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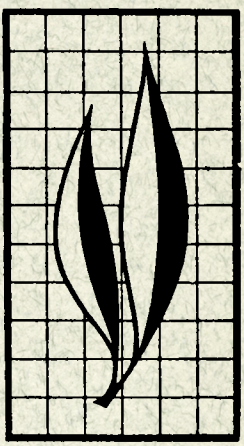

The present study on inheritance of bulb color in onions continues work begun 10 years ago at the United States Department of Agriculture. Results obtained in F_1, F_2, F_3, and backcross progenies of several varieties and lines are explained by assuming that five major genes, *I, C, G, L,* and *R* (each with two alleles) interact, and segregate independently of each other. The five genes act in a specific order on a biochemical pathway that leads to pigment formation. A diagram for such a pathway, showing the action of each gene, is proposed. Four of the genes, *I, C, L,* and *R,* were reported previously by other workers. (*L* and *R* are the designations given by us to the complementary genes reported by Jones and Peterson, 1952). The fifth gene, *G,* is proposed in the present study. The results of several of the crosses cannot be explained without its presence.

The density of golden yellow and red colors is apparently controlled by several microgenes; i.e., it is quantitatively inherited. Quantitative inheritance is not discussed in the analysis of the crosses, because this subject requires further investigation.

The study also further substantiates the presence of the four genes previously reported.

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Inheritance of Bulb Color in the Onion (*Allium cepa* L.)[1]

INTRODUCTION

INHERITANCE OF BULB COLOR in the onion is not a simple process. It results from the interaction of several genes, some of which are epistatic to the others. Bulb color ranges from white through various shades of yellow and red, to dark red and dark yellow. Intermediate colors that breed true are also known. Commercially, four color classifications are used: white, yellow, red, and brown.

A knowledge of how bulb color is inherited is of great value in a commercial breeding program because: (1) Bulb color is associated with disease resistance (Walker, 1923). (2) It may be used, with other varietal characteristics, for classification purposes. (3) It is also related to weight of the bulb. For example, Clarke, Jones, and Little (1944) indicated that an allele (*I*) may be directly or indirectly associated with smaller bulb size. (4) The onion industry has special color requirements for onions that are to be dehydrated, and uses white cultivars extensively.

The attractiveness of a cultivar depends largely upon the bulb color (Jones and Mann, 1963). Tschermak (1916) reported that dark yellow and red bulb colors are dominant to white in the F_1 generation. Furthermore, a complex segregation was observed in the F_2, and in the F_3 some white individuals produced white and colored bulbs. Yellow was found to be sometimes dominant over red and white, but a recessive yellow also occurs (Meunissier, 1918).

Reiman (1931) made a detailed study of the inheritance of bulb color in the onion. He showed that yellow and red are dominant to a *recessive* white in the F_1 and later generations, but he also observed a *dominant* white, which accounts for the complex segregation that Tschermak (1916) found in the F_2 and F_3 generations. Furthermore, Reiman postulated a working hypothesis for color inheritance. He proposed a series of multiple alleles in which *W* is a gene for red pigment, W^y a gene for yellow, and *w* a gene for white, with *W* dominant over W^y and *w*.

Genetic studies by Clarke, Jones, and Little (1944) make it necessary to modify Reiman's earlier conclusions. These workers postulated a new hypothesis that fits their data and Reiman's data equally well. In addition, it has the advantage of explaining certain results that cannot be explained on the basis of multiple alleles. The hypothesis is based on three independent pairs of factors for the development of pigment in the onion bulb. The first is a color-inhibiting factor, *I*, that is incompletely dominant over *i*. Genes *I* and *i* are present in addition to Reiman's multiple alleles, and are inherited independently of the allelic series. The *I* gene, when present in the homozygous condition (*II*), inhibits

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the expression of the color whether the other genes are present or not. All *II* plants produce white bulbs regardless of other factors. The second is a basic factor for color, *C*, that is completely dominant to its alternative, *c*, and is necessary for the production of any pigment. Therefore, all *cc* plants produce white bulbs regardless of other color factors that may be present. The third factor is *R* vs. *r*. In the presence of *C*, the dominant *R* leads to the production of red pigment, and the recessive allele, *r*, produces a yellow pigment. Bulbs with the genotype *IiCCrr* are cream or buff in color, but those with *IICCrr* are white. Plants that breed true for red and yellow are *iiCCRR* and *iiCCrr*, respectively. Two types of white are known, recessive and dominant. Recessive white can be *iiccRR*, *iiccRr*, or *iiccrr*, in the genotype, while plants that are *II*– in the genotype are dominant white.

Davis (1954) published a method for distinguishing recessive-white from dominant-white onion bulbs that saves at least two years in determining their genetic constitution by normal breeding methods. The method is based on Reiman's (1931) observations, in which he reported that the yellow pigment is a flavone, which ranges in color from pale to deep yellow. The dominant white *II*, not the recessive white, produces the almost colorless flavone. If the latter is present, exposure of the outer, fleshy onion scales to concentrated ammonia fumes induces a chemical change that results in a deep yellow color in a few seconds.

Jones and Peterson (1952) reported complementary factors for light red bulb color, but assigned no symbols to these genes. We have therefore designated them *L* and *R* in this paper. In crosses between the true-breeding yellow Brazilian cultivar 'Pera Baia' and three yellow cultivars of American origin, 'Early Yellow Globe,' 'Ebenezer,' and 'Yellow Globe Danvers,' all the F_1 bulbs are light red. After selfing of F_1 plants, the F_2's, separately and combined, showed a ratio of light red to yellow of 9:7.

Jones and Mann (1963) indicated that when some recessive white cultivars are crossed, colored bulbs, i.e., light red and/or yellow, appear in the F_1 generation, thus indicating complementary factors for yellow and light red bulb colors. No reference nor data to support these observations were given. Furthermore, Jones and Mann referred to the occasional appearance of chartreuse bulbs in certain cultivars, such as 'Australian Brown' and 'Giza No. 6.'

The present study, designed to obtain additional information on the genetic basis of color heritability, proposes a scheme for inheritance of bulb color that can provide explanations for the modified Mendelian ratios: 12:3:1, 9:7, 9:3:4, and 13:3. It is a continuation of a study begun over 10 years ago at the United States Department of Agriculture. The original materials used were provided by Dr. Elmo Davis, of the Plant Industry Station, Beltsville, Maryland.

MATERIALS AND METHODS

All the materials used were varieties and lines belonging to the species *Allium cepa* L. Whenever the genotype—according to Clarke, Jones, and Little's (1944) hypothesis—was known, it is indicated either in the tables or in the discussion of results. Table 1 shows the materials used in the spring of 1962.

These materials were crossed in all possible combinations. Then F_1's were selfed and backcrossed to both parents when possible. Later, some of the F_2 plants were selfed to get F_3 populations. The same procedure was followed with other materials received in the fall of 1962 from Dr. Davis (table 2). In the spring of 1964, other materials were crossed in all possible combinations to get F_1 data (table 3). Fortunately, some of the F_1 plants bloomed in the first year, and these were selfed to get F_2 populations in the summer of 1966. The latter are included in the results. The F_1 data for cross 5 (p. 617) are not discussed, however, because time limitations prevented carrying them further to the F_2.

TABLE 1

ONION VARIETIES AND LINES USED FOR CROSSING STUDIES
(Spring, 1962)

Lot no.*	Pedigree	Color†
457 (S ms ms)	B7-165A	white
458 (N ms ms)	B7-165B	white
851 (S ms ms)	'Red Globe' A *ii CCRR*	red
852 (N ms ms)	'Red Globe' B *ii CC RR*	red
938 (S ms ms)	'Pera Baia' #13 A ck	golden yellow
939 (N ms ms)	'Pera Baia' #13 B	golden yellow
426	P 54-306 B	golden yellow
888	P 52-353 B × rec. white B2218B F_2 massed *iiccrr*	white
931	B 15-108 B × (WP × AB F_2)F_2 massed	golden yellow
937	WSS × (wh. Persian × AB F_2)F_3	golden yellow
959	PI 174021	golden yellow
960	PI 174021 S_1	golden yellow

* U.S.D.A. identification.
† All golden yellow colors listed are without pink color in the first fleshy leaves underneath the dry scales.

Handling of plants

Seeds of the various crosses and parental lines were planted in flats in the greenhouse in September and October. Three or four weeks before transplanting, the flats were moved outdoors. Transplanting was usually done in December and January. Some pruning was done to both vegetative and root systems. The plants were placed approximately 4 inches apart in the field. Bulbs to be planted the following year were stored in flats in the bulb house (at 20 to 25° C), after being cleaned by pruning the tops and the root systems.

Cross- and self-pollinations were performed according to the procedures de-

TABLE 2

ONION VARIETIES AND LINES USED FOR CROSSING STUDIES
(Spring, 1963)

Gr. 1962 lot no.*	Pedigree	Source of seed	Color
623	B59-527	B2273-2279 sc 10 Belts. 1960	white
626	B58-806	B4278 Belts. 1960	homozygous chartreuse
627	B58-812	B2703-27 10 Belts. 1960	golden yellow homozygous†
639	B57-92	B1862-1867 sc 4 Belts. 1961	white
733	(B12132B × L303B) × Imp Sp F_2 pink	Gr 1049 sc 134	pink
955	B12132B × (chart × Imp Sp) F_2	B 1004 Belts. 1961	chartreuse
962	B12132B × 'Pera Baia' #13 F_2	B 1033 Belts. 1961	pink
967	'Pera Baia' #13 A × B2215C F_2	B 1064 Belts. 1961	pink
993	'Mexican White' × B 12132B F_2	B 1206 Belts. 1961	pink
347	B 2647A	B4295-4302 Belts. 1960	red and intermed. red *iiCCRR*

* U.S.D.A. identification.
† Without pink color in the first fleshy leaves under the dry scales.

TABLE 3
ONION VARIETIES AND LINES USED FOR CROSSING STUDIES
(Spring, 1964)

Lot no.*	Pedigree	Color
Gr 87.....	B 59-527 C	white
Gr 32.....	Chieftain	golden yellow
Gr 493.....	B4038 A	chartreuse
Gr 505.....	B 60-5036 A	pink
Gr 571.....	'Pera Vermalha' A	pink and golden yellow
Gr 685.....	Ia 1408 A	red
Gr 787.....	B 79-717B	rec. white
Gr 1015.....	B 62-715C	dom. white
Gr 1033.....	B 62-813C	pink and intermed. red

* U.S.D.A. identification.

scribed by Jones and Emsweller (1933) and Jones (1946), with slight modifications. Both types of pollination were made under wire-screen cages of about 8 inches in diameter and 12 to 14 inches in height.

Selfing was accomplished by caging the entire umbel before any flowers opened, to prevent contamination with foreign pollen. Blow flies were introduced into the cage several times during the flowering period to insure self-pollination.

For cross-pollination, umbels that were to be used as female parents were enclosed in paper bags when the first flowers opened. After several days, all flowers already open were removed, and emasculation was then performed on succeeding newly-opened flowers twice each day, at 8 to 9 a.m. and 5 to 7 p.m. After about 50 to 150 flowers had been emasculated, all remaining unopened flowers were removed from the umbel, which was then placed in a wire-screen cage. The male inflorescence was covered with a paper bag during the emasculation period, to prevent pollen contamination. It was then cut, placed in water, and enclosed in the cage with the female umbel. Flies were added to accomplish pollination.

In 1962 and 1963 some crosses were made by using sterile male plants as female parents. In such cases, female and male umbels were enclosed in the same cage, without emasculation, with flies present to aid pollination.

Color classification

In previous studies of the inheritance of bulb color (Reiman, 1931; Clarke, Jones, and Little, 1944; Jones and Peterson, 1952), three types of color were analyzed—white, yellow, and red. The bulb colors used in the present study were classified as: white, buff, chartreuse, golden yellow (normal), dark golden yellow, pink, and red (figs. 1 and 2). For purposes of comparison, the following list indicates corresponding color plates from Maerz and Paul (1930).

COLOR	PLATE, COLUMN, ROW
white	17 A, 1
buff	11 C, 2 and D, 2
chartreuse	11 L, 1
golden yellow (normal)	10 F through L 7
dark golden yellow	13 L, 12
pink	4 J, 8 and K, 8
red	6 J, 6 and K, 6

It was possible to classify bulbs into one of the above-mentioned categories according to the general phenotype of the color. Difficulties in classification were sometimes encountered, however, because several shades were present in the bulb skin, resulting from the influence of several environmental conditions on the phenotype of the bulb color. Some of these shades can be observed in figures 1 and 2. Some abnormalities in the phenotype of color were observed in a single bulb during the course of the study; for example, the occasional occurrence of more than one color in the skin. Chartreuse and shades of golden yellow might be found in the same bulb. In another example, the outer, dry scales of two bulbs might have the same phenotype (for example, dark golden yellow),

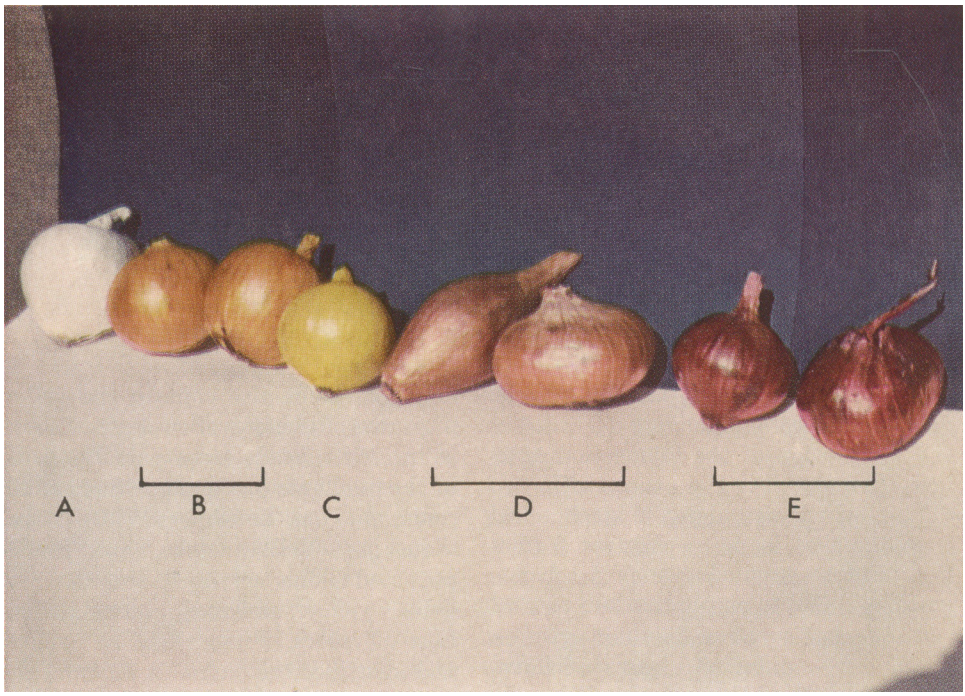


Fig. 1. Bulbs of different colors: A, white; B, golden yellow; C, chartreuse; D, pink; E, red.

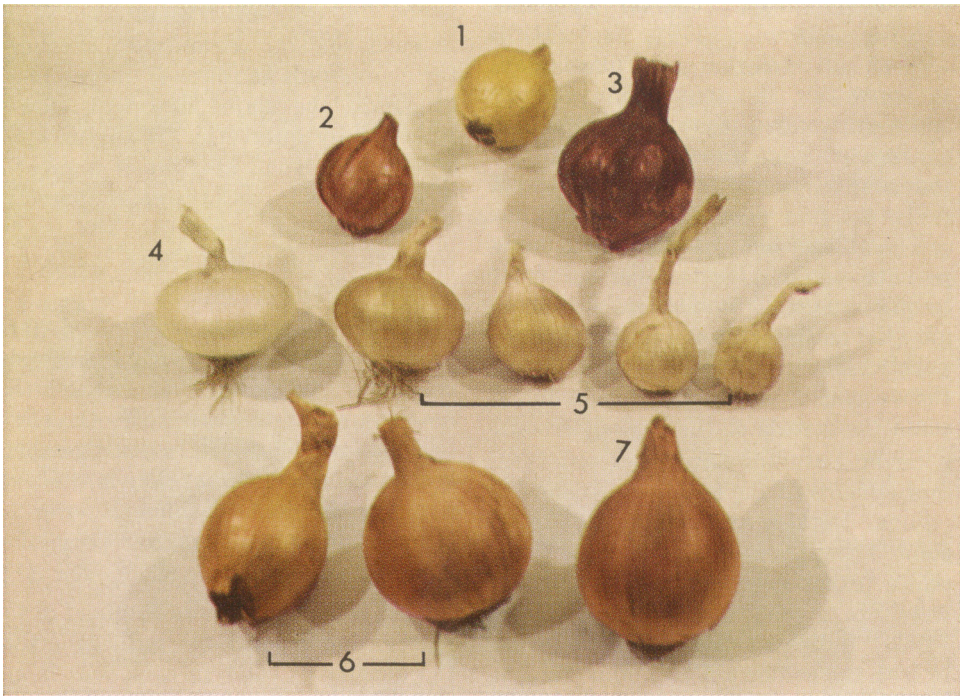


Fig. 2. Bulbs varying in color from white through red: 1, chartreuse; 2, pink; 3, red; 4, white; 5, buff; 6, golden yellow; 7, dark golden yellow.

but the color of the first fleshy leaves would be different—light yellow in the first bulb but pink in the other. These are referred to in this paper as without or with pink beneath, respectively. It should be mentioned that the classification of bulbs depends largely on the subjective sensitivity and experience of the investigator.

HYPOTHESIS FOR EXPLAINING INHERITANCE OF BULB COLOR

A scheme to account for the inheritance of bulb color in onions necessitates the assumption of the interaction of at least five major genes, each with two alleles, which act along a biochemical pathway that leads to pigment formation. Before proposing such a scheme, we should like to emphasize two points:

First, the literature does not agree on whether the different classes of flavonoids are formed through parallel pathways from a single intermediate or whether they are formed sequentially, without a common precursor. Krugman (1956), Alston (1958), and Hillis (1955) indicated that some plants seem to carry out the sequential pathway while others synthesize the two classes of flavonoids—anthoxanthins and anthocyanins—as end products of parallel pathways.

The biogenesis of flavonoid compounds and the inheritance of bulb color in onions seem to fit more closely the sequential pathway theory rather than the parallel scheme of biosynthesis, and that theory can be successfully used to explain the results of the various crosses.

Several studies have been published on pigments of the major bulb colors in onions. Perkin and Hummel (1896) showed that the coloring matter of onion scales (exact color and name of cultivar were not given) is quercetin. Walker (1923) indicated that quercetin exists in both the golden yellow and red scales, and that the red scales also have an anthocyanin. A report (unpublished) by the present authors showed that pink and red scales also contain the yellow pigments of golden yellow scales. Brandwein (1965) made a comparative study of the pigments of three cultivars of the common onion, 'Southport White Globe,' 'Southport Yellow Globe,' and 'Southport Red Globe,' corresponding to white, golden yellow, and red in our classification of colors. From them he isolated and identified the flavonols, flavonol glycosides, and anthocyanin glycosides. 'Yellow Globe' and 'Red Globe' had the greatest amounts of flavonoids; 'White Globe' had only small quantities. Within each cultivar, Brandwein arranged the compounds as follows: quercetin-4′-glucoside, the major flavonoid, closely followed by quercetin 3,4′-diglucoside; a relatively small amount of quercetin 4′-7-diglucoside; and traces of quercetin 3-glucoside and quercetin. The major compound of the 'Red Globe' cultivar is peonidin 3-arabinoside.

The second point to be emphasized in connection with the working hypothesis, as stated earlier, is that light, intermediate, and dark shades of both yellow and red bulb colors can be distinguished, and it was thought that they may segregate in a Mendelian fashion either in the F_2 or F_3 or in the backcross progenies.

In many cases, however, a range of golden yellow or red was obtained in the segregating generations, indicating that the density of color in each case is apparently quantitatively inherited. The *environmental* factors also seem to have an effect on the color density.

For example, a range of one color was encountered in cross 6:

P_1, 347, red
Proposed genotype:
iiCCLLRR
P_2, 963, pink
Proposed genotype:
iiCCL-R-
F_1, 3 intermediate red with tendency toward pink
F_2, 162 bulbs ranging from pink to red

Similar results also appeared in cross 20 (Appendix table 1). Such segregation indicates quantitative inheritance.

An accurate means of measuring pigment density is desirable, since it was difficult to classify bulbs with the unaided eye. Additional research remains to be done with a suitable measure for determining color density, and with parents representing the two extremes of the density range.

The results of the crosses made in the present study can be explained easily if we assume that the appearance of golden yellow or red color is initiated by five major genes, and that the increasing density from light to dark is a matter of accumulation of microgenes, each with a small, i.e., quantitative effect. These genes, discussed below, segregate independently of each other, and act in the following *specific* order:

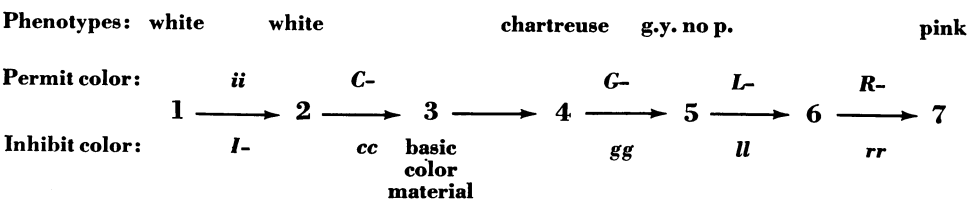
I-i. The *I* gene, named by Reiman (1931), inhibits pigment formation. It is partially dominant to its recessive allelomorph, *i*, which allows color expression when present as the homozygous recessive. *II* bulbs are white *regardless* of other color genes. It should be noted that this gene can act at either the beginning of the biochemical pathway that leads to pigment formation, or, possibly, at the end, by destroying the pigment.

C-c. This allelic pair was named as a basic color factor by Clarke, Jones, and Little (1944), with the dominant *C*, either homozygous or heterozygous, being necessary for pigment formation. The homozygous recessive *cc* bulbs are white *regardless* of other color genes present.

G-g. In this gene, proposed by us, the dominant *G*, either homozygous or heterozygous, produces golden yellow color without pink beneath, provided *iiC-* are present. The homozygous recessive *gg* is responsible for the appearance of chartreuse color if *iiC-* genes are present, and regardless of other color genes present.

L-l and **R-r.** Jones and Peterson (1952) reported that when crosses were made between a golden yellow variety, 'Pera Baia,' from Brazil, and three golden yellow varieties of American origin, all the F_1 bulbs were light red. When they were selfed, a ratio of 9 light red:7 golden yellow was obtained in F_2, indicating a complementary interaction of two genes for light red. Jones and Peterson did not assign symbols for these two allelic pairs, but Clarke, Jones, and Little (1944) indicated the presence of allelic pair *R-r*, with the dominant *R* being necessary for the production of red pigment, and its recessive homozygous allele for golden yellow pigment. Apparently, therefore, *R-r* is one of two allelic pairs necessary for light red bulb color and for which we suggest the symbols *L-l* and *R-r*. For these two allelic pairs, either homozygous or heterozygous dominant, to produce the red pigment requires only the presence of *iiC-G-*. This complementary interaction between *L* and *R* genes was confirmed during the analysis of other crosses (Appendix tables 1, 2, and 3), and the evidence will be reported at a later date.

The diagram (p. 614) represents the scheme for inheritance of bulb color. The numbers 1 through 7 represent the compound, or group of compounds, involved in the biochemical pathway. As indicated, the appearance of color is not a simple process, but results from a complicated interaction among several genes, some of which are epistatic.



RESULTS: EVIDENCE FOR A NEW COLOR GENE

The existence of a new gene was determined during analysis of several crosses made in the present study. Table 4 shows the parents for five crosses, and the cross results. Abbreviations used in analysis of crosses are:

g.y.p. = golden yellow with pink beneath

g.y. no p. = golden yellow without pink beneath

chart = chartreuse

I-, *C-*, *G-*, *L-*, or *R-* indicates that the gene is present in either the homozygous dominant or heterozygous condition

Cross 1. Pedigrees of the two parents in this cross are given in table 5. It may be noted (table 4) that a new class of color, normal golden yellow, appeared in the F_1 and then reappeared in F_2, together with white and chartreuse bulbs, in a ratio suggesting that normal golden yellow is dominant over chartreuse. This finding also indicates that a biochemical step leading to the formation of golden yellow color was blocked in the homozygous chartreuse parent, Gr 626, as a result of the presence of a new homozygous recessive gene, and that the dominant allele of that gene was supplied to F_1 bulbs by the other parent, Gr 623, which is white because of the presence of *cc*, and regardless of other color genes. Positive evidence that the parent Gr 623 has the dominant allele in homozygous condition is clear from crosses 10, 11, 13, and 22 (Appendix table 1). There is no other way to explain the results of cross 1 unless we assume the presence of the new gene with two alleles that act after *I-i* and *C-c* genes in the biochemical pathway of pigment formation. We have given the symbol *G-g-* to the new gene, with

TABLE 4

INHERITANCE OF BULB COLOR IN CERTAIN ONION CROSSES

Cross no.	Parents	F_1 (one plant)	F_2				
			White	Chartreuse	g.y. no p.	Total no. bulbs	Proposed ratio
1.....	Gr 623 × Gr 626 rec. white homozyg. chart	g.y. no p.	64	43	163	270	g.y.:chart:white 9:3:4
2.....	B1915 × B1386 chart pink	g.y. no p.	...	13	37	50	g.y.:chart 3:1
3.....	B1847 × B1963 g.y. no p. g.y. no p.	g.y. no p.	...	101	327	428	g.y.:chart 3:1
4.....	B1145 × B1750 chart red	chart	...	125	...	125	All one class.
5.....	493 × 32 chart g.y. no p.	200 g.y. no p.*					

* Indicates the dominance relationship between g.y. no p. and chart. colors. F_2 information not available for this cross.

TABLE 5

PEDIGREES AND PROPOSED GENOTYPES OF TWO ONION PARENTS, Gr 623 AND Gr 626

Year			B12132B × L303BF *iiCCrr* *iiccrr*	B4038B chartreuse		P_1 172700 red
1956.....	p74-9-32C *iiCCrr*		P5130	P5053		P550
1957.....	Gr 674 g.y.		B1252 g.y.	B1145 chart	×	B1750 red
1958.....	B255 g.y.	×	B380 white		B806 one chart bulb	
1959.....		B527 g.y.			Gr 927 125 chart bulbs	
1960.....		Gr 201 g.y.			B4278 chart	
1961.....		B2273-2279 g.y.				
1962.....		Gr 623* g.y. and white			Gr 626† chart	

* Gr 623 white used as parent in the cross. Proposed genotype, *iiccrr*, rec. white.
† Proposed genotype, *iiCC-*, homozygous chartreuse.

G allele completely dominant over *g*. It is logical also to assume that the Gr 626 parent has *rr*, since the other parent, Gr 623, is *rr*, and the F_1 and F_2 showed no evidence of pink or red.

On the basis of these assumptions, the genetic structure of the bulbs involved in the cross may be analyzed as follows:

P_1, Gr 623, rec. white, *iiccGGrr-* × P_2, Gr 626, homozyg. chart, *iiCCggrr-*

F_1, g.y. no p., *iiCcGgrr-*, self-crossed, yielding

F_2 ratio of:

9 *iiC-G-rr* g.y.p.
3 *iiC-ggrr-* chart
4 *iiccG-rr-* (3) white
iiccggrr- (1) white

The observed numbers of F_2 bulbs compared with the expected 9:3:4 ratio were:

EXPECTED	OBSERVED
151.88	163 normal g.y. no p.
50.62	43 chart
67.50	64 white
270.00	270

Goodness of fit was calculated by the chi-square method, with P between 0.5 and 0.3. The deviation of the observed from the expected ratio is not significant, and the results indicate that *G* is necessary for the appearance of g.y. no p. color. Apparently such a gene acts in the pigment biosynthesis after the *I-i* and *C-c* genes and before the *R-r* gene.

Cross 2. Pedigrees of the parents of this cross were:

SEED
P_1, B4038B chart
BULBS
P_1, P5056 all chart
SEED
P_2, 'Imperial Spanish Red'
BULBS
P_2, P5151
37 g.y.:16 p.

The cross was between chartreuse bulbs (B1915) from P5056 and pink bulbs (B1386) from P5151. The fact that all bulbs obtained from seeds of B4038B were chartreuse indicates homozygosity for that color. Therefore, the proposed genotype of B1915 parent can be *iiCCgg* if we assume the existence of a gene that controls the biochemical pathway between chartreuse and golden yellow, as indicated in cross 1.

Selfed seeds of the 'Imperial Spanish

Red' line segregated into bulbs with golden yellow and pink colors, indicating heterozygosity for genes controlling pink. When the pink bulbs were selfed, the progeny were 4 pink: 3 normal golden yellow without pink beneath, a close fit to the 9:7 ratio in which P = 0.7 to 0.8. Complementary factors for light red (pink) bulb color have also been reported by Jones and Peterson (1952). The proposed genotype of the B1386 parent can therefore be *iiCC-GGLlRr.*

Results of cross 2 (table 4) are easily explained if we assume that the difference in color between chartreuse and golden yellow with no pink beneath is controlled by a single major gene with two alleles, *G-g,* with *G* completely dominant over *g.* Based on this assumption, the results of this cross were analyzed as follows:

P_1, B1915, chart, *iiCCggllrr* × P_2, B1386, pink, *iiCCGGLlRr*
F_1, g.y. no p., *iiCCGgllrr,* self-crossed, yielding
F_2 ratio of:
3 *iiCCGGllrr* (1) g.y. no p.
iiCCGgllrr (2) g.y. no p.
1 *iiCCggllrr* chart

The observed numbers of F_2 bulbs compared with the expected 3:1 ratio were:

Expected	Observed
37.5	37 g.y. no p.
12.5	13 chart
50.0	50

By adjusted chi-square test, the observed results were a close fit to the expected ratio. Results of this cross confirm the existence of *G-g* which controls the difference between chartreuse and golden yellow with no pink and which acts independently in the biochemical pathway of the pigment formation after *I-i* and *C-c* genes and before *L-l* and *R-r.*

Cross 3. Pedigrees of the parents of this cross were:

Seed
P_1, B12132B
iiCCrr
Bulbs
P3322
Seed
P_2, 'Southport Yellow Globe'
iiCCrr
Bulbs
P5179

The following year, bulbs from P3322 and P5179 were used for cross 3:

B1847, g.y. no p × B1963, g.y. no p.

The results of cross 3 (table 4) can be explained if we assume that *G-g* is necessary for the expression of g.y. no p. and that it segregates independently of other bulb-color genes, one parent being *GG* and the other, *Gg.* Based on that assumption, the cross results were analyzed as follows:

P_1, B1847, g.y. no p.
Proposed genotype:
iiCCGg-rr ×
P_2, B1963, g.y. no p.
Proposed genotype:
iiCCGG-rr
F_1, g.y. no p., possible genotype:
iiCCGg-rr
F_2 ratio of:
3 *iiCCGG-rr* (1) g.y. no p.
iiCCGg-rr (2) g.y. no p.
1 *iiCCgg-rr* chart

The observed numbers of F_2 bulbs compared with the expected 3:1 ratio were:

Expected	Observed
321	327 g.y. no p.
107	101 chart
428	428

By adjusted chi-square test, the observed results were a close fit to the expected ones, with P between 0.5 and 0.3. Again, the results of this cross indicate the existence of *G-g,* as in the case of crosses 1 and 2.

Cross 4. Pedigrees of the parents of this cross were:

SEED
P_1, B4038B chart
BULBS
P5053
SEED
P_2, 172700 red
BULBS
P550

The following year, bulbs from P5053 and P550 were used for cross 4:

B1145 chart × B1750 red

with the following results:

F_1, 1 bulb, chart
F_2, 125 bulbs, chart

As with crosses 1, 2, and 3, the presence of *G-g* is assumed, on the basis of which, the following analysis of cross 4 is made:

P_1, B1145, chart
Proposed genotype:
iiCCgg ×
P_2, B1750, red
Proposed genotype:
iiCCGgL-R-
F_1, chart, possible genotype, *iiCCgg*
F_2, expected all chart
(actual count, 125 chart bulbs)

The above findings provide additional evidence that *G-g* is necessary for both the appearance of g.y. no color beneath and the expression of genes *L* and *R*.

Cross 5. In this cross, P_1, 493, chart, and P_2, 32, g.y. no p., yielded 200 F_1 g.y. no p. The F_1 bulbs were not selfed to produce F_2 plants, because of time limitations. The results of cross 5, as shown in F_1, are useful, however, since they indicate that golden yellow without pink beneath seems to be completely dominant over chartreuse, as was suggested in crosses 1 to 4.

The remaining crosses were analyzed genotypically and phenotypically (Appendix tables 1–4) according to the proposed hypothesis. Goodness of fit was tested by the chi-square method, which was adjusted when only one degree of freedom was present.

Although the two parents Gr 959 and Gr 960 (crosses 9 and 7, respectively, Appendix table 1) were classified by Dr. Davis as champagne color, they are included in the golden yellow with no pink group. The dry scales of these two parents are very close to golden yellow, but with some very light redness. However, the first fleshy leaves under the dry scales do not show pinkish color.

It is reasonable to consider golden yellow with pink beneath as bulbs with pink color for two reasons: First, their potential ability to form pink color is indicated by its presence in the first fleshy leaves. The appearance of golden yellow in the dry scales may be attributed to an increase in density of golden yellow pigment as a result of the accumulation of several small genes; this in turn tends to hide the pink color in the dry scales. Second, the data can be explained logically if we consider these bulbs to be in the pink group.

Approximately 40 to 50 per cent of the crosses in the present study were successful. The lack of success with the rest of the crosses may have resulted mainly from the plants' failure to set seed at any generation, damping-off of plants in the seedling stage, and the inability of seed to germinate.

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APPENDIX TABLE 1

CROSSES INVOLVING SELFING OF F_1 ONION PLANTS TO OBTAIN F_2 SEGREGATING GENERATION

Cross no.	Lot no., color, proposed genotype		F_1	F_2 segregating generation	χ^2 P
	P_1	P_2			
7	888 rec. white *iiccGG**	960 g.y. no p. *iiCCGG**	g.y. no p. *iiCcGG**	81 g.y. no p. 23 white 1 *iiCCGG** } g.y. no p. 2 *iiCcGG** } 1 *iiccGG** white	0.3–0.5
8	426 g.y. no p. *iiCCGG**	888 rec. white *iiccGG**	g.y. no p. *iiCcGG**	18 g.y. no p. 3 white 1 *iiCCGG** } g.y. no p. 2 *iiCcGG** } 1 *iiccGG** white	0.2–0.3
9	931 g.y. no p. *iiCCGGllrr*	959 g.y. no p. *iiCCGGLLrr*	g.y. no p. *iiCCGGLlrr*	77 g.y. no p. (range in density) All expected to be g.y. no p.	
10	623 rec. white *iiccGGllrr*	962 pink *iiCCGGLlRr*	9 g.y. no p. 2 pink Fits expected 3:1 ratio.	159 g.y. no p. (range in density) 59 white Fits expected 3:1 ratio.	0.3–0.5
11	623 rec. white *iiccGGllrr*	627 g.y. no p. *iiCCGGll–*	7 g.y. no p. *iiCcGGll–*	216 g.y. no p. 71 white Fits expected 3:1 ratio.	0.8–0.9
12	623 rec. white *iiccGGllrr*	967 pink *iiCCGGLlRr*	g.y. no p. possible F_1 *iiCcGGll–*	183 g.y. no p. 71 white Fits expected 3:1 ratio.	0.2–0.3
13	627 g.y. no p. *iiCCGGll*	639 white *iiccGGll*	4 g.y. no p. all *iiCcGGll*	89 g.y. no p. 39 white Fits expected 3:1 ratio.	0.1–0.2
14	962 pink *iiCCGGL–R–*	967 pink *iiCCGGLlRr*	2 pink possible F_1 *iiCCGGLlRr*	137 pink 88 g.y. no p. Fits expected 9:7 ratio.	0.1–0.2
15	639 white *iiccGGllRR*	962 pink *iiCCGGL–R–*	10 pink possible F_1 *iiCcGGLlRR*	119 pink or g.y. no p. 47 g.y. no p. 57 white Fits expected 9:3:4 ratio.	0.5–0.7
16	733 pink *iiCCGGLlRr*	993 pink *iiCcGGLlRr*	g.y. no p. possible F_1 *iiCcGGllrr*	206 g.y. no p. 67 white Fits expected 3:1 ratio.	0.8–0.9
17	B1045 white *IICCGGLLRR*	B1186 white *IiCCGGLLrr*	white 1 *IICCGGLLRr* 1 *IiCCGGLLRr*	12 white† 6 pink 1 g.y. no p. Fits expected 12:3:1 ratio. F_1 selfed plant was *IiCCGGLLRr*	0.3–0.5
18	B1247 pink *iiCCGGLLRR*	B1430 g.y. no p. *iiCCGGLLrr*	40 pink all *iiCCGGLLRr*	178 pink 47 g.y. no p. Fits expected 3:1 ratio	0.1–0.2

APPENDIX TABLE 1—*Continued*

Cross no.	Lot no., color, proposed genotype		F_1	F_2 segregating generation	χ^2 P
	P_1	P_2			
19	P1502 g.y. no p. *iiCCGGLLrr*	B1720 g.y. no p. *iiCCGGllRR*	pink all *iiCCGGLlRr*	58 pink 50 g.y. no p. Fits expected 9:7 ratio	0.5–0.7
20	505 pink *iiCCGGLLRR*	1033 inter. red *iiCCGGLLRR*	inter. red all *iiCCGGLLRR*	25 bulbs ranging from pink to red 3 g.y. no p. (possibly a contamination). All *iiCCGGLLRR* (indicates quantitative inheritance for density of redness).	
21	87 white *iiccGG–rr*	32 g.y. no p. *iiCCGG–rr*	g.y. no p. all *iiCcGG–rr*	76 dark g.y. no p. 25 white Fits expected 3:1 ratio.	0.8–0.9

* Indicates a block in the biochemical pathway of the pigment beyond the genes listed.
† It was difficult to distinguish accurately between white and buff color, and the bulbs were considered white.

APPENDIX TABLE 2

CROSSES INVOLVING BACKCROSSING OF F_1 PLANTS TO ONE PARENT TO OBTAIN BACKCROSS SEGREGATING GENERATION

Cross no.	Lot no., color, proposed genotype		F_1	One F_1 plant backcrossed to:	Backcross segregating generation	χ^2 P
	P_1	P_2				
22	623 rec. white *iiccGGll*	627 homozygous g.y. no p. *iiCCGGll*	7 g.y. no p. *iiCcGGll*	627 *iiCCGGll*	44 g.y. no p. All expected to be g.y. no p.	
23	955 chart *iiC–gg—*	993 pink *iiCCGGLLRR*	16 pink 1 g.y. no p. (contaminated) possible F_1 *iiC–GgL–R–*	993 *iiCCGGLLRR*	28 pink All expected to be pink.	
24	955 chart *iiC–gg—*	962 pink *iiCCGGLlRr*	pink with some chart interaction possible F_1 *iiCCGgLlRr*	962 *iiCCGGLlRr*	35 pink 21 g.y. no p. Fits expected 9:7 ratio.	0.3–0.5
25	627 g.y. no p. *iiCCGGll*	639 white *iiccGGll*	4 g.y. no p. *iiCcGGll*	627 *iiCCGGll*	37 g.y. no p. (range in density) 1 white (possibly a contamination) All expected to be g.y. no p.	
26	627 g.y. no p. *iiCCGGll*	733 pink *iiCCGGLLRR*	3 pink *iiCCGGLlRr*	733 *iiCCGGLLRR*	29 pink All expected to be pink.	
27	962 pink *iiCCGGLlRr*	967 pink *iiCCGGL–R–*	pink possible F_1 *iiCCGGLlRr*	962 *iiCCGGLlRr*	9 pink or g.y. no p. 6 g.y. no p. Fits expected 9:7 ratio.	0.5–0.7
28	347 inter. red *iiCCGGLLRR*	733 pink *iiCCGGLlRr*	8 pink all *iiCCGGL–R–*	733 *iiCCGGLlRr*	51 pink 16 g.y. no p. Fits expected 3:1 ratio if genotype of backcrossed F_1 plant was *iiCCGGLLRr* or *iiCCGGLlR*	0.7–0.8

Appendix Table 3

CROSSES INVOLVING BACKCROSSING OF ONE F_1 PLANT TO ONE PARENT TO OBTAIN BACKCROSS SEGREGATING GENERATION, THEN SELFING A BACKCROSS PROGENY TO OBTAIN ONE MORE SEGREGATING GENERATION

Cross no.	Lot no., color, proposed genotype		F_1	F_1 backcrossed to:	Backcross segregating generation	χ^2 P	Segregating generation from selfing one of the backcross progeny	χ^2 P
	P_1	P_2						
29	938 g.y. no p. *iiCCGGLLrr*	937 g.y. no p. *iiCCGGllRR*	pink *iiCCGGLlRr*	937 *iiCCGGllRR*	5 g.y. no p. 6 pink 1 *iiCCGGllRR* } 1 *iiCCGGllRr* } 1 *iiCCGGLlRr* } 1 *iiCCGGLlRR* } Fits 1:1 ratio.	0.5–0.7	173 g.y. no p. 157 pink 51 g.y. no p. All expected to be g.y. no p. Fits expected 3:1 ratio if selfed plant was *iiCCGGLlRR*.	0.8–0.9
30	938 g.y. no p. *iiCCGGLLrr*	426 g.y. no p. *iiCCGGllRR*	pink *iiCCGGLlRr*	426 *iiCCGGllRR*	2 g.y. no p. 3 pink 1 *iiCCGGllRR* } 1 *iiCCGGllRr* } 1 *iiCCGGLlRR* } 1 *iiCCGGLlRr* } Fits 1:1 ratio.	0.5–0.7	166 g.y. no p. 158 pink 38 g.y. no p. All g.y. no p. Fits expected 3:1 ratio if selfed plant was *iiCCGGLlRR*.	0.05–0.1
31	426 g.y. no p. *iiCCGGllRR*	959 g.y. no p. *iiCCGGLLrr*	pink *iiCCGGLlRr*	426 *iiCCGGllRR*	3 pink 2 g.y. no p. 1 *iiCCGGLlRR* } 1 *iiCCGGLlRr* } 1 *iiCCGGllRr* } 1 *iiCCGGllrr* } Fits 1:1 ratio.	0.5–0.7	67 pink 40 g.y. no p. 121 g.y. no p. Fits expected 9:7 ratio if selfed plant was *iiCCGGLlRr*. All g.y. no p.	0.1–0.2
32	938 g.y. no p. *iiCCGGLLrr*	939 g.y. no p. *iiCCGGLlrr*	g.y. no p. *iiCCGGLLrr*	939 *iiCCGGLLrr*	1 g.y. no p. All *iiCCGGLLrr*		179 g.y. no p. 1 g.y. no p. (possibly a contamination) All g.y. no p. (*iiCCGGLLrr*)	

APPENDIX TABLE 4

CROSSES TO OBTAIN F_2 AND F_3 SEGREGATING GENERATIONS

Cross no.	Lot no., color, proposed genotype		F_1	F_2 segregating generation	χ^2 P	F_3 segregating generation	χ^2 P
	P_1	P_2					
33	938 g.y. no p. *iiCCGGLLrr*	426 g.y. no p. *iiCCGGllRR*	pink *iiCCGGLlRr*	14 pink 10 g.y. no p. Fits expected 9:7 ratio	0.7–0.8	206 pink 52 g.y. no p. Fits expected 3:1 ratio if genotype of F_2 pink was *iiCCGGLlRR*.	0.05–0.1
34	426 g.y. no p. *iiCCGGll*	931 g.y. no p. *iiCCGGll*	g.y. no p. *iiCCGGll*	1 g.y. no p. All g.y. no p.		264 g.y. no p. All *iiCCGGll*	
35	P 74-1 g.y. no p. *iiCCGG–rr*	P 61-1 rec. white *iiccGG–rr*	g.y. no p. *iiCcGG–rr*	277 g.y. no p. 90 white Fits expected 3:1 ratio.	0.8–0.9	15 white All expected to be *iiccGG–rr* which is white in phenotype.	

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