red	*bbRr*
N.Y. 15305	Ontario × Thompson Seedless	white	*bbrr*
N.Y. 21552	Fredonia × Black Monukka	black	*Bbrr*
N.Y. 21553	Fredonia × Black Monukka	red	*bbRr*
N.Y. 33873	Ontario × Black Monukka	white	*bbrr*
N.Y. 33905	Ontario × Black Monukka	red	*bbRr*
N.Y. 36806	Bell × Interlaken Seedless	white	*bbrr*
N.Y. 45910	Bath × Interlaken Seedless	red	*bbRr*
N.Y. 46101	Van Buren × N.Y. 33905 (Ontario × Black Monukka)	black	*Bbrr*

Discussion

The 2-gene hypothesis proposed for the inheritance of grape fruit color is an example of dominant epistasis, black fruit color being dominant and epistatic to red and white fruit color. Although not studied here, color subclasses within the white, red and black categories probably result from one or more modifying color genes.

Wagner (6) has proposed that 3 independent genes are responsible for fruit color in grapes. He suggested that at least two dominant alleles at separate loci (*XxYyzz*, *XxyyZz* or *xxYyZz*) give red fruit and that white fruit was the result of either *xxyyzz* or *Xxyyzz* (or *xxYyzz* or *xxyyZz*) genotypes. However, he was unable to present precise genotypes for the varieties studied and did not determine the phenotypic consequence of more than 2 dominant alleles or of homozygous dominant loci.

Support for the present hypothesis can be found in the literature. Black-fruited seedlings were not found by Snyder and Harmon (4) in the selfed progeny of 3 red-fruited varieties and the ratio of white- to red-fruited seedlings approached 1:3, suggesting that the 3 red-fruited varieties studied, 'Castiza', 'Chasselas Rose de Falleaux', and 'Emperor', have the genotype *bbRr*. In the selfed and crossed progenies of white- and red-fruited varieties Wagner (6) did not obtain black-fruited seedlings. He obtained a 1:1 ratio of white- to red-fruited seedlings when crossing 'Muscat Rose' × 'Muscat Ottonel', indicating that 'Muscat Rose' has the genotype *bbRr*. A white- to red-fruited seedling ratio of 1:3 obtained by Wagner (6) when he crossed 'Chasselas Rose' × 'Muscat Rose' suggests that 'Chasselas Rose' also has the genotype *bbRr*. Snyder and Harmon (4) selfed 3 black-fruited varieties, 'Mission', 'Mondeuse', and 'Zinfandel', and obtained only white- and black-fruited seedlings in a ratio approaching 1:3, suggesting that these varieties have the genotype *Bbrr*.

Certain genotypes, *bbRR*, *BbRr*, and *BB – –*, were conspicuously absent from the parents studied as all red-fruited parents had the genotype *bbRr* and all black-fruited varieties had the genotypes *Bbrr* or *BbRR*. An explanation for these findings is lacking but perhaps with a wider survey of varieties the remaining genotypes will be found. For example, the *V. vinifera* variety 'Petit Syrah', selfed by Snyder and Harmon (4), produced only black-fruited seedlings, indicating that it is probably homozygous dominant for the black gene.

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