

# INHERITANCE OF BULB COLOR IN THE ONION

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Received February 17, 1944

**I**N THE onion the color of the bulb ranges from white to dark red and dark yellow, a great assortment of shades of red and yellow being known. The attractiveness of a variety depends to a large degree upon the bulb color. Furthermore, colored bulbs are highly resistant to the onion smudge organism, *Colletotrichum circinans* (Berk.) Vogl., whereas white bulbs are susceptible. For these reasons it is important to understand the mode of inheritance of different colors.

Genetic studies in this subject have been published, but in this paper data from additional crosses are presented which necessitate a modification of the conclusions drawn from this earlier work.

## REVIEW OF LITERATURE

TSCHERMAK (1916) found that dark yellow and red bulb colors are dominant to white, with a complex segregation in the F<sub>2</sub>. MEUNISSIER (1918) reported that sometimes yellow is dominant over red and over white, although a recessive yellow also occurs.

RIEMAN (1931) has made a more detailed study of the inheritance of bulb color in the onion. He postulated a series of multiple alleles—namely, *W* a gene for red pigment, *W<sup>y</sup>* a gene for yellow pigment, and *w* a gene for white. *W* is dominant over both *W<sup>y</sup>* and *w*. In addition, there are the genes *I* and *i*, inherited independently of this allelic series. *I* is incompletely dominant over *i* and inhibits both red and yellow so that all plants homozygous for *I* are white. Both red and yellow bulbs lack the inhibitor *I*, the homozygous red onions being *ii WW* and the homozygous yellow being *ii W<sup>y</sup> W<sup>y</sup>*.

## MATERIALS AND METHODS

To determine the mode of inheritance of red, yellow, and white bulb color crosses were made between a large number of commercial varieties and inbred strains. Flies were used to facilitate crossing, as described by JONES and EMSWELLER (1934). Several populations were grown in the field at Milpitas, Calif., in 1934, while the second author was a member of the staff of the College of Agriculture, UNIVERSITY OF CALIFORNIA, but most were grown since 1936 in the greenhouses at the Plant Industry Station, Beltsville, Md. F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub>, and backcross and backcross selfed populations have been examined. For convenience in summarizing, comparable populations have been pooled in the tables.

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The goodness-of-fit to Mendelian ratios was calculated by the chi-square method.

## EXPERIMENTAL RESULTS

In reciprocal crosses between red and yellow varieties the F<sub>1</sub> bulbs were red, showing that red is dominant over yellow (table 1). The ratios obtained were in close agreement with the expected ratios of 3 red: 1 yellow for the F<sub>2</sub> and 1 red: 1 yellow for the backcross populations. The genes differentiating red pigment from yellow were designated by RIEMAN (1931) as *W-W<sup>v</sup>*.

TABLE 1  
*Inheritance of bulb color in the onion in crosses involving the C and R genes.*

PEDIGREE	GENOTYPE	GENERATION	OBSERVED			EXPECTED RATIO	P
			RED	YELLOW	WHITE		
Red×yellow.....	<i>ii CC RR×ii CC rr</i>	F <sub>1</sub>	All				
Yellow×red.....	<i>ii CC rr×ii CC RR</i>	F <sub>1</sub>	All				
F <sub>1</sub> red selfed.....	<i>ii CC Rr</i> selfed	F <sub>2</sub>	2,353	756		3:1	0.40
F <sub>1</sub> red×yellow....	<i>ii CC Rr×ii CC rr</i>	B <sub>1</sub>	214	226		1:1	.58
Yellow×white....	<i>ii CC rr×ii cc rr</i>	F <sub>1</sub>		All			
F <sub>1</sub> yellow selfed....	<i>ii Cc rr</i> selfed	F <sub>2</sub>		638	216	3:1	.85
White×F <sub>1</sub> yellow....	<i>ii cc rr×ii Cc rr</i>	B <sub>1</sub>		14	14	1:1	1.00
Yellow selfed.....	<i>ii Cc rr</i> selfed	B <sub>1</sub> (X)		94	36	3:1	.48
Red×white.....	<i>ii CC RR×ii cc RR</i>	F <sub>1</sub>	All				
F <sub>1</sub> red selfed.....	<i>ii Cc RR</i> selfed	F <sub>2</sub>	421		154	3:1	.33
F <sub>2</sub> red selfed.....	<i>ii Cc RR</i> selfed	F <sub>3</sub>	121		43	3:1	.72
Red×F <sub>1</sub> red.....	<i>ii CC RR×ii Cc RR</i>	B <sub>1</sub>	All				
F <sub>1</sub> red×white....	<i>ii Cc RR×ii cc RR</i>	B <sub>1</sub>	86		69	1:1	.18
Yellow×white....	<i>ii CC rr×ii cc RR</i>	F <sub>1</sub>	All				
White×yellow....	<i>ii cc RR×ii CC rr</i>	F <sub>1</sub>	All				
F <sub>1</sub> red selfed.....	<i>ii Cc Rr</i> selfed	F <sub>2</sub>	1,019	375	482	9:3:4	.21
Yellow×white....	<i>ii CC rr×ii cc Rr</i>	—	15	19		1:1	.49
Red×white.....	<i>ii Cc Rr×ii cc Rr</i>	—	59	25	80	3:1:4	.57

In certain crosses between yellow and white plants the F<sub>1</sub> bulbs were yellow, the F<sub>2</sub> produced a ratio of 3 yellow: 1 white, and the backcross produced 1 yellow: 1 white (table 1). When yellow-bulbed plants from the backcross were selfed, they also produced 3 yellow: 1 white. This indicates that in these particular crosses white bulb color behaves as a simple monogenic recessive to yellow. RIEMAN (1931) used the gene symbols *W<sup>v</sup>* and *w* to differentiate yellow from recessive white.

Some crosses between red and white produced red F<sub>1</sub> plants. On selfing they produced F<sub>2</sub> bulbs in the ratio 3 red: 1 white. When backcrossed to the red parent, the progeny were all red, whereas when backcrossed to the white parental strain, the progeny were 1 red: 1 white. According to RIEMAN'S nomenclature, the genes involved in this case are *W* and *w*.

Several yellow  $\times$  white crosses were also obtained in which all the  $F_1$  plants were red. When the  $F_1$  plants were selfed, a satisfactory fit to the dihybrid ratio 9 red:3 yellow:4 white was obtained in the  $F_2$  (table 1). These  $F_1$  and  $F_2$  results cannot be accounted for by RIEMAN's multiple allele hypothesis. Consequently, it is postulated that a basic color factor  $C$  is involved in the above red  $\times$  white and yellow  $\times$  white crosses, and the genes differentiating red color from yellow in the presence of  $C$  have been designated  $R-r$ . Recessive white plants  $cc$  may carry either  $R$  or  $r$ .

A different yellow  $\times$  white cross gave red and yellow plants in equal numbers. This ratio of 1 red:1 yellow can be accounted for by assuming that the white plant involved in the cross was heterozygous for the  $R$  factor, the parental genotypes being  $CC rr$  (yellow)  $\times$   $cc Rr$  (white).

An  $F_1$  red plant known to have the genetic constitution  $Cc Rr$  was crossed with a white plant belonging to the genotype  $cc Rr$ . A satisfactory fit was obtained to the ratio 3 red:1 yellow:4 white (table 1).

In some crosses between red and white the  $F_1$  plants are not as red as in the crosses previously described but are intermediate in color. This behavior is found in crosses involving dominant white gene  $I$ , as previously described by RIEMAN (1931). This gene is incompletely dominant so that some color develops in the heterozygous  $Ii$  plants, the amount of pigmentation depending apparently on what other color genes are carried by the plant. It was not possible to distinguish with certainty  $Ii CC RR$  from  $Ii CC rr$ . All plants involved in the crosses shown in table 1 belong to the genotype  $ii$ . Data from crosses involving the inhibitor  $I$  are shown in table 2. In the cross  $ii CC RR \times II CC RR$  the  $F_1$  plants are intermediate and the  $F_2$  segregate in the ratio 1 white:2 intermediate:1 red. Frequently it is difficult to differentiate between the white and intermediate classes, so that the ratio becomes 3 white and intermediate:1 red. When tested in the  $F_3$  generation, all white and red  $F_2$  plants bred true; all intermediate plants again segregated. When the  $F_1$  intermediate was backcrossed to dominant white, a satisfactory fit to the expected ratio of 1 white:1 intermediate was obtained. A similar ratio was obtained from the reciprocal backcross. Some of the intermediate plants from the backcross were selfed. As shown in table 2, they gave an extremely poor fit to the ratio 1 white:2 intermediate:1 red, but this was probably the result of difficulty in distinguishing between whites and intermediates, since a satisfactory fit was obtained when the white and intermediate classes were grouped together to give the ratio 3 white and intermediate:1 red. When an intermediate plant from a cross between dominant white and red ( $II CC rr \times ii CC RR$ ) was backcrossed with the red parent, a satisfactory fit to the expected ratio of 1 intermediate:1 red was obtained.

Intermediate plants belonging to the genotype  $Ii CC rr$ , obtained from the cross  $II CC rr$  (white)  $\times$   $ii CC rr$  (yellow), cannot always be distinguished with certainty from pure white. When the whites and intermediates were grouped together in the  $F_2$ , a satisfactory fit was obtained to the ratio 3 white and intermediate:1 yellow (table 2). The backcross  $Ii CC rr$  (intermediate)

$\times ii CC rr$  (yellow) also gave a satisfactory fit to the expected ratio 1 intermediate: 1 yellow. A satisfactory fit to the ratio 3 white and intermediate: 1 yellow was also obtained by selfing an intermediate plant selected from a backcross population.

TABLE 2  
*Inheritance of bulb color in the onion in crosses involving the I gene.*

PEDIGREE	GENOTYPE	GENERATION	OBSERVED				EXPECTED RATIO	P
			WHITE	INTER-MEDIATE	RED	YELLOW		
Red $\times$ white . . . . .	$ii CC RR \times II CC RR$	F <sub>1</sub>	All				1:0	
F <sub>1</sub> intermediate selfed . . . . .	$Ii CC RR$ selfed	F <sub>2</sub>	63	156	58		1:2:1	0.10
F <sub>1</sub> intermediate selfed . . . . .	$Ii CC RR$ selfed	F <sub>2</sub>	35*		6		3:1	.13
F <sub>2</sub> intermediate selfed . . . . .	$Ii CC RR$ selfed	F <sub>3</sub>	339	727	321		1:2:1	.16
F <sub>2</sub> intermediate selfed . . . . .	$Ii CC RR$ selfed	F <sub>3</sub>	107*		41		3:1	.46
F <sub>1</sub> intermediate $\times$ white . . . . .	$Ii CC RR \times II CC RR$	B <sub>1</sub>	333	363			1:1	.26
White $\times$ F <sub>1</sub> intermediate . . . . .	$II CC RR \times Ii CC RR$	B <sub>1</sub>	31	32			1:1	.90
Intermediate selfed . . . . .	$Ii CC RR$ selfed	B <sub>1</sub> (X)	136 (564*)	428	187 (187)		1:2:1 (3:1)	.01- (.95)
Intermediate $\times$ red . . . . .	$Ii CC Rr \times ii CC RR$	B <sub>1</sub>		297	265		1:1	.18
F <sub>1</sub> intermediate selfed . . . . .	$Ii CC rr$ selfed	F <sub>2</sub>	737*		252		3:1	.73
Intermediate $\times$ yellow . . . . .	$Ii CC rr \times ii CC rr$	B <sub>1</sub>		92	72		1:1	.12
Intermediate selfed . . . . .	$Ii CC rr$ selfed	B <sub>1</sub> (X)	10*		5		3:1	.47

\* Includes intermediates, which were not distinguished from whites.

F<sub>2</sub> populations segregating for both the *I-i* and *R-r* genes were obtained from both red  $\times$  white ( $ii CC RR \times II CC rr$ ) and white  $\times$  yellow ( $II CC RR \times ii CC rr$ ) crosses. These populations gave a satisfactory fit to the ratio 12 white and intermediate: 3 red: 1 yellow (table 3). From selfing the F<sub>1</sub> intermediates from the cross  $II cc RR$  (white)  $\times$   $ii CC rr$  (yellow) a satisfactory fit to the trihybrid ratio 52 white and intermediate: 9 red: 3 yellow was obtained (table 3). No populations segregating for only the *I-i* and *C-c* genes were tested. However, if the red and yellow classes are pooled in the foregoing case, a satisfactory fit to the expected ratio 13 white and intermediate: 3 colored is obtained, the P value being 0.55. The backcross  $Ii Cc$  (intermediate)  $\times$   $II cc$  (white) gave a satisfactory fit to the ratio 3 white: 1 intermediate (table 3).

TABLE 3

*Inheritance of bulb color in the onion in crosses involving the I, C, and R genes.*

PEDIGREE	GENOTYPE	GENER- ATION	OBSERVED				EX- PECTED RATIO	P
			WHITE	INTER- MEDI- ATE	RED	YEL- LOW		
F <sub>1</sub> intermediate selfed (from red×white) . . . . .	<i>Ii CC Rr</i> selfed	F <sub>2</sub>	94*		19	11	12:3:1	0.35
F <sub>1</sub> intermediate selfed (from white×yellow) . . . . .	<i>Ii CC Rr</i> selfed	F <sub>2</sub>	2,921*		701	259	12:3:1	.35
F <sub>1</sub> intermediate selfed (from white×yellow) . . . . .	<i>Ii Cc Rr</i> selfed	F <sub>2</sub>	338*		52	20	52:9:3	.72
F <sub>1</sub> intermediate×white . . . . .	<i>Ii Cc†×II cc†</i>	B <sub>1</sub>	33	14			3:1	.46

\* Includes intermediates, which were not distinguished from whites.

† These plants may have carried either *R* or *r*.

In an F<sub>2</sub> population segregating for both white and colored bulbs, an association was found between the color of the bulb and its weight in grams. During a study of the effect of length of photoperiod on bulbing, an F<sub>2</sub> population from the cross Southport White Globe (*II CC RR*)×Early Grano (*ii CC rr*) was grown in the greenhouse under 13-, 14-, and 15-hour photoperiods. The bulbs were classified according to color into three groups: (1) white, (2) intermediate, and (3) red and yellow. The white bulbs belonged to the genotype *II*; the intermediate bulbs to *Ii*, the *I* factor being only incompletely dominant over red and yellow; and the red bulbs to *ii*. It was difficult to distinguish always between the *II* and *Ii* genotypes, so an occasional bulb may have been erroneously classified. The individual bulbs were weighed in grams, and it was found (table 4) that for each photoperiod the white bulbs (*II*) weighed less than the red and yellow ones, the difference being sufficiently great to exceed the 1 percent level of significance.

TABLE 4

*Weight of white and colored F<sub>2</sub> onion bulbs from the cross Southport White Globe ×Early Grano, grown in 13-, 14-, and 15-hour photoperiods.*

COLOR	GENO- TYPE	13-HOUR	14-HOUR	15-HOUR
		Grams	Grams	Grams
White . . . . .	<i>II</i>	43.8±2.32	39.7±1.59	36.7±1.56
Intermediate . . . . .	<i>Ii</i>	50.0±1.41	43.0±.94	45.0±.80
Red and yellow . . . . .	<i>ii</i>	56.1±2.66	47.6±1.59	45.4±1.52

## DISCUSSION

As evidence that the genes *W*, *W<sup>v</sup>*, and *w* form a series of alleles, RIEMAN showed that a simple monohybrid relationship exists between the genes *W* and

*w* and likewise between *W* and *W<sup>v</sup>*. Unfortunately, as RIEMAN pointed out, all of his yellow  $\times$  white crosses involved white plants carrying the inhibitor *I* so that the relationship between *W<sup>v</sup>* and *w* was not definitely established. In this paper data are presented which show that in certain crosses, in which the inhibitor *I* is not involved, a simple monohybrid relationship exists between yellow and white. This completes the proof that the genes for red and yellow are alleles but does not necessarily establish the validity of RIEMAN's multiple allele hypothesis, since the recessive white class can be explained in another way. It may be assumed that there is a basic color factor *C*, which is essential for pigment formation, so that plants possessing *C* are colored and those with *c* are white. In the presence of *C* the dominant gene *R* produces red pigment, and the recessive *r* produces yellow. Red varieties carry the genes *i C R*, yellow varieties *i C r*, and recessive white may be either *i c R* or *i c r*. All varieties which carry the dominant inhibitor *I* are white, regardless of the presence or absence of the *C* and *R* factors.

This hypothesis fits RIEMAN's data equally well as did his multiple allele hypothesis and has the advantage of explaining certain results presented in this paper, which cannot be accounted for by the assumption of multiple alleles. All the *F*<sub>1</sub> plants from certain yellow  $\times$  recessive white crosses (*ii CC rr*  $\times$  *ii cc RR*) had red bulbs. Furthermore, all three color classes segregated in the *F*<sub>2</sub>—namely, red, yellow, and white. Since these results are contrary to those expected on RIEMAN's hypothesis, data on the color of bulb in the onion are interpreted in this paper on the basis of three independent pairs of factors: *C-c*, *R-r*, *I-i*.

The data presented in table 4 show that there is a correlation between weight and color of bulb, the white bulbs tending to be smaller than the colored ones. This suggests that, in this particular cross, the gene *I* either has a direct effect on the size and weight of the bulb or else is genetically linked with one or more growth factors which influence the weight of the bulb. This point is of considerable practical importance and deserves further study because it will be impossible to secure large white onions carrying the *I* factor if this gene is directly responsible for the smaller bulb size. On the other hand, if the difference in size is the result of a linkage between *I* and a factor for growth, it should be possible to secure some crossing over, and to establish stocks of large-size bulbs which are also homozygous for *I*.

#### SUMMARY

Three pairs of genes are involved in the development of pigment in the onion bulb—namely: (1) *C-c*, a basic color factor, the dominant *C* gene being necessary for the production of any pigment. Consequently, all *cc* plants produce white bulbs. (2) *R-r*, in the presence of *C*, the dominant *R* gene is responsible for the production of red pigment; its allele *r* is responsible for yellow pigment. (3) *I-i*, an inhibiting factor *I* is partially dominant over *i*. All *II* plants produce white bulbs.

In one cross a correlation was found between color and weight of bulbs, sug-

gesting either that the gene *I* is genetically linked with one or more growth factors or that this gene is directly responsible for smaller bulb size.

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