INHERITANCE OF SEED COLOR IN LACTUCA SATIVA[1]

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INTRODUCTION

The mature fruit of lettuce is an achene or naked seed, the color of which is determined by the color of its pericarp. The pigments that give the seed its particular color seem to be localized in the pericarp tissues.[2]

The mode of inheritance of seed color is of immediate practical importance to those breeding lettuce for disease resistance, climatic adaptation, and desirable commercial characteristics. Unlike flowers of most other food crops, those of lettuce can be emasculated only with extreme difficulty, if at all. In making crosses the breeder must remove the maternal parent's own pollen from the stigmas after the anthers have dehisced, but before the pollen tubes have entered the stigmatic tissues. As it is generally almost impossible to remove every grain of the maternal parent's pollen, both selfed and hybrid seed develop in heads in which pollen removal is attempted. Therefore, the breeder must know the mode of inheritance of some easily recognizable character by which he can distinguish hybrid from selfed plants in the F_1 generation. Seed color is a character that can be used to advantage for this purpose.

The cultivated varieties of lettuce (*Lactuca sativa* L.) may be roughly divided into 3 groups on the basis of their achene color. Of the 114 varieties of lettuce listed by Tracy [3] in 1904, 81 were indicated to have white, 30 black, and 3 yellow seed. Since then the trend has been even more toward the white-seeded varieties, until now there are only a few important varieties of the black-seeded type and no important varieties in the yellow-seeded group.

In the white-seeded group, the color is fairly constant except for discolorations caused by premature harvesting, dampness, and other environmental factors. In the black-seeded group the achenes range in color from reddish brown through dark brown to black. These different shades probably have a genetic basis; however, the differences are not great enough to permit accurate classification in view of the minor color variations caused by environmental factors. There are also some shade variations among varieties in the yellow group

Some data have been published by Durst [4] and Thompson [5] on the inheritance of factors for black and white seeds, but no report that deals with the factors for yellow seed has been found. The data of Durst and Thompson agree that black behaves as a monogenic factor

[1] Received for publication September 11, 1942.

[2] Borthwick, H. A. Unpublished data on the morphology of lettuce seed.

[3] Tracy, W. W., Jr. American varieties of lettuce. U. S. Bur. Plant Indus. Bul. 69, 103 pp., illus. 1904.

[4] Durst, C. E. Inheritance in lettuce. Ill. Agr. Expt. Sta. Bul. 356, pp. [237]-341, illus. 1930.

[5] Thompson, R. C. Genetic relations of some color factors in lettuce. U. S. Dept. Agr. Tech. Bul. 620, 38 pp., illus. 1938.

dominant to white. It is the purpose of this paper to show the relation of the factors that control the inheritance of the three colors, but no effort was made in this study to account for the inheritance of the minor color variations within the three large groups.

MATERIALS AND METHODS

The data presented were obtained from numerous hybrid populations of lettuce stocks being grown at the Bureau of Plant Industry Station, Beltsville, Md., for breeding heat-tolerant and disease-resistant varieties. The plants were grown either in 10-inch clay pots or in 1-foot by 2-foot by 3-inch cypress planting flats in a screened greenhouse. The possibility of contamination by insects was kept at a minimum by frequent spraying and fumigation.

The parent stocks had been grown for at least two generations previous to the cross from which seed-color records were kept and were known to be homozygous for the particular color type. The parent stocks used for the black phenotype were from a strain of Grand Rapids that has been maintained by the Division of Fruit and Vegetable Crops and Diseases for many years. For the white phenotype the variety Chavigne from Vilmorin-Andrieux & Cie., Paris, France; Iceberg from the Ferry-Morse Seed Co., San Francisco, Calif.; and a hybrid selection from a breeding stock were used. The variety Giant Summer from the Ferry-Morse Seed Co. was used for the yellow-seeded parent type.

In all cases the flower heads of the maternal parent were depollinated with water and dried before the desired pollen was applied by brushing the washed stigmas with the pollen-laden styles of flowers from the male parent.

GENETIC RELATIONS OF FACTORS FOR ACHENE COLOR

WORKING HYPOTHESIS

The breeding behavior of the three color types indicates that achene color in lettuce is inherited in a manner similar to that of the factors (*CcAa*) for coat color in rodents in which an F_2 generation from a cross between a black (*CCaa*) and an albino (*ccAA*) consists of 9 agouti, 3 black, and 4 albino.

This requires the presence of an independent allelomorphic pair in addition to those previously suggested by Durst [6] and Thompson [7]. In these two reports the genetic factor for black was represented by the symbol *WW* and the white by the symbol *ww*. This new pair of allelomorphs has been given the symbol *Yy*. The symbolized genotypes and their phenotypic expressions are *WWYY*, black; *wwYY*, yellow; *WWyy*, white; and *wwyy*, white. All four of these homozygous genotypes have been isolated, and their genetic constitution has been studied.

CROSS INVOLVING BLACK- AND YELLOW-SEEDED PARENTS

Grand Rapids × *Giant Summer* (*cross No. 122*).—Pollen from flowers of the yellow-seeded variety Giant Summer (*wwYY*) was applied to washed stigmas of flowers of the black-seeded variety Grand Rapids (*WWYY*). The cross was made in this way so that it might be pos-

[6] See footnote 4.
[7] See footnote 5.

sible to isolate at an early stage the hybrids from the selfed plants in the resulting progenies. Such isolation is possible because, as Thompson has shown,[8] the spotted anthocyanin leaf type of Giant Summer is dominant to the absence of pigment in the leaves of Grand Rapids.

A population of 93 F_2 plants was grown, with a ratio of 73 black-seeded to 20 yellow-seeded resulting. This is a satisfactory fit to a 3 to 1 ratio.

F_3 progenies were grown from both black- and yellow-seeded F_2 plants. Progenies from the F_2 yellow-seeded plants were all yellow-seeded. In the progenies from the black-seeded F_2 plants there were some families that were all black-seeded and other families with black- and yellow-seeded plants in the ratio of approximately 3 black-seeded to 1 yellow-seeded. The results from the F_2 and F_3 generations are given in tables 1 and 2, respectively.

TABLE 1.—*Records for F_2 progenies from selfed F_1 plants from crosses involving black-, yellow-, and white-seeded varieties of lettuce*

Phenotypes and cross	Parental varieties and assumed genotypes	F_1 plants	F_1 seed color	F_2 progenies				Assumed ratio	χ^2
				Black	Yellow	White	Total		
Black-seeded × yellow-seeded:		*Number*		*Number*	*Number*	*Number*	*Number*		
No. 122	Grand Rapids (*WWYY*) × Giant Summer (*wwYY*).	17	Black	73	20	0	93	3:1	[1] 0.5198
Black-seeded × white-seeded:									
No. 12	Grand Rapids (*WWYY*) × Iceberg (*WWyy*).	27	do	89	0	19	108	3:1	4.0000
No. 396	Grand Rapids (*WWYY*) × hybrid (*wwyy*).	35	do	88	42	52	182	9:3:4	[2] 4.5866
White-seeded × yellow-seeded:									
No. 21	Chavigne (*WWyy*) × Giant Summer (*wwYY*).	42	do	96	36	46	178	9:3:4	.4549
No. 40	Hybrid (*wwyy*) × Giant Summer (*wwYY*).	28	Yellow	0	42	13	55	3:1	.0958

[1] χ^2 for 1 degree of freedom (3:1 ratio) at 1-percent level, 6.635; at 5-percent level, 3.841.
[2] χ^2 for 2 degrees of freedom (9:3:4 ratio) at 1-percent level, 9.210; at 5-percent level, 5.991.

CROSSES INVOLVING BLACK- AND WHITE-SEEDED PARENTS

Grand Rapids × Iceberg (cross No. 12).—The white-seeded variety Iceberg (*WWyy*) was used as the pollen parent in a cross with the black-seeded Grand Rapids (*WWYY*). All the 27 F_1 plants grown to maturity produced black seed. The F_2 progenies segregated in the ratio of approximately 3 black- to 1 white-seeded. In the F_3 generation all the white-seeded F_2 plants gave families that produced only white seed. The black-seeded F_2 plants gave some families that were all black-seeded and other families that were black- and white-seeded in the ratio of approximately 3 black to 1 white. The F_2 and F_3 data are given in tables 1 and 2, respectively.

Grand Rapids × white-seeded hybrid (cross No. 396).—The white-seeded parent (*wwyy*) used in this cross was isolated from an F_3

[8] See footnote 5.

TABLE 2.—*Records for F_3 progenies from selfed F_2 plants from crosses involving black-, yellow-, and white-seeded varieties of lettuce*

Phenotypes and cross	Parental varieties and assumed genotypes	F_2 families	F_2 seed color	F_3 progenies				Assumed ratio	χ^2
				Black	Yellow	White	Total		
		Number		*Number*	*Number*	*Number*	*Number*		
Black-seeded × yellow-seeded:									
No. 122	Grand Rapids (*WWYY*) × Giant Summer (*wwYY*)	6	Black	49	0	0	49		
		11	do	62	15	0	77	3:1	[1] 1.1409
		3	Yellow	0	31	0	31		
Black-seeded × white-seeded:									
No. 12	Grand Rapids (*WWYY*) × Iceberg (*WWyy*).	9	Black	51	0	0	51		
		15	do	75	0	20	95	3:1	.7895
		4	White	0	0	44	44		
No. 396	Grand Rapids (*WWYY* × hybrid (*wwyy*).	9	Black	87	0	0	87		
		10	do	71	28	0	99	3:1	.5690
		15	do	111	0	30	141	3:1	1.0425
		37	do	197	71	96	364	9:3:4	[2] .6788
		17	Yellow	0	127	36	163	3:1	.7383
		5	do	0	47	0	47		
		27	White	0	0	259	259		
White-seeded × yellow-seeded:									
No. 21	Chavigne (*WWyy*) × Giant Summer (*wwYY*).	6	Black	56	0	0	56		
		18	do	126	47	0	173	3:1	.4952
		13	do	98	0	29	127	3:1	.3760
		29	do	151	50	80	281	9:3:4	2.0405
		11	Yellow	0	91	17	108	3:1	4.9382
		8	do	0	77	0	77		
		35	White	0	0	341	341		
No. 40	Hybrid (*wwyy*) × Giant Summer (*wwYY*).	3	Yellow	0	29	0	29		
		12	do	0	70	17	87	3:1	1.5209
		5	White	0	0	35	35		

[1] χ^2 for 1 degree of freedom (3:1 ratio) at 1-percent level, 6.635; at 5-percent level, 3.841.
[2] χ^2 for 2 degrees of freedom (9:3:4 ratio) at 1-percent level, 9.210; at 5-percent level, 5.991.

population of the cross No. 21 between the white-seeded Chavigne and the yellow-seeded Giant Summer. As indicated in the discussion of cross No. 21, one-fourth of the F_2 plants produced white seed. According to the hypothesis, one-fourth of these F_2 white-seeded plants should be of the double-recessive (*wwyy*) genotype. Seven of these F_2 white-seeded segregates were tested by backcrossing to the yellow-seeded Giant Summer, and one of these was found to be of the double-recessive genotype, as indicated by an all yellow-seeded F_1 generation and an F_2 generation that gave 3 yellow-seeded to 1 white-seeded. This double recessive was then crossed with Grand Rapids (*WWYY*). The F_1 plants of this cross were black-seeded, and the F_2 segregated approximately 9 black-seeded, 3 yellow-seeded, and 4 white-seeded.

The F_3 progenies from the white-seeded F_2 plants were all white-seeded. Some progenies from the black-seeded F_2 plants produced only the black-seeded type; some produced 3 black-seeded to 1 yellow-seeded; some 9 black-seeded, 3 yellow-seeded, and 4 white-seeded; and some 3 black-seeded to 1 white-seeded. Some progenies of yellow-seeded F_2 plants produced all yellow-seeded F_3 and others 3 yellow-seeded to 1 white-seeded. The F_2 and F_3 data are given in tables 1 and 2, respectively.

CROSSES INVOLVING YELLOW- AND WHITE-SEEDED PARENTS

Chavigne × Giant Summer (cross No. 21).—The yellow-seeded variety Giant Summer (*wwYY*) was used as the pollen parent in a cross with the white-seeded variety Chavigne (*WWyy*). The F_1

hybrid plants all produced black seed. The F_2 population segregated 9 black-seeded, 3 yellow-seeded, and 4 white-seeded. The F_3 progenies from white-seeded F_2 plants gave only white seed. The F_3 progenies from yellow-seeded F_2 plants gave some families that were all yellow-seeded and other families that segregated with a moderately significant departure from 3 yellow- to 1 white-seeded. F_3 progenies from black-seeded F_2 plants were all black-seeded, 3 black-seeded to 1 yellow-seeded, 3 black-seeded to 1 white-seeded, or 9 black-seeded to 3 yellow-seeded to 4 white-seeded. The F_2 and F_3 data are presented in tables 1 and 2, respectively.

White-seeded hybrid × *Giant Summer (cross No. 40).*—The yellow-seeded Giant Summer (*wwYY*) was used as the pollen parent in a backcross to the white-seeded F_3 selection (*wwyy*) from Chavigne × Giant Summer. The F_1 backcrossed plants all produced yellow seed, and the F_2 population from these segregated 3 yellow- to 1 white-seeded. The F_3 progenies from the white-seeded F_2 plants were all white-seeded. From the F_2 yellow-seeded plants some families that were all yellow-seeded and other families that segregated 3 yellow-seeded to 1 white-seeded were obtained. F_2 and F_3 data are presented in tables 1 and 2, respectively.

DISCUSSION

The 3 to 1 ratio of black to white seed in the F_2 generation, as suggested by Durst [9] and by Thompson,[10] holds only in the case of the white-seeded phenotype having the *wwYY* constitution. With the double-recessive white-seeded (*wwyy*) the F_2 from a cross with a black-seeded variety gives the ratio of 9 black-seeded, 3 yellow-seeded, to 4 white-seeded.

Many varieties of lettuce of the cultivated form (*Lactuca sativa*) have come under the writer's observation in the lettuce-breeding program of the United States Department of Agriculture, and breeding data on seed color have been recorded on many of these. None of the white-seeded varieties on which breeding behavior records are available are of the double-recessive (*wwyy*) type. This type must be very rare among fixed varieties.

SUMMARY

Data from the F_1 generation and from F_2 and F_3 progenies of crosses involving the three seed-color types in lettuce—black, yellow, and white—are presented.

The data have been analyzed for an explanation of the inheritance of the factors that control pericarp color in lettuce seed. The analysis indicates that the expression of black, yellow, and white seed color in cultivated lettuce (*Lactuca sativa*) is controlled by two pairs of allelomorphs, which have been assigned the symbols *Ww* and *Yy*. The inheritance is similar to that of the factors (*CcAa*) for coat color in rodents in which the F_2 from a cross between black and albino parents gives 9 agouti, 3 black, and 4 albino. In the present case the F_2 progenies from a cross between a white-seeded (*WWyy*) and the yellow-seeded (*wwYY*) segregated 9 black-seeded, 3 yellow-seeded, and 4 white-

[9] See footnote 4.
[10] See footnote 5.

seeded. This gives one true-breeding black genotype (*WWYY*), one true-breeding yellow genotype (*wwYY*), and two true-breeding white genotypes (*WWyy*) and (*wwyy*).

The double-recessive white-seeded genotype (*wwyy*) is rare, if present at all, among commercial varieties of lettuce. A homozygous line of this genotype was obtained only by the use of testers on the white-seeded segregates from a yellow-seeded by a white-seeded cross in which the white-seeded was of the *WWyy* genotype.