

# The Genetics of Flower Colours in *Pharbitis Nil.*

By  
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With Plate XVI.

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## Introduction.

The Japanese morning glory (*Pharbitis Nil*) is a favorable material for the genetic study, for the reason that it includes many distinguishable characters. In regard to the flower colour of this plant a number of genetic papers have been published by some Japanese investigators. Sô (1915) described the genetics of purple, red and white flowers, without numerical data. TAKEZAKI (1916) first detected two complementary genes for the production of the flower colour, by crossing two whites. MIYAZAWA (1918, 1921), crossing his so-called dark red (dusky) with white, obtained results showing the recessive nature of white to coloured, dark red to normal (blue) and red to purple. Afterwards, IMAI (1919) studied the recessive nature of dusky to normal; and in other papers (1921 a,b), he reported in more detail on the complementary genes studied by TAKEZAKI. MIYAKE and IMAI (1920) described the relation between light and dark colours. The writer (HAGIWARA 1923) showed the relation of blue, purple (including

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magenta), red and dark red (dusky), giving three genes: purple, magenta and dusky. Afterwards the writer extended the study, partly proving his previous results, and identified the corresponding variation in the broken (dusky) colour series (1928a). He (1928b) found another new broken colour (duskish), which is due to a gene, not allelomorphic to dusky mentioned above. Furthermore, he (1928a, 1929a,b, 1930) detected a gene, the dominant allelomorph of which is complementary in the production of the coloured flower with the two, previously detected genes. Recently, IMAI (1930) published a paper, in which he gave the confirmation of the facts reported hitherto on the interrelations of the normal four colours, dusky, duskish and whites.

In this paper, the writer will describe the interrelation of the various flower colours in detail.

### Flower Colour Series.

The flower colour series includes blue, purple, magenta, red, slate, gray, plum, drab, terra-cotta, vinaceous, and also light yellow and white. Depending on the fact that we find only the description of light blue in old Chinese and Japanese books, we may regard the light blue flower as the original form of this plant.

The general flower colours exhibited by anthocyanin pigments may be gathered under the two groups, pure and broken colours, the former containing blue, purple, magenta and red, and the latter including slate, gray, plum, drab, terra-cotta and vinaceous. In the following lines, the respective colours are indicated by the directions according to Ridgway's colour standards.

Group	Colour	Ridgway's	Colour No.
Pure Colours	Blue	nearly	45
	Purple	"	55-59
	Magenta	"	61-63
	Red	"	65-69
Broken Colours I	Slate	"	49'''-57'''
	Plum	"	61'''-65'''
	Terra-cotta	{ I	1'''-9'''
		{ II	7'''
Broken Colours II	Gray	"	57''''
	Drab	"	1'''
	Vinaceous	{ I	1'''
		{ II	1'''

The other group contains white and light yellow, in which no anthocyanin pigment is developed. Such flowers can be classified into several forms by the colours of the flower tube, stem and seed; namely, white with coloured tube (Fig. 9), white with coloured stem (Fig. 11), white with white tube (Fig. 10), white bearing white seed, and creamish (Fig. 12). In the present paper the writer, however, will reserve the description of the data on this group which will be reported in the future.

In Tokyo the seeds of this plant are generally sown in early May and its flowers bloom from July to October. Corollas are very thin in texture and their colour changes by sunshine. Such colours as blue and purple are liable to change into reddish. Therefore, the observation on flower colours must be made very early in the morning.

### Experiments.

The experiments, the results of which will be described here, concern the twelve flower colour phenotypes of the pure colours and the broken colours, disregarding the other points, such as the intensity, pattern etc.

#### I. PURE COLOURS.

The genetic interrelations among four colour groups—blue, purple, magenta and red—were brought to light by the data involving twenty-five crosses, the results of which are presented in the following six sections.

**PURPLE VERSUS BLUE.** Six different crosses were made between purple and blue flowers, giving  $F_1$  plants which bore blue flowers. In  $F_2$ , purple flowers reappeared in one-fourth of the total, as shown in Table I.

TABLE I.

$F_2$  plants from the cross of purple and blue.

Cross	Blue	Purple	Total
41×54	63	22	85
56×57	40	13	53
135×118	39	11	50
92.3×100.2	71	27	98
431.1×419.51	49	15	64
419.51×A	40	11	51
Total	302	99	401
Expected	300.75	100.25	401

Blue behaves as a dominant character to purple, and a recessive gene  $p$ . (previously  $b$ ) is responsible for purple.

MAGENTA VERSUS BLUE. Crossing a blue flowered plant (No. 85.1) with a magenta flowered plant (No. 70.2)  $F_1$  plants bearing blue flowers were obtained. In  $F_2$ , 15 blue and 4 magenta were recorded, showing that blue is a simple dominant character to magenta, though the numbers observed were very few. An  $F_3$  obtained by selfing blue  $F_2$  plants confirms this point, as shown by the data in Table II.

TABLE II.

$F_3$  of cross 85.1×70.2.

$F_2$ flower	No. families	Blue	Magenta	Total
Blue	5	83	—	83
	9	166	68	234

Therefore, magenta differs by one gene from the normal. Let us designate the gene by  $m$ , (previously  $p$ .)

RED VERSUS PURPLE. From the experiments above shown, we learned the fact that purple and magenta are simple recessives to blue. In the present section let us describe the results in their relation to the inheritance of red.

The  $F_1$  plants obtained by the cross between red and purple flowers bore purple corolla; and in  $F_2$ , a simple segregation occurred, giving purple and red flowers in the ratio 3:1, as shown in Table III.

TABLE III.

$F_2$  plants from the cross of red and purple.

Cross	Purple	Red	Total
72×41	52	13	65
56×72	100	41	141
468.18×499.47	33	9	47
A×R.1	35	11	46
56×V-Y	46	16	62
Total	271	90	361
Expected	270.75	90.25	361

The further generation of cross 468.18 × 499.47 was observed, giving expected results as shown in Table IV.

TABLE IV.

F<sub>3</sub> of cross 468.18 × 499.47.

F <sub>2</sub> flower	No. families	Purple	Red	Total
Purple	11	99	—	99
	27	369	125	494
Red	7	—	70	70

Hence, red is a simple recessive to purple in inheritance. From the fact that the F<sub>1</sub> bore purple flowers but not reversional blue flowers, we may conclude that the red flower cannot contain the dominant allelomorph for purple.

RED VERSUS MAGENTA. The writer made three crosses between red and magenta, and obtained purple flowers as F<sub>1</sub>. In F<sub>2</sub>, magenta hybrids gave magenta and red segregates in a monohybrid ratio, indicating that red is recessive to magenta. The numerical data are shown in Table V.

TABLE V.

F<sub>2</sub> plants from the cross of red and magenta.

Cross	Magenta	Red	Total
60 × 72	27	10	37
103.3 × 60	30	8	38
129.3 × 133	28	9	37
Total	85	27	112
Expected	84.0	28.0	112

Therefore, the red flower cannot include either *P*, nor *M*<sub>2</sub> in its gene complex.

RED VERSUS BLUE. The cross between blue and red is expected to give a key to understanding interrelation among four groups of the pure flower colours. The  $F_1$  plants bore blue flowers; and in  $F_2$ , the segregation occurred into blue, purple, magenta and red, as shown by the data in Table VI.

TABLE VI.

$F_2$  plants from the cross of red and blue.

Cross	Blue	Purple	Magenta	Red	Total
72 × 53	61	23	25	13	122
85.1 × 103.6	25	6	6	5	42
130.2 × 100.3	25	5	4	3	37
100.3 × 103.7	22	7	5	6	40
127 × 110	20	5	6	1	32
233.36 × 457.15	27	8	8	5	48
159 × V	49	10	13	10	82
233.36 × 428.15	33	9	10	5	57
Total	262	73	77	48	460
Expected	258.75	86.25	86.25	28.75	460

$$\chi^2 = 15.87$$

$$P = 0.001$$

The segregation occurred with a remarkable deviation, but it does not deny the assortment of two genes, purple and magenta. Red is double recessive, that is  $p_r m_r$ . The further generation of 53  $F_2$  plants, obtained by the cross 233.36 × 428.15, was observed, giving the results as shown in Table VII.

TABLE VII.

$F_3$  of cross 233.36 × 428.15.

$F_2$ flower	No. families	Blue	Purple	Magenta	Red	Total
Blue	3	34	—	—	—	34
	10	69	—	28	—	97

F <sub>2</sub> flower	No. families	Blue	Purple	Magenta	Red	Total
Blue	10	112	35	—	—	147
	9	82	29	29	16	156
Purple	3	—	53	—	—	53
	4	—	76	—	23	99
Magenta	5	—	—	50	—	50
	5	—	—	45	13	58
Red	5	—	—	—	112	112

The F<sub>3</sub> data cover the theory proposed above, namely, red is double recessive to blue.

MAGENTA VERSUS PURPLE. Magenta and purple being recessive to blue, what result will be obtained by crossing the two recessives? The cross gave reversional blue flowers as F<sub>1</sub>; and in F<sub>2</sub>, segregation occurred as indicated by the data in Table VIII.

TABLE VIII.

F<sub>2</sub> plants from the cross of magenta and purple.

Cross	Blue	Purple	Magenta	Red	Total
56 × 60	189	53	60	25	327
468.18 × 499.49	19	5	6	1	31
499.25 × 499.9	34	10	10	2	56
499.25 × 499.17	28	8	10	3	49
409.16 × 415.32	60	27	28	4	119
415.43 × 454.2	40	16	17	5	78
Total	370	119	131	40	660
Expected	371.25	123.75	123.75	41.25	660

$$\chi^2 = 0.64$$

$$P = 1$$

The segregation occurred in accordance with a dihybrid ratio. Since the genotype of  $F_1$  is  $P,p,M_gm_g$ , the  $F_2$  segregation should be 9 blue, 3 purple, 3 magenta and 1 red in every 16. The  $F_3$  generation of 61  $F_2$  plants from the cross  $415.43 \times 454.2$  was raised, and the data obtained are shown in Table IX.

TABLE IX.

$F_3$  of cross  $415.43 \times 454.2$ .

$F_2$ flower	No. families	Blue	Purple	Magenta	Red	Total
Blue	4	63	—	—	—	63
	8	64	—	24	—	88
	10	137	33	—	—	170
	17	289	78	86	28	481
Purple	3	—	32	—	—	32
	3	—	35	—	10	45
Magenta	6	—	—	65	—	65
	6	—	—	109	33	142
Red	4	—	—	—	79	79

The results perfectly cover the expectation developed on the basis of dihybrid.

From the experimental data shown in the foregoing pages the genotypes of the four pure flower colours are considered as follows:

Blue .....  $P,M_g$   
 Purple .....  $p,M_g$   
 Magenta .....  $P,m_g$   
 Red .....  $p,m_g$

So far as the writer's experiments went, no exceptional cases beyond the assumption were found.



## II. BROKEN COLOURS.

The broken colours have a dull hue, contrasting to pure colours, which have a bright hue. As mentioned before, the broken colours are classified into two groups—broken I and broken II. In both broken colour series, there occur variations corresponding to the pure colour series.

In connection with the broken colours, 39 crosses were made, the results being described in the following two parts.

## BROKEN COLOUR I.

The dull colours, corresponding to magenta and red, are difficult to detect in some cases. Therefore, the writer gathered them into a terra-cotta group, though they were classified into terra-cotta I and terra-cotta II in other cases.

SLATE VERSUS BLUE. Four crosses were made between slate and blue. All  $F_1$  plants bore blue flowers; and in  $F_2$ , blue and slate were segregated after a monohybrid fashion, the data obtained being shown in Table X.

TABLE X.

$F_2$  plants from the cross of slate and blue.

Cross	Blue	Slate	Total
44 × 37.4	43	10	53
124.2 × 100.23	30	8	38
141 × X	49	13	62
233.36 × 455.22	36	13	49
Total	158	44	202
Expected	151.5	50.5	202

Slate is, therefore, a simple recessive to blue, and the character is due to a gene dusky or  $d_y$  (formerly  $k^1$ ). Consequently slate is considered to carry a genetic complex  $P, M, d_y$ .

SLATE VERSUS PURPLE. The  $F_2$  plants obtained by two crosses between

slate and purple bore blue flowers, differing from both parents. In  $F_2$  segregation took place dihybridly, as shown in Table XI.

TABLE XI.

$F_2$  plants from the cross of slate and purple.

Cross	Blue	Purple	Slate	Plum	Total
58×41	53	21	11	3	88
51A×56	43	19	16	4	82
615.58×499.26	16	9	9	1	35
Total	112	49	36	8	205
Expected	115.31	38.44	38.44	12.81	205

$$\chi^2 = 4.96$$

$$P = 0.18$$

From the double heterozygous constitution of the  $F_1$  blue flowers we should expect 9 blue, 3 purple, 3 slate, and 1 plum in every 16  $F_2$ . The expectations in the above table were calculated from such a ratio; therefore, plum is double recessive, that is  $p.M_d y$ .

PLUM VERSUS SLATE. The  $F_1$  hybrids obtained by crossing plum with slate bore slate flowers, and they segregated into slate and plum in a ratio 3:1, as shown by the data in Table XII.

TABLE XII.

$F_2$  plants from the cross of plum and slate.

Cross	Slate	Plum	Total
141×41/C.1	87	35	122
Expected	91.5	30.5	122

The result indicated in the table confirms the fact that the genotype of plum is purple dusky or  $p.M_d y$ . The  $F_3$  generation was raised, and the data are gathered in Table XIII.

TABLE XIII.

F<sub>3</sub> of cross 141 × 41/C.1.

F <sub>2</sub> flower	No. families	Slate	Plum	Total
Slate	8	97	—	97
	28	298	86	384
Plum	12	—	162	162

The results confirm the simple recessive nature of plum to slate.

PLUM VERSUS PURPLE. An F<sub>1</sub> obtained by crossing plum (No. 419.17) with purple (No. 407.24) bore purple flowers; and in F<sub>2</sub>, 33 purple and 12 plum were segregated, giving a 3 : 1 ratio as expected.

PLUM VERSUS BLUE. Crossing blue (No. 233.36) with plum (No. 41/C.1), blue flowers were produced as F<sub>1</sub>. In F<sub>2</sub>, 11 blue, 5 purple, 3 slate and 2 plum were segregated, according to an expected dihybrid ratio. Though the data are small, they may confirm, together with the results given in previous sections, the double recessive nature of plum.

SLATE VERSUS MAGENTA. A cross was made between slate and magenta, and reversional blue-flowered F<sub>1</sub> plants were obtained. In F<sub>2</sub>, segregation occurred as shown in Table XIV.

TABLE XIV.

F<sub>2</sub> plants from the cross of slate and magenta.

Cross	Blue	Magenta	Slate	Terra-cotta	Total
37.4 × 70.2	27	7	9	1	44
530.10 × 516.41	75	24	17	6	122
Total	102	31	26	7	166
Expected	93.4	31.1	31.1	10.4	166

$$\chi^2 = 2.74$$

$$P = 0.57$$

The parental constitutions in this cross are considered to be  $P_rM_yd_y$  for slate and  $P_r m_y D_y$  for magenta. Therefore, dihybrid segregation may be expected in  $F_2$ , the assortment being concerned with the two genes,  $m_y$  and  $d_y$ . The segregated terra-cotta flowers correspond to the double recessives. The theory will be proved by the  $F_3$  data, which are presented in Table XV.

TABLE XV.

$F_3$  of cross 37.4 × 70.2.

$F_2$ flower	No. families	Blue	Magenta	Slate	Terra-cotta	Total
Blue	2	31	—	—	—	31
	5	67	—	25	—	92
	7	72	33	—	—	105
	13	141	38	42	15	236
Magenta	3	—	23	—	—	23
	3	—	37	—	15	52
Slate	3	—	—	36	—	36
	3	—	—	58	20	78
Terra-cotta	1	—	—	—	22	22

Inspecting the data shown in the above table, the double recessive nature ( $P_r m_y d_y$ ) of terra-cotta is clear.

TERRA-COTTA I VERSUS BLUE. The  $F_1$  hybrids obtained by crossing terra-cotta with blue bore blue flowers, and they segregated into four forms in  $F_2$  as shown by the data in Table XVI.

TABLE XVI.

$F_2$  plants from the cross of terra-cotta I and blue.

Cross	Blue	Magenta	Slate	Terra-cotta I	Total
233.1 × 416.37	39	20	21	6	86
Expected	48.4	16.1	16.1	5.4	86

$$\chi^2 = 4.33$$

$$P = 0.23$$

The result is practically the same with that shown in Table XIV.

TERRA-COTTA II VERSUS PLUM. Two crosses were made between plum and terra-cotta II. The  $F_1$  plants thus obtained bore plum flowers. In  $F_2$ , segregation occurred into the two parental forms, the data being presented in Table XVII.

TABLE XVII.

$F_2$  plants from the cross of terra-cotta II and plum.

Cross	Plum	Terra-cotta II	Total
419.243 × 419.12	20	8	28
424.9 × 41/C.1	41	11	52
Total	61	19	80
Expected	60.0	20.0	80

In these crosses, the difference between plum and terra-cotta lies in one gene, therefore a monohybrid segregation is expected.

TERRA-COTTA II VERSUS RED. From the experimental data above shown, the genotype of terra-cotta I is regarded as  $P_r m_y d_y$ . In addition to this, another terra-cotta form occurs as a triple recessive, that is  $p_r m_y d_y$ . The evidence supporting this fact will be found in this and the following sections. Crossing red with terra-cotta II,  $F_1$  bearing red flowers were obtained; and in  $F_2$ , simple segregation took place, as shown in Table XVIII.

TABLE XVIII.

$F_2$  plants from the cross of terra-cotta II and red.

Cross	Red	Terra-cotta II	Total
421.17 × 423.9	35	9	44
457.12 × 423.9	72	26	98
468.2 × 603.11	20	7	27
Total	127	42	169
Expected	126.75	42.25	169

In these crosses, the terra-cotta parent must be a triple recessive.

TERRA-COTTA II VERSUS SLATE. All  $F_1$  plants from two crosses between terra-cotta II and slate bore slate flowers, and they segregated into two parental forms and plum flowers. The numerical data of these three forms in segregation are shown in Table XIX.

TABLE XIX.

$F_2$  plants from the cross of terra-cotta II and slate.

Cross	Slate	Plum	Terra-cotta	Total
423.1 × 455.4	50	11	19	80
141 × 423.9	30	7	19	56
Total	80	18	38	136
Expected	76.5	25.5	34.0	136

$$\chi^2 = 2.83$$

$$P = 0.25$$

The slate, plum and terra-cotta segregates occurred in practical accordance with a ratio of 9 : 3 : 4. Therefore, terra-cotta flowers thus produced contain both  $P_r m_y d_y$ - and  $p_r m_y d_y$ -carrying forms. The  $F_3$  from cross 423.1 × 455.4 was examined, giving the results shown in Table XX.

TABLE XX.

$F_3$  of cross 423.1 × 455.4.

$F_2$ flower	No. Families	Slate	Plum	Terra-cotta	Total
Slate	5	65	—	—	65
	6	76	29	—	105
	5	54	—	17	71
	19	247	86	108	441
Plum	2	—	12	—	12
	4	—	29	9	38
Terra-cotta	16	—	—	368	368

By raising  $F_3$  plants, the writer called attention to the fact that there is some difference in hue between terra-cotta segregated from plum and that segregated from slate, as shown in Plate XVI. So that, terra-cotta may be classified, possibly, into terra-cotta I bearing the gene-complex  $P, m_y d_y$ , and terra-cotta II bearing the gene-complex  $p, m_y d_y$ .

PLUM VERSUS RED. A red-flowered strain (No. 457.12) was crossed with a plum-flowered strain (241.35), and purple  $F_1$  plants were obtained, the character of the hybrids being different from both parents. In  $F_2$  only 21 plants were raised. The segregation, however, occurred in approximate accordance with the ratio 9:3:3:1 of dihybrid, which involves  $m_y$  and  $d_y$ . Actually  $F_2$  consisted of 13 purple, 4 red, 3 plum and 1 terra-cotta II.

TERRA-COTTA II VERSUS PURPLE. From two crosses between terra-cotta II and purple, the writer got  $F_1$  bearing purple flowers. In  $F_2$ , purple, red, plum and terra-cotta II were segregated as shown in Table XXI.

TABLE XXI.

$F_2$  plants from the cross of terra-cotta II and purple.

Cross	Purple	Red	Plum	Terra-cotta II	Total
499.25 × bpr	98	34	30	8	170
423.9 × 499.25	22	5	2	3	32
Total	120	39	32	11	202
Expected	113.6	37.9	37.9	12.6	202

$$\chi^2 = 1.51$$

$$P = 0.68$$

The results are according to our expectation.

TERRA-COTTA II VERSUS MAGENTA. As terra-cotta II carried  $p, m_y d_y$ , the  $F_1$  hybrids obtained by crossing it with magenta bore magenta flowers. In the subsequent generation, segregation took place as to the three phenotypes, magenta, red and terra-cotta, the data of which are given in Table XXII.

TABLE XXII.

$F_2$  plants from the cross of terra-cotta and magenta.

Cross	Magenta	Red	Terra-cotta	Total
437 × 407.36	21	8	18	47
499.26 × D.R5	30	10	20	60
Total	51	18	38	107
Expected	60.2	20.0	26.8	107

$$\chi^2 = 6.29$$

$$P = 0.04$$

The  $F_1$  plants being  $P_p M_g m_y D_y d_y$ , we may expect an  $F_2$  segregating magenta, red and terra-cotta in the ratio 9:3:4. This expectation is approximately satisfied by the  $F_2$  data.

#### BROKEN COLOUR II.

Broken colour II, including gray, drab, vinaceous I and vinaceous II, is due to another broken colour gene, duskish. Sometimes, difficulty in the distinction between vinaceous I and vinaceous II occurs in this group, as observed in the corresponding case of broken colour I. In such a case, vinaceous I and vinaceous II are gathered under a vinaceous group.

GRAY VERSUS BLUE. Two crosses between a gray strain bearing yellow leaf and a blue strain bearing green leaf, gave hybrids with green leaves and blue flowers. These hybrids resulted in normal dihybrid segregation as regards the above characters. The numerical data are shown in Table XXIII.

TABLE XXIII.

$F_2$  plants from the cross of gray flower with yellow leaf and blue flower with green leaf.

Cross	Green leaf		Yellow leaf		Total
	Blue	Gray	Blue	Gray	
123 × 118	24	8	8	3	43
489.10 × 487.18	30	8	10	4	52
Total	54	16	18	7	95
Expected	53.44	17.81	17.81	5.94	95

$$\chi^2 = 0.38$$

$$P \approx 1$$

The segregating number in regard to the flower colour is 72 blue and 23 gray, corresponding to the ratio 3:1. It is sure that the dull colour is not due to a gene  $d_y$  which is linked closely with yellow leaf gene, but is due to another one  $d_k$  (previously  $k^2$ ). Hence, gray refers to the gene-complex  $P M_g d_k$ .

VINACEOUS II VERSUS PURPLE. Hybrids bearing purple flowers were



given as  $F_1$  by crossing vinaceous II with purple in both reciprocal ways. The  $F_2$  segregation from these hybrids is shown in Table XXIV.

TABLE XXIV.

$F_2$  plants from the cross of vinaceous II and purple.

Cross	Purple	Red	Drab	Vinaceous II	Total
667.7 × 499.25	108	34	31	13	186
499.25 × 611.11	47	18	20	11	96
Total	155	52	51	24	282
Expected	158.6	52.9	52.9	17.6	282

$$\chi^2=2.50$$

$$P=0.48$$

These figures show the segregation of a dihybrid ratio. Vinaceous II is a duskish flower carrying two recessive genes,  $m_g$  and  $d_k$ . Drab is another duskish  $F_2$  class, which corresponds to purple duskish or  $p_r M_g d_k$ .

VINACEOUS II VERSUS MAGENTA. Crossing a vinaceous strain (No. 681.15) with a magenta strain (No. 499.26), the writer got  $F_1$  bearing magenta flowers; and in  $F_2$ , magenta, red and vinaceous were segregated in a ratio 9:3:4, as shown in Table XXV, with the numerical data of 14  $F_3$  families segregated in the same manner.

TABLE XXV.

Segregating data for  $p_r$  and  $d_k$ .

Source	Magenta	Red	Vinaceous	Total
499.26 × 681.15	45	16	23	84
Its 14 $F_3$ families	333	90	130	553
Total	378	106	153	637
Expected	358.31	119.44	159.25	637

$$\chi^2=2.84$$

$$P=0.25$$

In  $F_3$  raising, vinaceous was segregated in one-fourth of the total from magenta and red  $F_2$ , respectively. Vinaceous flowers from both magenta and red  $F_2$  so closely resemble each other that we cannot distinguish them in this cross. Vinaceous II has a gene-complex  $p_r m_y d_k$ , corresponding to red duskish, while vinaceous I has a gene-complex  $P_r m_y d_k$ , corresponding to magenta duskish.

VINACEOUS II VERSUS BLUE. The  $F_1$  plants obtained by crossing a vinaceous II strain (No. 666.7) with a blue strain (No. 667.6) bore blue flowers, and they gave rise to an  $F_2$  consisting of 27 blue, 9 purple, 8 magenta, 2 red, 7 gray, 3 drab and 3 vinaceous. These data are in approximate accordance with the expectation from the ratio 27:9:9:3:9:3:4, in which the three genes,  $p_r$ ,  $m_y$  and  $d_k$ , are working. Though the data are small in number, it is clear that there occur four kinds of dull colours, corresponding to four pure colours, and that vinaceous II is a triple recessive as to the genes,  $p_r m_y d_k$ .

BROKEN COLOUR I VERSUS BROKEN COLOUR II. As described before, dusky ( $d_y$ ) and duskish ( $d_k$ ) are not allelomorphic. Therefore, hybrids from the crossing between both broken colours should bear normally coloured flowers. These facts were reported by the writer (1928b) and IMAI (1930). Experimental data confirming these points are collected in Table XXVI.

TABLE XXVI.

$F_2$  plants from the cross of broken colour I and II.

Cross	Pure colour	Broken colour	Total
424 × 241.21	37	18	55
455.21 × 419.5	19	13	32
N. k × K. 13	37	24	61
666.9 × k. 12	110	92	202
Total	203	147	350
Expected	196.9	153.1	350

A cross made between a purple strain (No. 455.2) and a drab strain (No. 419.189) gave purple flowered hybrids. In  $F_2$ , 49 purple, 14 plum and 18 drab were recorded, showing the segregation of pure and broken

colours in a ratio 9:7. These  $F_2$  data, together with the  $F_3$ , confirm the genotype of the drab strain to be  $p, M_y d_y d_k$ . The  $F_3$  data are summarized in Table XXVII.

TABLE XXVII.

$F_3$  of cross 455.2  $\times$  419.189.

$F_2$ flower	No. families	Purple	Plum	Drab	Total
Purple	6	362	—	—	362
	5	200	61	—	261
	5	228	—	107	335
	11	208	67	97	372
Plum	5	—	182	—	182
	5	—	196	63	259
Drab	7	—	—	446	446

The data shown above may support a supposition that the genotypes,  $P, M_y d_y d_k$ ,  $P, m_y d_y d_k$  and  $p, m_y d_y d_k$ , may result in gray, vinaceous I, vinaceous II, respectively; though experimental results confirming them are not yet obtained.

### Genes for Flower Colours.

Summing up the experimental results above mentioned, four genes are responsible for the production of the flower colour variations, namely:

$d_y$  (formerly  $k^1, dy^1$ )...concerns the production of dull colour; namely, dusky.

$d_k$  ( „  $k^2, dy^2$ )...concerns the production of another dull colour; namely, duskish.

$p_r$  ( „  $b$  )...results in purple, modifying the normal blue.

$m_y$  ( „  $p$  )...modifies blue into magenta.

These four genes are active when the other three genes,  $C_a$  (formerly  $C^a$ ),  $C$  and  $R$ , which are complementary for the development of the flower colour, are also present. The genetic construction of the flower colours are shown below.

Group	Hue	Genetic construction
Pure colours	Blue .....	$P_r M_g D_y D_k$
	Purple .....	$p_r M_g D_y D_k$
	Magenta .....	$P_r m_g D_y D_k$
	Red .....	$p_r m_g D_y D_k$
Broken colours I	Slate .....	$P_r M_g d_y D_k$
	Plum .....	$p_r M_g d_y D_k$
	Terra-cotta	$\begin{cases} \text{I} & \dots\dots\dots P_r m_g d_y D_k \\ \text{II} & \dots\dots\dots p_r m_g d_y D_k \end{cases}$
Broken colours II	Gray .....	$P_r M_g D_y d_k, P_r M_g d_y d_k$
	Drab .....	$p_r M_g D_y d_k, p_r M_g d_y d_k$
	Vinaceous	$\begin{cases} \text{I} & \dots\dots\dots P_r m_g D_y d_k, P_r m_g d_y d_k \\ \text{II} & \dots\dots\dots p_r m_g D_y d_k, p_r m_g d_y d_k \end{cases}$

Looking over the colour series, we see that purple, magenta and slate are simple recessive to blue; red and plum are double recessive to the same; gray is either simple or double recessive; terra-cotta and drab are either double or triple recessive; and vinaceous is either double or triple or quadruple recessive, according to its genotype.

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### Summary.

1) So far studied, the flower colour series in Japanese morning glory (*Pharbitis Nil*) include blue, purple, magenta, red, slate, gray, plum, drab, terra-cotta I, terra-cotta II, vinaceous I, vinaceous II, white and yellow; and they may be classified under the three groups, pure colour, broken colour and white.

2) The pure colour, which is bright in hue, contains blue, purple, magenta and red. The broken colour, which is dull in hue, contains eight colours under two classes, each of which includes four dull hues, corresponding

to four normal pure colours. That is, the one, broken colour I (dusky) contains slate, plum, terra-cotta I and terra-cotta II, and the other, broken colour II (duskish) contains gray, drab, vinaceous I and vinaceous II. In both broken colour groups, however, two dull hues which correspond to magenta and red, are so slightly different that their classification is difficult in some cases, especially in the broken colour II.

3) These flower colours are due to anthocyanin pigments in the cells of the corollas, while the white group has no anthocyanin pigments in the corollas except flower tubes, in which sometimes a full amount of anthocyanin pigments occurs.

4) The results from 64 crossing experiments determined the four genes—purple ( $p$ ) (formerly  $b$ ), magenta ( $m_y$ ) (formerly  $p$ ), dusky ( $d_y$ ) (formerly  $k^1$ ,  $d_y^1$ ) and duskish ( $d_k$ ) (formerly  $k^2$ ;  $d_y^2$ ) which are active only with the co-existence of the other three complementary genes,  $C_a$  (formerly  $C^a$ ),  $C$  and  $R$ , for the development of the flower colour.

5) The genetic construction for twelve colours is shown as follows: In pure colour group, blue ( $P, M_y D_y D_k$ ) purple ( $p, M_y D_y D_k$ ), magenta ( $P, m_y D_y D_k$ ) and red ( $p, m_y D_y D_k$ ); in broken colour I, slate ( $P, M_y d_y D_k$ ), plum ( $p, M_y d_y D_k$ ) terra-cotta I ( $P, m_y d_y D_k$ ) and terra-cotta II ( $p, m_y d_y D_k$ ); and in broken colour II, gray ( $P, M_y D_y d_k$ ,  $P, M_y d_y d_k$ ), drab ( $p, M_y D_y d_k$ ,  $p, M_y d_y d_k$ ), vinaceous I ( $P, m_y d_y d_k$ ,  $P, m_y D_y d_k$ ) and vinaceous II ( $p, m_y D_y d_k$ ,  $p, m_y d_y d_k$ ).

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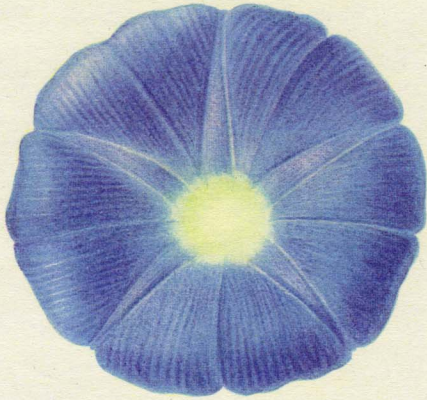
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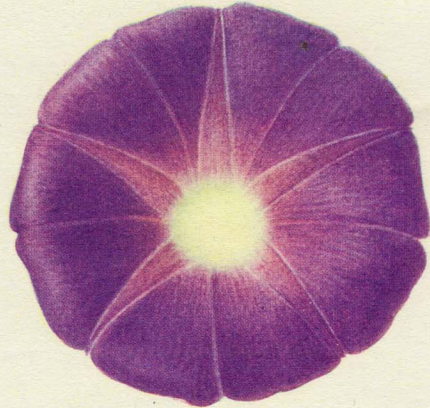
#### EXPLANATION OF PLATE XVI.

All the figures are drawn in about  $\frac{3}{4}$  natural size.

- Fig. 1. Blue flower.
- Fig. 2. Purple flower.
- Fig. 3. Magenta flower.
- Fig. 4. Red flower.
- Fig. 5. Slate flower.
- Fig. 6. Plum flower.
- Fig. 7. Terra-cotta I flower.
- Fig. 8. Terra-cotta II flower.
- Fig. 9. White flower with coloured tube and green stem.
- Fig. 10. White flower with white tube and green stem.
- Fig. 11. White flower with white tube and coloured stem.
- Fig. 12. Creamish flower with white tube and green stem.
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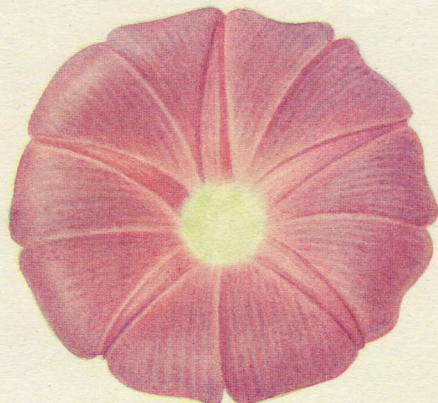
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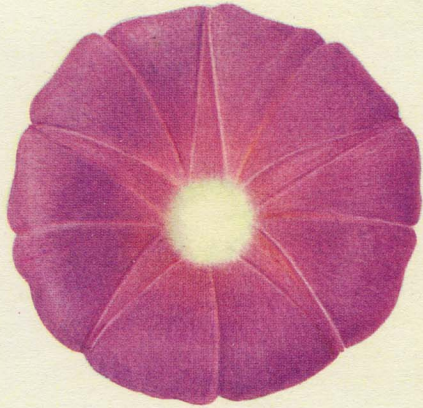


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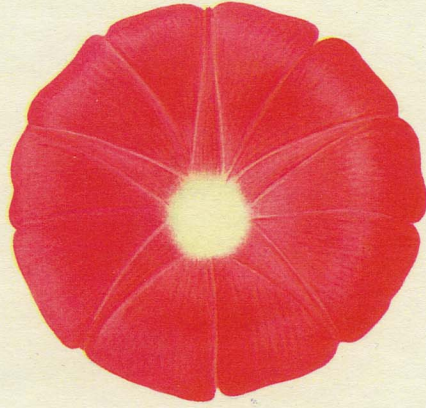


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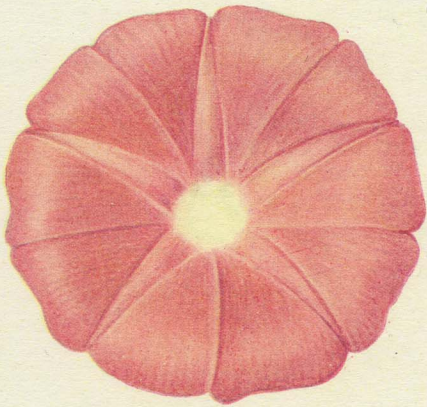




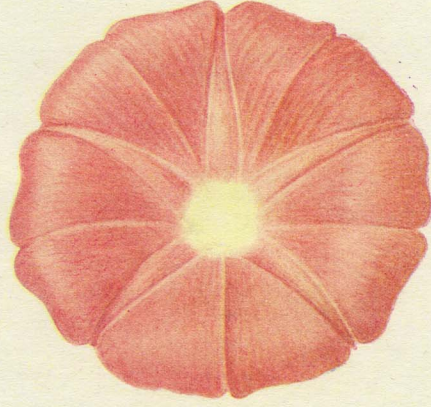
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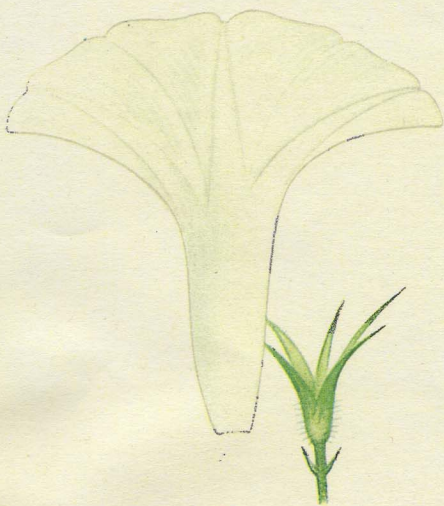
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