

# INHERITANCE STUDIES IN PISUM

## I. INHERITANCE OF COTYLEDON COLOR<sup>1</sup>

DR. ORLAND E. WHITE

CURATOR OF PLANT BREEDING, BROOKLYN BOTANIC GARDEN

### INTRODUCTION

MODERN students of genetics such as Baur, East, Morgan, Emerson, and others classify all variations in animals and plants into three general categories on the assumption that organisms are made up of unit factors, in the same way that a chemist thinks of rocks and minerals as being composed of elements. These three categories of variation are:

1. Variation resulting from changes in environment.
2. Variation due to "loss" or "gain" of new factors through crossing.
3. Variation due to mutation.

### THE PROBLEM

The present paper has to do largely with data on variations in *Pisum* belonging to the first and second categories mentioned above. An attempt is being made definitely to work out the Mendelian or factorial constitution of the genus *Pisum* with reference to all those characters by which its few species and numerous varieties are distinguished. In order satisfactorily to accomplish this object, all or nearly all the known varieties of the genus *Pisum* must be considered. In this paper only the inheritance of cotyledon color is considered. Further papers

<sup>1</sup>Published as Brooklyn Botanic Garden Contributions, No. 10. These studies on the genetics of *Pisum* are being carried on in collaboration with the Office of Forage Crop Investigations and the Office of Horticultural and Pomological Investigations, U. S. Department of Agriculture. Based in part on a paper given at the Twentieth Anniversary Celebration, New York Botanical Garden, September 9, 1915.

will deal with other characters and the modifications of various characters through crossing.

Of more than two hundred and fifty varieties and species upon which the writer has been conducting experiments, the great majority have seeds which in the mature condition possess yellow cotyledons, but in such an array of varieties, it was soon noticed that the shades of yellow varied from a light greenish yellow to that of a deep orange. Roughly one could divide these forms with yellow cotyledons into light and deep yellows, but any one particularly "keen" on forming a series showing continuous variation, could easily grade the varieties so as to present a series without breaks from light greenish yellow to deep orange yellow. All the wild varieties and species so far examined have yellow cotyledons, which favors the assumption that yellow cotyledon is the oldest color character. Many of the cultivated varieties and especially the so-called blue "field peas" such as Wisconsin Blue and Prussian Blue and the majority of those known as "garden peas" have green cotyledons when the seed is mature. What has been stated regarding the gradations of color in yellow cotyledon varieties is equally true of those with green cotyledons. Roughly classified, there are dark and light green forms, but the various varieties can be arranged in a continuous series representing every shade from very dark green to light yellowish green.

Among the numerous green and yellow cotyledon varieties, when grown under the same environment, there are, however, many varieties to which certain distinct shades of either green or yellow are peculiar. Some varieties have characteristically deep orange cotyledons, others have light yellow cotyledons, and still others breed true to the shades between these two extremes. With the group of green cotyledon varieties, the same state of affairs holds true. Classification of yellows and greens is still further complicated because some varieties with light yellow cotyledons grade into the light greens and *vice versa*, even though both are grown under the same conditions.

The following table (Table I) gives the names of varieties of greens and yellows representing the classes dark

TABLE I

VARIETIES OF PISUM CLASSIFIED ACCORDING TO SHADES OF COTYLEDON COLOR  
WHEN GROWN UNDER THE SAME CONDITIONS

*Yellow Cotyledons*

Cotyledon Shade	Variety	Pedigree Stock No.	Source
Orange yellow	Black-Eyed Marrowfat	14	Vaughan Seed Co.
	First of All	22	P. Henderson & Co.
	Petit Pois	25	P. Henderson & Co.
	Späte Gold	29	Haage & Schmidt
	Henderson's Perfection Sugar	60	P. Henderson & Co.
	Agnes	147	S.P.I. 22036
	Admiral	159	S.P.I. 29323
	Khaba	176	S.P.I. 20380
Yellow	Mummy	1	H. Eckford, Wem, Eng.
	White Marrowfat	23	P. Henderson & Co.
	Elephanten	31	Haage & Schmidt
	Wachs Schwert	32	Haage & Schmidt
	Gold von Blöcksberg	34	A. D. Darbishire
	" <i>P. Jomardi</i> "	40	Cambridge (Eng.) Bot. Gard.
	<i>P. elatius</i>	41	Cambridge (Eng.) Bot. Gard.
	Prosperity	71	P. Henderson & Co.
	Pois géant sans parchemin	107	Vilmorin & Cie
	Abyssinian Black	132	S.P.I., <sup>2</sup> Dept. of Agriculture
	<i>Pisum formosum</i>	137	H. Winkler
	Openshaw	208	S.P.I. 25439
Light yellow	Archer	209	S.P.I. 22037
	Goldkönig	30	Haage & Schmidt
	<i>Pisum humile</i> ?	33	A. Sutton
	Benton	138	S.P.I. 18396
	Killarney	150	S.P.I. 22078
	Khauaka	165	S.P.I. 31808

*Green Cotyledons*

Cotyledon Shade	Variety	Pedigree Stock No.	Source
Green to light green to yellowish green	Alaska	15	Vaughan Seed Co.
	Telephone	26	P. Henderson & Co.
	Laxtonian	27	P. Henderson & Co.
	Acacia (wrinkled)	38	W. Bateson
	Everbearing	62	P. Henderson & Co.
	Yorkshire Hero	65	Thorburn & Co.
	Duke of Albany	93	Sutton & Sons
	Hundredfold	97	Sutton & Sons
(Fade easily)	Alfred	140	S.P.I. 12888
	Blue Prussian	154	S.P.I. 19787
Yellowish green	Acacia (wrinkled)	38	W. Bateson
	Duke of Albany	93	Sutton & Sons
	Hundredfold	97	Sutton & Sons

Dark green	Market Split Pea	35	New York City Markets
	Acacia (Smooth)	39	W. Bateson
	Velocity	59	Vaughan Seed Co.
	Braunschweiger	88	Haage & Schmidt
	French Grey	149	S.P.I. 27003
	Rosenberg	161	S.P.I. 10274
	Alaska	193	S.P.I. 29366
	Scotch Beauty	198	S.P.I. 27004
	Wisconsin Blue	207	S.P.I. 22049
Green	Express	20	A. D. Darbshire
	Nott's Excelsior	21	P. Henderson & Co.
	Aldermann	28	Haage & Schmidt

yellow, yellow, light yellow, dark green, green, light green, and yellowish green, when these varieties are all grown under approximately the same conditions. Any one can distinguish between dark green and dark yellow, but one well acquainted with the color of cotyledons in *Pisum* would have difficulties in distinguishing between light yellowish greens and light yellows. The classification made is admittedly arbitrary, though based on the same sort of acquaintanceship with these colors as that of a nurseryman with varietal differences in bulbs or varietal characters in leafless nursery trees. The point which it is desired to emphasize by the foregoing remarks is that these shades of cotyledon color are distinctly *varietal* characters, and are always characteristic of the respective varieties when these varieties are all grown together under any one of the several specific<sup>3</sup> environments in which the pea cultures at the Brooklyn Botanic Garden have been grown.

#### THE RELATION OF ENVIRONMENT TO COTYLEDON COLOR

One other perplexing factor enters into the study of cotyledon color in *Pisum*—the difficulty of being certain that all varieties under observation mature their seed under as nearly as possible identical environments, a factor that many geneticists experimenting with other plant forms are prone to neglect. Some varieties of peas

<sup>2</sup> S.P.I. stands for Office of Foreign Seed and Plant Introduction, U. S. Department of Agriculture, to which I am very much indebted for help in collecting varieties and species of the genus *Pisum*.

<sup>3</sup> These environments will be described in detail in a later paper.

gradually change from green to yellow when maturing, while others appear to change very suddenly, but only if plenty of sunlight and no over-supply of moisture is present. This is particularly true of some of the deep orange varieties, such as Späte Gold (P 29). The seed of this variety remains very dark green until the general appearance of the vine leads you to suppose it is ripe, but if plenty of sunlight is present and not too much moisture, and the pods are allowed to remain for a few days, the dark green changes to a very deep orange, and this deep orange is characteristic of Späte Gold when grown commercially.

With the green cotyledon varieties, one is bothered by fading of the green to a sort of washed-out yellow in many varieties, if the vines are not harvested at exactly the right time. Express, Velocity and many of the wrinkled sorts (see Hurst, 1904) are particularly subject to change under these conditions.

The above mentioned difficulties regarding the proper maturing of pea seed have been considered quite fully by Bateson, Darbishire, Lock, Tschermak and other workers in genetics. Hurst (1904) and Lock (1905) particularly have studied the tendency of certain varieties such as Telephone with green cotyledons to fade easily, even when harvested carefully, but left exposed to light. Bateson and Kilby (1905, p. 58) have studied the so-called "piebald" peas (peas with green or yellow cotyledons partly spotted or tinged with both colors) and find them to largely result from environmental conditions such as failure to ripen properly or from bleaching after ripening. "Piebald" peas are characteristic of certain varieties of peas, in which the green fades much faster upon exposure to light or moisture or to both than in ordinary green cotyledon types. "Piebald" peas of one pod, according to Bateson and Kilby, are always tinged on the same surface. Injuries causing the death of the cotyledon tissue (Bateson, 1905) (Tschermak, 1902) also are a cause of yellow spots on peas from green cotyledon varieties.

THE PIGMENTS OF COTYLEDON COLOR IN *PISUM*

Bunyard (see Darbishire, p. 131) has shown that both yellow and green cotyledon varieties have a yellow and a green pigment in their cotyledons when the seed is immature, but the yellow cotyledon varieties possess a factor (an enzyme perhaps), which causes the green pigment to fade on the maturity of their seeds. Thus green pigment is epistatic to yellow pigment, since, when both are present, only the green is in evidence.

THE GENETICS OF COTYLEDON COLOR IN *PISUM**Historical*

As early as 1729, according to Darwin (1876, I, p. 428) white (yellow cotyledon) and blue (green cotyledon) peas were found in the same pod and these results were understood to be due to chance crossing. Wiegmann, Goss (1824) and others observed that varieties of *Pisum* breeding true to blue peas when crossed with pollen from varieties breeding true to white peas, always showed a direct and immediate effect of the pollen parent. Gärtner (1849) and later hybridists incorrectly regarded this phenomenon as xenia, believing that tissues of the parent generation were affected so that the color of the seed was changed. The fact that the change in color was due to an embryonic character of a new hybrid generation seems never to have occurred to them. The true significance of these facts were never understood by Knight, Goss, Gärtner, nor any of the hybridizers before Mendel's time. Knight distinguished between cotyledon colors and seed coat colors, and Goss and others had observed practically everything regarding crosses between green cotyledon and yellow cotyledon peas except the numerical proportion of one to the other in the  $F_2$  generation. Darwin (1876, p. 348) mentions some observations of Masters, which, if authenticated, show a complex state of affairs in the inheritance of cotyledon color, since Masters claims to have obtained both yellow (white) and green (blue)

peas from a certain pea plant and when these two kinds were planted separately each continued to produce the two kinds through four generations, that being as far as the experiment was carried. In the light of the data I present below his observations may be correct, he having possibly secured one of the yellow forms such as I have found.

Mendel (1865) found when peas with yellow cotyledons were crossed with green cotyledon forms that the first generation offspring all had yellow cotyledons, but each one of these yellow cotyledon  $F_1$  plants produced  $F_2$  seeds, approximately three fourths of which had yellow cotyledons and one fourth green cotyledons. Either color of parent could be used as the seed or female parent, and the result was the same. Further, the  $F_2$  greens in  $F_3$  only produced greens, while the  $F_2$  yellows when planted, in some cases gave only yellows, in other cases both yellows and greens in the proportion of 3 Y:1 G. The actual data by which Mendel supported these statements are as follows: fifty-eight crosses on 10 plants were made, and in every case, yellow was dominant to green in the  $F_1$  generation of these crosses. 258  $F_1$  plants produced 8,023  $F_2$  seeds of which 6,022 were yellow and 2,001 had green cotyledons, an actual ratio of 75.1 yellow to 24.9 green or 3.01 Y:1 G. Mendel is careful to call attention to the wide variability in the ratio of yellows to greens when the  $F_2$  peas of each  $F_1$  plant are considered separately, the variation ranging from 32 Y:1 G on one plant to 20 Y:19 G on another. Between these extremes, there were some among the 10  $F_1$  plants of which he gives the ratios, that closely approximated the theoretical 3:1 ratio. I call attention to this great variability that Mendel found because some geneticists of late, apparently not having noted that Mendel himself observed these same facts, have referred to this as a new phenomenon. Only average ratios from large numbers were considered by Mendel, as small numbers tended to obscure the significance of the facts. Of the 8,023  $F_2$  seeds secured by Mendel,

519 seeds with yellow cotyledons were used to grow an  $F_3$  progeny. Of these, 166  $F_2$  seeds bred true or produced only seeds with yellow cotyledons, while 353 produced both yellows and greens in the proportion of 3 Y : 1 G. 353 to 166 gives a ratio of 2.13 to 1. Mendel (p. 327) especially calls attention to the difficulties involved in classifying the two colors of seeds, and notes, as I have done in the preceding paragraphs, that the seeds of pure green varieties and of segregate greens, have a tendency to bleach, another fact that several critics of Mendelian methods seem to have overlooked or forgotten.

Mendel's work has been substantiated by a large number of trained investigators, as well as by a host of teachers and amateurs. The results for cotyledon color in *Pisum* obtained by seven well-known geneticists are given below (Table II).

TABLE II

Hybrid Generation	Observer	Yellow	Green	Percentage of Green
Second. . . . .	Mendel	6,022	2,001	24.9
	Correns	1,394	453	24.5
	Tschermak	3,580	1,190	24.9
	Bateson	11,903	3,903	24.7
	Hurst	1,310	445	25.4
	Lock	1,438	514	26.2
	Darbishire	1,089	354	24.9
Third. . . . .	Correns	1,012	344	25.5
	Tschermak	3,000	959	24.2
	Lock	3,082	1,008	24.6
	Darbishire	5,662	1,856	24.7
Fourth. . . . .	Correns	225	70	23.7
	Lock	2,400	850	26.1
Total. . . . .	56,064	42,117	13,947	24.9

These results approximate very closely the ratio of 3 Y : 1 G demanded by Mendel's theory. Darbishire (1913, p. 62) in testing out 140  $F_2$  progeny with yellow cotyledons, secured 98  $F_3$  plants heterozygous for green and yellow cotyledons, and 42 breeding true or homozygous for yellow cotyledons, a proportion of 2.3 heterozygous  $F_2$  plants to 1 homozygous  $F_2$  yellow. Many varieties gathered from all over the world were used in these

<sup>4</sup> These data are taken from Darbishire (1913).



studies and all gave similar results. With these facts before us, there can be no denying the validity of Mendel's law as regards inheritance of cotyledon color in *Pisum*. The criticism has sometimes been made that the  $F_2$  segregate yellows and greens were a little less green and a little less yellow owing to the association of the unit factor materials of the two pigments in the  $F_1$  generation. In other words, segregation was not complete; the

TABLE IIIa

CROSSES OF DOMINANT YELLOW WITH GREEN ( $F_2$  GENERATION)<sup>6</sup>

Crosses	Cotyledon Color	
	Yellow	Green
(P1-4 × P39-3)-1 .....	76	34
(P21-1 × P1-1)-1 .....	129	41
(P23-5 × P39-3)-1 .....	60	16
(P26-1 × P1-1)-1 .....	23	7
(P26-1 × P1-1)-2 .....	16	0
(P26-1 × P1-1)-3 .....	32	10
(P26-1 × P1-1)-4 .....	34	6
(P27-1 × P1-1)-1 .....	33	10
(P28-1 × P1-1)-1 .....	48	6
(P28-1 × P1-1)-2 .....	37	22
(P28-2 × P1-2)-1 .....	46	17
(P29-1 × P35-7)-1 .....	11	4
(P32-1 × P35-2)-1 .....	65	16
(P34-2 × P35-7)-1 .....	103	34
(P35-3 × P1-4)-1 .....	9	4
(P35-3 × P1-4)-2 .....	49	16
(P39-1 × P32-1)-1 .....	63	17
(P40-1 × P59-1)-1 .....	91	30
(P40-1 × P59-1)-2 .....	68	29
(P41-1 × P21-1)-1 .....	103	30
(P41-1 × P21-1)-2 .....	81	25
(P62-1 × P41-3)-1 .....	40	17
(P62-1 × P41-3)-2 .....	74	22
(P65-1 × P41-3)-1 .....	71	29
(P72-1 × P41-5)-1 .....	143	54
(P72-1 × P41-5)-2 .....	142	47
Total actually obtained .....	1,647	543
Total—theoretically expected .....	1,642.4	547.5
Ratio (theoretical) .....	75 yellow	25 green
Ratio (actually obtained) .....	75.2 yellow	24.8 green

<sup>6</sup> Pedigree numbers such as -1, -2, etc., following the pedigree stock number of the variety as, *e. g.*, P28-1 refer to plant numbers. P28-1, *e. g.*, is progeny plant No. 1 of stock variety P28. P28-1-1 is plant No. 1 of the second generation from pure inbred stock P28. The seed or maternal parent in a cross is always given first, *e. g.*, P28-1 ♀ × P29-1 ♂.

determiner for green pigment was not able to produce as dark a green in  $F_2$  green segregates as in peas of the green cotyledon parent race. This is true undoubtedly in some few cases, but in still others, Hurst (1904), Darbishire (1913) and myself have been unable to find any distinction in shading by comparing the segregates with the grandparental seeds of both colors. In those cases where there has been found a difference, the observers probably failed to take into account all the environmental factors.

### NEW DATA

In my own investigations<sup>5</sup> on the heredity of cotyledon color, the  $F_1$  and  $F_2$  generations from over 79 crosses involving combinations of 40 varieties and species of *Pisum* have given results similar to those secured by other workers except in the case of crosses involving a variety of German pea, "Goldkönig," obtained from Haage & Schmidt. The data for most of these crosses are given in Tables IIIa, IIIb, IIIc.

TABLE III b

CROSSES OF DOMINANT YELLOW AND RECESSIVE YELLOW ( $F_2$  GENERATION)<sup>7</sup>

Crosses	Cotyledon Color		
	Yellow	Green	Yellowish Green
(P22-3-1 × P30-A-5)-1.....	26	7	
(P22-3-1 × P30-A-5)-2.....	18	6	
(P22-3-1 × P30-A-5)-3.....	11	3	
(P22-6-1 × P30-A-3)-1.....	17	5	
(P30-1 × P1-1)-1.....	73	16	2
(P30-2 × P1-1)-1.....	51	5	6
(P30-2 × P1-1)-2.....	62	8	3
(P30-3 × P32-1)-1.....	52	10	3
(P40-2 × P30-4)-1.....	98	15	7
(P41-1 × P30-6)-1.....	49	12	1
Total—actually obtained.....	457	87	22
		109	
Total—theoretically expected.....	459.2 yellow : 106.2 green		
Ratio.....	13 yellow : 3 green		

<sup>5</sup> All varieties of peas have been inbred for at least two generations and all the ordinary precautions against differentiating environmental factors, insect pollination, etc., in use by geneticists have been employed.

<sup>7</sup> The investigations of Mendel, Bateson, Lock, Tschermak and others

TABLE III c

CROSS OF GREEN  $\times$  RECESSIVE YELLOW ( $F_2$  GENERATION)<sup>8</sup>

Cross	Yellow or Yellowish	Green
(P21-15-1 $\times$ P30-A-2)-1 .....	2 + 1?	12
(P21-15-1 $\times$ P30-A-2)-2 .....	4 + 1?	22
(P30-5-4 $\times$ P38-20-1)-1P .....	15 + 1?	30
(P30-5-4 $\times$ P38-20-1)-2P .....	15	13 + 4?
(P30-5-4 $\times$ P38-20-1)-1 .....	2 + 2?	16
(P30-5-1 $\times$ P38-20-1)-1 .....	7 + 1?	26
(P35-1 $\times$ P30-3)-1 .....	9	22
(P35-1 $\times$ P30-3)-2 .....	0	20
(P35-9-1 $\times$ P30-5-4)-1 .....	1	6
(P35-9-1 $\times$ P30-5-4)-2 .....	4	29
(P35-9-1 $\times$ P30-5-4)-3 .....	1 + 1?	8
(P35-10-2 $\times$ P30-5-6)-1 .....	1	12
(P35-10-2 $\times$ P30-5-6)-2 .....	1 + 1?	26
(P35-10-2 $\times$ P30-5-6)-3 .....	0	10
Total actually obtained, 326....	70	256
Total theoretically expected ....	81.5	244.5
Ratio .....	1 yellow : 3 green	

The variety "Goldkönig" breeds true to yellow cotyledons and wrinkledness. When crossed with varieties breeding true to green cotyledons, the  $F_1$  generation was invariably green. In most of the crosses, the seed parent was the green variety, but reciprocals have been obtained in two cases.

The crosses were:

Goldkönig  $\times$  Acacia and reciprocal

Goldkönig  $\times$  Market Split Pea and reciprocal

have always shown cotyledon color in peas to be inherited independently of roundness and wrinkledness of cotyledons. The data given in Tables III b and III c give reason to believe there is linkage or partial coupling involved. Round yellow  $\times$  wrinkled yellow (Goldkönig) gives practically only three classes in  $F_2$ —round yellow, wrinkled yellow, and round green. All four classes appeared in only one cross, where a single wrinkled green was obtained. Round green  $\times$  wrinkled yellow (Goldkönig) gave all the expected classes except round yellow, which was absent from the  $F_2$  progeny of all the eight crosses examined. Wrinkled yellow (Goldkönig)  $\times$  wrinkled green and reciprocal gave wrinkled yellows and wrinkled greens approximating the expected ratio.

<sup>8</sup> The cotyledon colors of the peas concerned in Tables III b and III c were for the most part independently determined by two separate people, and these determinations when compared, differed but slightly, and only in very few cases. For help in these determinations, I am indebted to Mr. Montague Free of the Brooklyn Botanic Garden staff.

Nott's Excelsior  $\times$  Goldkönig  
Aldermann  $\times$  Goldkönig  
Scotch Beauty  $\times$  Goldkönig  
Sutton's Main Crop  $\times$  Goldkönig

An  $F_2$  generation has been grown from the first three of these crosses with the results (see Table IIIc) approximating a ratio of 3 G:1 Y or the reverse of the common result. Practically all of the green seeds are distinct greens, but among those classed as yellows are several doubtful cases, and these are marked questionable. An  $F_3$  generation is being grown which will decide whether I have erred in considering these doubtful cases as yellow cotyledon peas in which the greenish color results possibly from lack of enough sunlight during the ripening period.

When the "Goldkönig" yellow was crossed with other varieties having yellow cotyledons, the  $F_1$  progeny all had yellow cotyledons, but in the  $F_2$  generation, a certain proportion of peas with distinctly green cotyledons appeared, the  $F_2$  ratio in the progeny of the ten different  $F_1$  plants, showing considerable variation, but averaging 13 yellow seeds to 3 green seeds, provided all yellows having any considerable amount of green pigment are classified as greens. The number of  $F_2$  generation progeny obtained was small, totaling only 566, of which 457 had yellow cotyledons, 87 distinctly green cotyledons and 22 seeds had yellowish green cotyledons. All were grown under conditions insuring their maturity, but under these conditions (greenhouse cultures) the amount of moisture present is such as possibly to cause some of the true greens to bleach. Further justification for classifying the 22 doubtful greens as true greens comes from the fact that all the varieties having yellow cotyledons used in these crosses with the exception of Goldkönig are varieties with distinctly bright yellow cotyledons, which grown under the same conditions and often side by side with the crosses, *never* show any green coloring matter in the coty-

ledons of their mature seeds. The crosses of dominant yellow with Goldkönig were:

“*Pisum Jomardi*”  $\times$  Goldkönig  
 Goldkönig  $\times$  “Mummy Pea”  
 Goldkönig  $\times$  Wachs Schwert  
 “*Pisum elatius*”  $\times$  Goldkönig  
 First of All  $\times$  Goldkönig  
 Gold von Blöcksberg  $\times$  Goldkönig  
 Späte Gold  $\times$  Goldkönig  
 Benton  $\times$  Goldkönig

All the yellows other than Goldkönig yellow gave the ordinary Mendelian ratios when crossed with varieties having green cotyledons. No greens were obtained from crosses between varieties having yellow cotyledons, other than those with Goldkönig.

#### THEORETICAL INTERPRETATION

Interpreted in Mendelian terms the above data are brought into accord with other data on the inheritance of cotyledon color in *Pisum* by regarding all varieties of peas, both with yellow and with green cotyledons, as possessing a factor for yellow pigment (Y), while the dominant yellow varieties possess a factor for green pigment (G) and a factor (I) which causes the green pigment to fade on the maturity of the seed. The German variety “Goldkönig” may be regarded as lacking both the factor for causing green pigment and the factor for causing that pigment to fade on the maturity of the seed, while the green varieties lack only the factor (I). Green pigment masks yellow pigment, hence may be regarded as epistatic to yellow pigment.

Regarded thus:

- (1) YYGGII = dominant yellow varieties
- (2) YYggii = recessive yellow varieties
- (3) YYGGii = green varieties

Crossed with each other these give:

(1 × 2) = YYGgIi (F<sub>1</sub>) yellow, (F<sub>2</sub>) 13 Y : 3 G

(1 × 3) = YYGGIi (F<sub>1</sub>) yellow, (F<sub>2</sub>) 3 Y : 1 G

(2 × 3) = YYGgii (F<sub>1</sub>) green, (F<sub>2</sub>) 1 Y : 3 G

The hereditary substances responsible for yellow pigment, of course, have not been isolated and may take the form of more than one factor, but I have represented these as Y, to make my interpretation clearer. The essential point in the interpretation is that all the hereditary differences in cotyledon color in *Pisum* so far discovered may be pictured as due to the presence or absence of two genetic factors.

TABLE IV

FACTORIAL COMPOSITION OF F<sub>2</sub> PLANTS OF THE THREE CROSSES AND THE APPEARANCE OF THE F<sub>3</sub> PROGENY

*Dominant Yellow × Recessive Yellow and Reciprocals*

F <sub>2</sub> Ratio	13 Y : 3 G	Character of F <sub>3</sub> Progeny
9 yellow	1 YYGGII	Breeds true to yellow cotyledons
	2 YYGGIi	3 Y : 1 G
	2 YYGgII	Breeds true to yellow but heterozygous for G
	4 YYGgIi	13 Y : 3 G
3 green	1 YYGgii	Breeds true to green cotyledons
	2 YYGgii	1 Y : 3 G
3 yellow	1 YYggII	Breeds true to yellow cotyledons
	2 YYggIi	Breeds true to yellow but heterozygous for I
1 yellow	1 YYggii	Breeds true to yellow cotyledons

*Dominant Yellow × Green and Reciprocals*

F <sub>2</sub> Ratio	3 Y : 1 G	Character of F <sub>3</sub> Progeny
3 yellow	1 YYGGII	Breeds true to yellow cotyledons
	2 YYGGIi	3 Y : 1 G
1 green	1 YYGGii	Breeds true to green cotyledons

*Recessive Yellow × Green and Reciprocals*

F <sub>2</sub> Ratio	1 Y : 3 G	Character of F <sub>3</sub> Progeny
1 yellow	1 YYggii	Breeds true to yellow cotyledons
3 green	1 YYGGii	Breeds true to green cotyledons
	2 YYGgii	1 Y : 3 G

Regarded thus, the F<sub>2</sub> plants of all crosses so far made in *Pisum*, involving cotyledon color, can be represented by the gametic formulæ given in Table IV. The char-

acter of the  $F_3$  progeny, *providing this interpretation of the facts regarding cotyledon color in *Pisum* holds*, is also indicated in this table.

Additional data on the inheritance of cotyledon color in *Pisum* will be given in a succeeding paper.

#### CONCLUSIONS AND SUMMARY

Variation in cotyledon color in *Pisum* belongs to all three of the categories of variation mentioned in the forepart of this paper, although there are no definite data as regards the origin of the green cotyledon and the "recessive" yellow cotyledon varieties.

1. Variations in cotyledon color due to environment are:

(a) Yellow cotyledon varieties producing seeds with green cotyledons, because of immaturity, absence of sufficient sunlight, excess moisture at the period of ripening of the seed, etc.

(b) Green cotyledon varieties, especially those with wrinkled seeds, producing seeds which fade or bleach to yellow or yellowish green owing to excess of moisture and sunlight after the seed has matured.

2. Variations due to innate or hereditary differences probably arising as mutations are:

(a) Different degrees or intensities of yellow and green coloring in the different varieties of *Pisum*. These different intensities are characteristic of particular varieties when all varieties under consideration are grown under approximately the same environment.

3. Hereditary distinctions as regards cotyledon color in *Pisum* may be represented by the presence and absence of two factors, a factor (I) causing green pigment to fade when the variety matures its seed, and a factor (G) causing the production of green pigment. All varieties of *Pisum* so far experimented with, have yellow pigment in their cotyledons and the determiner or determiners responsible for this pigment may be graphically represented by (Y). As the presence of green pigment masks

yellow pigment, green may be regarded as epistatic to yellow.

4. The majority of varieties with yellow cotyledons when crossed with varieties having green cotyledons, have yellow cotyledon  $F_1$  offspring, the  $F_2$  generation breaking up into yellow and green cotyledon plants in the ratio of 3 Y:1 G.

The yellow cotyledon variety "Goldkönig" when crossed with green cotyledon varieties has green cotyledon  $F_1$  offspring, in  $F_2$  giving a ratio of approximately 1 Y:3 G, just the reverse of the ordinary result.

"Goldkönig" crossed with other varieties having yellow cotyledons has yellow cotyledon  $F_1$  offspring, in  $F_2$  giving a ratio of approximately 13 yellow seeds: 3 green seeds.

With these facts in view, "dominant yellows" may be represented by the formula YYGGII, "recessive yellows" (Goldkönig) by the formula YYggii, and green cotyledon forms by the formula YYGGii. These formulæ account for all the facts so far discovered in experiments on the inheritance of cotyledon color in *Pisum*, except the data on linkage or coupling, referred to in page 539, note 7. These results will be discussed when more data are available.

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