The Genetics of Pharbitis purpurea.

By

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With Plate VIII.

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Introduction.

Pharbitis Nil, the Japanese morning glory, which exhibits remarkable variation in its foliage and flowers, has been a favorable genetic subject with us for many years, but only few papers dealing with the genetics of *Pharbitis purpurea,* a species closely related to the Japanese mornig glory, can be found in the literature. Though *Ph. purpurea* shows less variability in its forms compared with the Japanese morning glory the investigation of its genetics is of importance for a comparative study. The plants of this species, however, grow luxuriantly under common field culture, and it is troublesome to keep the vines from entwinning with each other. In my study, much labor was devoted to the raising of *Ph. Nil,* so less time was given to *Ph. purpurea.* Under such circumstances, I failed to take the record on a large scale, especially on the F_4 plants of a cross, with which I was chiefly concerned, though I had cultivated a sufficient number of progenies.

The first paper which deals with the genetics of *Ph. purpurea* was

[Jour. Coll. Agric., Vol. IX, No. 3, 1927.]

published by BARKER[1]. This was followed by my Japanese papers[2]. The former author, however, made an experimental series by observing only a relatively small number of offspring in his crossings, therefore he left various points open for a subsequent final decision. The present paper contains only a few additional data to those, with which I had dealt previously in my Japanese papers, but it seems advisable to publish these data in English, as I have started further investigations on this plant, and it will take two or three years before I can make further reports.

Stem Color.

The qualities of the stem appear in the following three forms :

Condition	Denomination (abbreviation)
1. Colored intensely	Colored stem (c. s.)
2. Faintly colored, but the leaf axil colored deeply	Faintly colored stem (f. c. s.)
3. Entirely colorless	Green stem (g. s.)

The three forms breed true to their respective types when they are selfed[3], and with such pure strains the following results were obtained in making hybridization experiments.

COLORED STEM *versus* FAINTLY COLORED STEM. The F_1 plants obtained by both reciprocal matings have invariably self-colored stems, demonstrating the recessiveness of the faintly colored condition with dark axils. Table I gives the F_2 segregation of such crossings.

TABLE I.

The F_2 data of the cross, colored stem × faintly colored stem, and its reciprocals.

Cross	Stem color of parents	Colored stem	Faintly colored stem	Total
R′. S. × W. D.	c. s. × f. c. s.	105	48	153
W. D. × R′. S.	f. c. s. × c. s.	34	19	53
W. D. × R. S.	f. c. s. × c. s.	59	16	75
Total		198	83	281
Expected		210.75	70.25	281

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[1] Heredity studies in the morning-glory (*Ipomea purpurea* [L.] Roth). Cornell University Agricultural Experiment Station, Bulletin 392 : 1–38. 1917.

[2] IMAI, Y.——Genetic studies in morning glories. III. Bot. Magazine, Tokyo. 34 : 217–247. 1920. (In Japanese.) Genetic studies in morning glories. VI. Ibid. 36 : 45–48. 1922. (In Japanese.)

[3] I made hand-pollination to obtain selfed seeds, as we cannot raise sufficient seeds leaving flowers under bagging on account of the different length of the pistil and stamens in a flower.

The segregation occurred quite in accordance with the simple ratio of monohybrid[1]; namely, 3 colored stems : 1 faintly colored stem. I made the F_3 examination with one of these three matings to verify the results gained in the foregoing generation. On selfing 112 F_2 plants, which comprised 75 colored and 37 faintly colored stems, we recorded F_3 summarized in Table II.

TABLE II.

A summary of the F_3 data of the cross, R'. S. × W. D., showing the segregation of colored and faintly colored stems.

Character of F_2	Number of pedigree	Colored stem	Faintly colored stem	Total
Colored stem	28	882	—	882
	47	1264	432	1696
	Expected	1272	424	1696
Faintly colored stem	37	—	1086	1086

Thus the colored F_2 stems composed of 28 homozygotes and 47 heterozygotes, where we expect 25 and 50, respectively, and the segregation of two forms into 1264 colored and 432 faintly colored stems is remarkably approaching the simple ratio, on which we should expect 1272 and 424 for each. The F_4 data also confirmed the one-factor segregation. Namely: On selfing 3 F_3 plants having colored stems, offspring of No. 30, which bred true to the colored stem in F_3, we obtained 45 F_4 with colored stems. Nos. 9, 34 and 35 were the F_3 pedigrees making segregation of stem forms in question. On examining the F_4 progenies of 15 plants from these pedigrees, I found the result shown in Table III.

TABLE III.

Some F_4 data repeating the F_3 feature as to the inheritance of stem color.

Character of F_3	Number of pedigree	Colored stem	Faintly colored stem	Total
Colored stem	9	148	—	148
	5	88	32	120
	Expected	90	30	120
Faintly colored stem	1	—	10	10

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[1] A marked variation in intensity of the stem color occurred, but I did not make any classification on this point.

I selected 10 plants with faintly colored stems from the F_3 progenies of Nos. 14 and 72, both pedigrees being bred true to the faintly colored condition, and found the constancy of the form in the subsequent generation in observing 199 individuals, which had all faintly colored stems with dark axils. These F_4 data show nothing but the result we expected.

Besides selfing the hybrids, I made back-crossings with their parents. In back-crossing the F_1 plants with the colored stems, I obtained 79 plants quite deeply colored, as expected, whereas, when the same procedure was made with the faintly colored stem instead of the colored one, the segregation of two forms occurred in an equal ratio, as is shown in Table IV.

TABLE IV.

The back-crossing data of F_1, which were obtained by the cross, colored and faintly colored stems, with faintly colored stem.

	Colored stem	Faintly colored stem	Total
Observed	122	120	242
Expected	121	121	242

With the results above-cited we can safely conclude that the quantitative diversity of the colored and faintly colored stems[1] lies in a one-factor difference, i. e., the former is manifested by a dominant factor, *R*, while the latter by its recessive mate, *r*.

COLORED STEM *versus* GREEN STEM. The cross gave F_1 with colored stems, representing the recessiveness of the green condition, and selfing such hybrids I recorded F_2 shown in Table V.

TABLE V.

The F_2 data of the cross, colored stem × green stem, and its reciprocal.

Cross	Stem color of parents	Colored stem	Green stem	Total
R'. S. × St. S.	c. s. × g. s.	108	31	139
R'. S. × W. S.	c. s. × g. s.	83	24	107
W. S. × R. S.	g. s. × c. s.	108	32	140
W. S. × R'. S.	g. s. × c. s.	25	8	33
Total		324	95	419
Expected		314.25	104.75	419

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[1] A few strains of *Pharbitis Nil* have green stems with colored leaf axils and produce colored flowers. The condition is transmitted as a simple recessive to the fully colored stem bearing colored flowers.

The segregation occurred quite simple in accordance with a 3 : 1 ratio, which indicates the one-factor difference between colored and green stems[1] in their genotypes. The back-crossing experiments also proved this condition as is shown by the data in Table VI.

TABLE VI.

The back-crossing data of F_1, which were obtained by the cross, colored and green stems, with their parents.

Back-cross	Colored stem	Green stem	Total
F_1(R. S.×W. S.)×R. S.	30	—	30
F_1(R. S.×W. S.)×W. S.	59	55	114
Expected	57	57	114

The colored stem differs from the green stem by one factor, but the difference lies in a different relation to the factors involved in the case of colored *versus* faintly colored.

FAINTLY COLORED STEM *versus* GREEN STEM. The F_1 plants had quite distinct stems in their color from both parents, their stems being colored intensely. In F_2, the segregation occurred in three forms, colored, faintly colored and green stems, as is represented by the data in Table VII.

TABLE VII.

The F_2 data of the cross, green stem×faintly colored stem, and its reciprocal.

Cross	Stem color of parents	Colored stem	Faintly colored stem	Green stem	Total
St. S.×W. D.	g. s.×f. c. s.	125	33	58	216
W. S.×W. D.	g. s.×f. c. s.	105	32	49	186
W. D.×W. S.	f. c. s.×g. s.	70	21	32	123
Total		300	86	139	525
Expected		295.31	98.44	131.25	525

$\chi^2=2.103$ $P=0.353$

The three forms appeared in the relations of nearly 9 : 3 : 4, a slightly modified dihybrid ratio, which indicates the segregation of two factors in this case. As formerly assumed, the difference between colored and faintly

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[1] The green stem behaves also as a simple recessive to the colored condition in *Pharbitis Nil*, but sometimes the segregation occurs in more complicated ratios on account of the countenance of complemental factors.

colored stems is due to the allelomorphs of R and r, and that between colored and green stems to another set of factors. Now let us postulate the factors concerning the diversity of the latter case by S and s, which are responsible for the presence or absence of anthocyanin pigment in the stem. The effect of the allelomorphs R and r, therefore, is only discernible in the coexistence of S. Under such conditions, the genotypes of three stem forms are determined as follows :

Colored stem ... ... RS
Faintly colored stem ... ... rS
Green stem ... ... Rs or rs

The cross between faintly colored and green stems, therefore, is genetically designated as $rrSS \times RRss$, from which we should expect the segregation of 9 colored stems $(1RRSS+2RrSS+2RRSs+4RrSs)$, 3 faintly colored stems $(1rrSS \times 2rrSs)$ and 4 green stems $(1RRss \times 2Rrss \times 1rrss)$ in F_2.

Flower Color.

The flower-color series of *Ph. purpurea* contains blue, purple, red shades[1] etc., but the present paper is confined to the red shaded series of variation. The parents, with which my crossing experiments were made and the record of their hybrid progeny taken, are the following three strains :

1. White single flower with green stem (W. S.)
2. White double flower (Pl. VIII, fig. 1) with faintly colored stem (W. D.)
3. Intense-red single flower (Pl. VIII, fig. 2) with colored stem (R. S., R′. S.)

THE RESULT OF W. S. × R′. S. The F_1 plants bore flowers in an intermediate red (nearly the same as Pl. VIII, fig. 5) between two parents. In F_2, the segregation occurred quite simply, i. e., 1 intense : 2 intermediate : 1 white in every four, as is shown by the actual data in Table VIII.

TABLE VIII.

The F_2 data of the cross W. S. × R′. S. and its reciprocal, showing the simple segregation of flower color.

Cross	Intense-red flower	Intermediate-red flower	White flower	Total
W. S. × R′. S.	10	15	8	33
R′. S. × W. S.	25	58	24	107
Total	35	73	32	140
Expected	35	70	35	140

$\chi^2 = 0.386$ P = 0.849

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[1] BARKER made some experiments with various shaded flowers including flaked ones.

Thus we had monohybrid segregation in flower color at present crossing. In Table IX, I collected the F_3 data, which came to quite prove the nature recognized in the previous generation.

TABLE IX.

A summary of the F_3 data of the cross R′. S. × W. S., showing the segregation of flower color.

Character of F_2	Number of pedigree	Intense-red flower	Intermediate-red flower	White flower	Total
Intense-red flower	5	93	—	—	93
Intermediate-red flower	7 Expected	75 79.25	160 158.50	82 79.25	317 317
White flower	5	—	—	44	44

$\chi^2=0.338$ $P=0.867$

Thus the intense-red and white flowers employed as parents in the present crossing is due to one factor difference in their genotypes. The stem color of W. S. is green and all the white-flowered segregates in the hybrid progeny have colorless stems, indicating the fact that the color of stem and flower in this case is manifested by one and the same factor[1]. Generally speaking, the green stem factor *r* is concerned with the production of a white flower or a flower with white ground color on which flaking occurs as the case is in my St. S. strain.

The dominancy of a factor was much emphasized formerly and embodied into one of MENDEL'S laws under the term "law of dominance". The dominancy, however, is not always perfect and sometimes hybrids assume quite intermediate colors or forms. Usually the dominancy is recognized, but sometimes we may be able to detect some heterozygotic characteristics when the study is made more closely, or when the hybrids are surveyed statistically or anatomically. The dominancy, therefore, appears in various expressions within perfect and intermediate limits. CORRENS' case[2] of the flower color of *Mirabilis Jalapa* is a well-known example, in which the heterozygote shows an intermediate color of both parents. Usually the heterozygous flower of red (=crimson) and white is referred to as "pink" ("hell rose") in color. Recently KIERNAN and WHITE[3] protested against this terminology,

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[1] In *Pharbitis Nil*, green stems with green leaf axils invariably has white corollas, whereas colored stems bear colored flowers with some exceptions in which white flowers are the cases.

[2] Die neuen Vererbungsgesetze. Berlin. 1912.

[3] Inheritance in four o'clocks. Journ. Heredity. 17 : 383–386. 1926.

and sympathized with MARRYAT's "magenta"[1]. BAUR[2] demonstrated the analogy with his observation made in the flower color of *Antirrhinum majus*. In the Japanese morning glory, *Pharbitis Nil*, which is closely related to the species I am now discussing, no similar cases are known up to the present as to the inheritance of the flower color, though the hybrids at times assume an intermediate shade of the colors of both parents by the occurrence of a dominant diluting factor. This fact stands in curious contrast with the intermediate expression of the factor for the flower color in *Pharbitis purpurea*, as stated before.

THE RESULT OF R'. S. × W. D., ETC. One of the parents of this sort of matings, W. D., is a white feathering flower (Pl. VIII, fig. 1) yielding whitish or tan seeds, and its partners are intense-red single flowers (Pl. VIII, fig. 2) producing black seeds. The F_1 plants obtained by both reciprocal matings bore dilute-red flowers (Pl. VIII, fig. 3), representing an intermediate state of flower color of parents. The flower color of these hybrids, however, is somewhat lighter than the F_1 flowers of the previous crossing, in which the white-flowering parent is W. S. yielding black seeds instead of W. D. producing whitish seeds. In F_2, the segregation occurred in no simple way. Before entering into a general discussion on the segregation of the flower color in F_2, it is advisable to state the behavior of each factor in order. The first allelomorphic pair I am now going to discuss is a set designated by U and u. Table X concerns the dihybrid segregation of this and the R, r pairs of factors.

TABLE X.

The F_2 data of the cross W. D. × R. S. and the like, showing the difactorial segregation of flower color.

Cross	Colored stem			Faintly colored stem			Total
	I	II	III	I'	II'	III'	
R'. S. × W. D.	29	57	19	11	18	19	153
W. D. × R'. S.	9	23	2	5	10	4	53
W. D. × R. S.	13	36	10	1	9	6	73
Total	51	116	31	17	37	29	281
Expected	52.69	105.375	52.69	17.56	35.125	17.56	281

$\chi^2 = 17.626$ $P = 0.004$

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[1] Hybridization experiments with *Mirabilis Jalapa*. Rpts. Evol. Comm. Roy. Soc. 5 : 32-50. 1909.

[2] Einführung in die experimentelle Vererbungslehre. Berlin. 1919. See "Tafel II" and its explanation in text.

In the colored-stem group, (I) contains intense-red flowers (Pl. VIII, fig. 4) just as R′. S. or R. S., and flowers (Pl. VIII, fig. 5) a little lighter than these, (II) the dilute flowers (Pl. VIII, fig. 6) just as F_1 and (III) those (Pl. VIII, fig. 10) with spots on the middle of rays, the intensity of the spots varying to some extent (Pl. VIII, fig. 11), including so faint ones as hardly to be recognizable. The faintly-colored-stem group includes the corresponding three forms in somewhat lighter color than the former group; namely, (I′) contains intense-pink[1] (Pl. VIII, fig. 7) and pink flowers (Pl. VIII, fig. 8), (II′) flowers (Pl. VIII, fig. 9) having dilute color in their rays, on which the weak pink is shaded out toward the outer margin, and (III′) white flowers (Pl. VIII, fig. 12). The segregating ratio of these six forms, three of colored-stem group and three of faintly-colored-stem group, occurred in the approximation of a 3 : 6 : 3 : 1 : 2 : 1 ratio in the correspondence of I : II : III : I′ : II′ : III′, though the data may suggest the occurrence of weak coupling segregation. The F_3 examination was made and gave the results summarized in Table XI.

TABLE XI.

A summary of the F_3 data of the cross R′. S, × W. D., showing the difactorial segregation of flower color.

Character of F_2	Number of pedigree	Colored stem			Faintly colored stem			Total	Genetic constitution
		I	II	III	I′	II′	III′		
I	10	211	—	—	—	—	—	211	*SSUU*
	10	163	—	—	55	—	—	218	*SsUU*
	Expected	163.5	—	—	54.5	—	—	218	
II	12	137	280	115	—	—	—	532	*SSUu*
	Expected	133	266	133	—	—	—	532	
	$\chi^2=3.293$		P=0.197						
	27	227	464	224	85	144	84	1228	*SsUu*
	Expected	230.25	460.50	230.25	76.75	153.50	76.75	1228	
	$\chi^2=2.402$		P=0.790						
III	6	—	—	139	—	—	—	139	*SSuu*
	9	—	—	186	—	—	64	250	*Ssuu*
	Expected	—	—	187.5	—	—	62.5	250	
I′	8	—	—	—	362	—	—	362	*ssUU*
II′	13	—	—	—	117	251	142	510	*ssUu*
	Expected	—	—	—	127.5	255	127.5	510	
	$\chi^2=2\ 576$		P=0.285						
III′	14	—	—	—	—	—	209	209	*ssuu*

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[1] In F_2, however, actually I had no intense-pink flowers owing to linked assortment, of which I will speak later.

Table XII contains a summary of F_4 as to the inheritance of the characters in discussion.

TABLE XII.

A summary of F_4 bred from F_3 given in the previous table, showing the difactorial segregation of flower color.

Character of F_3	Pedigree number of F_3	Number of F_4 pedigree	Colored stem			Faintly colored stem			Total	Genetic composition
			I	II	III	I′	II′	III′		
I	9, 30, 34, 35	10	181	—	—	—	—	—	181	*SSUU*
	34, 35	4	81	—	—	29	—	—	110	*SsUU*
	Expected		82.5	—	—	37.5	—	—	110	
III	9, 34	2	—	—	17	—	—	—	17	*SSuu*
	35	1	—	—	7	—	—	3	10	*Ssuu*
	Expected		—	—	7.5	—	—	2.5	10	
I′	14, 72	6	—	—	—	86	—	—	86	*ssUU*
II′	72	2	—	—	—	18	30	8	56	*ssUu*
	Expected		—	—	—	14	28	14	56	
	$\chi^2=3.857$		P=0.148							
III′	35, 72	3	—	—	—	—	—	67	67	*ssuu*

With these results we can clearly understand the nature of the allelomorphs, *U* and *u*, which give three phenotypes by the intermediate expression of the heterozygotic character, and the allelomorphs *S* and *s* result in two flower color series of intense and dilute, within which the respective three forms are displayed. When we designate the genetic constitution of the parental intense-red and white flowers as *SSUU* and *ssuu* respectively, we should have the following segregation in F_2 which bred from doubly heterozygous F_1 hybrids.

$$\overbrace{\text{I} \qquad\quad \text{II} \qquad\quad \text{III}}^{\text{Colored stem}} \qquad\qquad \overbrace{\text{I}' \qquad\quad \text{II}' \qquad\quad \text{III}'}^{\text{Faintly colored stem}}$$

$$3\left\{\begin{matrix}1\ SSUU\\ 2\ SsUU\end{matrix}\right. : 6\left\{\begin{matrix}2\ SSUu\\ 4\ SsUu\end{matrix}\right. : 3\left\{\begin{matrix}1\ SSuu\\ 2\ Ssuu\end{matrix}\right. : 1\ \{\ 1\ ssUU : 2\ \{\ 2\ ssUu : 1\ \{\ 1\ ssuu$$

So the segregates (I) and (I′) have the *UU*-constitution, (II) and (II′) the *Uu*-constitution and (III) and (III′) the *uu*-one, and the monofactorial segregating data on this allelomorphic pair are shown in Table XII.

TABLE XIII.

A summary of the F_2, F_3 and F_4 data, showing the monofactorial segregation of the allelomorphs, *U* and *u*.

Generation	*UU*	*Uu*	*uu*	Total
F_2	68	153	60	281
F_3	401	801	425	1627
F_4	18	30	8	56
Total	487	984	493	1964
Expected	491	982	491	1964

$\chi^2 = 0.045$ $P = 0.932$

The segregation occurs in fair accordance with the ratio 1 : 2 : 1, as expected. The white flowers of this crossing are due to the combined manifestation of two recessive factors, *s* and *u*, therefore their segregation takes place with the proportion of one-fourth in some pedigrees propagated from the III- and the II′-flowers and with the proportion of one-sixteenth in some pedigrees bred from the II-flowers. In the coexistence of the factors *S*, *u* results in white flowers with spots on their rays, while the replacement of this by its recessive factor produces apparently white flowers by the fading out of the spots.

Next let us state the behavior of another allelomorphic pair, *D* and *d*. The factor *D*, a diluting qualifier, is plainly visible outwardly only in the *UU*-flowers, so its segregation cannot be phenotypically detected in the other flowers. The colored flowers used as one parent in each crossing, were of an intense *UU*-color and they are regarded as carrying the *SSUUdd*-constitution. The segregation of the dilute *UU*-flowers in the later hybrid generations indicates the countenance of the *D*-factor, the origin of which is attributed to the white-flowered parent. The white flowers, the partners of the colored flowers just described, therefore, are considered to be *ssuuDD*. From the triply heterozygous F_1 plants we should obtain the four phenotypes of color intensity in the classes I and I′ by the segregation of two allelomorphic pairs, *D*, *d* and *S*, *s*. Practically, however, no flowers carrying the *ssUUdd*-constitution appeared in F_2 owing to the occurrence of linkage between these two allelomorphic series. Before presenting the F_2 data on the segregation of these factors in question I will make clear the behavior of the factor *d* with the data of its monofactorial segregation. The F_2 flowers which are grouped under the forms I and I′ were intense red, red and pink, but contained no intense pink (cf. Plate VIII). Table XIV concerns the F_3 data of these F_2 flowers.

TABLE XIV.

The F_3 data of the intense-red, red and pink F_2 flowers, showing the behavior of the factor *d*.

Character of F_2	Number of pedigree	Red flower	Intense-red flower	Pink flower	Intense-pink flower	Total	Genetic composition
Red flower	2	46	—	—	—	46	*SSUUDD*
	7	98	47	—	—	145	*SSUUDd*
	Expected	108.75	36.25	—	—	145	
	1	5	—	3	—	8	*SsUUDD*
	Expected	6	—	2	—	8	
	8	106	48	47	4	205	*SsUUDd*
	Expected	106.68	47.07	47.07	4.18	205	
	$\chi^2=0.040$		P=0.992				
Intense-red flower	1	—	20	—	—	20	*SSUUdd*
	1	—	4	—	1?	5	*SsUUdd*
	Expected	—	3.75	—	1.25	5	
Pink flower	5	—	—	286	—	286	*ssUUDD*
	3	—	—	59	17	76	*ssUUDd*
	Expected	—	—	57	19	76	

Among these segregations the one indicated in the last of the "red flower" column shows the result of linkage between the factors, *s* and *d*. The origin of these factors can be attributed the one to one parent and the other to its partner, so we expect more chance of obtaining repulsion pedigrees than coupling ones in F_3. Actually all eight pedigrees, of which I made observation on the flower color, gave repulsion segregations.

Thus the behavior of the *D*, *d* allelomorphs can be visible when the flowers carry duplex constitution of the factor *U*. If we collect the data of the monofactorial segregation of this point from Table XIV we obtain 310 *D* and 116 *d* in the total of 426 flowers, in which we should expect 319.5 *D* and 106.5 *d*, respectively.

With these results we can safely recognize the countenance of the *D*, *d* allelomorphs in the present cases. In Table XV I collected the F_4 data confirming the previous observation.

From the foregoing description we recognize the three pairs of factors which determine the color variation exhibited in the hybrid progeny. Now let us present the F_2 data showing the triple segregation for the flower color in Table XVI.

TABLE XV.

The F_4 data showing the behavior of the factor *d*.

Character of F_3	Pedigree number of F_3	Number of F_4 pedigree	Red flower	Intense-red flower	Pink flower	Intense-pink flower	Total	Genetic composition
Red flower	30, 35	2	66	—	—	—	66	*SSUUDD*
	30, 35	4	36	13	—	—	49	*SSUUDd*
	Expected		36.75	12.25	—	—	49	
	34, 35	2	36	—	15	—	51	*SsUUDD*
	Expected		38.25	—	12.75	—	51	
	35	2	30	15	14	0	59	*SsUUDd*
	Expected		30.70	13.55	13.55	1.20	59	
	$\chi^2=1.386$		P=0.713					
Intense-red flower	9, 30, 34, 35	4	—	66	—	—	66	*SSUUdd*
Pink flower	14, 72	4	—	—	45	—	45	*ssUUDD*
Intense-pink flower	14, 72	2	—	—	—	29	29	*ssUUdd*

TABLE XVI.

The F_2 data of the cross, intense-red × white, showing the segregation of flower color.

Cross	Intense-colored series (Colored stem)				Dilute-colored series (Faintly colored stem)				Total
	Red flower	Intense-red flower	Dilute-red flower	Spotted flower	Pink flower	Intense-pink flower	Shaded flower	White flower	
R′. S. × W. D.	25	4	57	19	11	0	18	19	153
W. D. × R′. S.	5	4	23	2	5	0	10	4	53
W. D. × R. S.	9	4	36	10	1	0	9	6	75
Total	39	12	116	31	17	0	37	29	281
Expected	36.56	16.13	105.375	52.69	16.13	1.43	35.125	17.56	281

$\chi^2=20.250$ P=0.005

The F_2 data shown above are not simple because of the interaction of the factors and of linkage. The genetic constitution of the white-flowered parents is considered to be *ssuuDD*, while their partners, intense-red flowers, have the *SSUUdd*-constitution. On selfing the triply heterozygous F_1 hybrids we should expect the following segregation (see Table XVII), if the gametic ratio of present linkage is applied to be 1 : 2.5, which quite fairly satisfied the actual data as will be seen in Tables XIV and XV.

TABLE XVII.

The theoretical F_2 segregation corresponded to the actual data shown in Table XVI.

Genotype		Phenotype		Color series
Constitution	Ratio	Flower color	Ratio	
SSUUDD	1.00	Red	25.50	Intense-colored series (Colored stem)
SsUUDD	5.00			
SSUUDd	5.00			
SsUUDd	14.50			
SSUUdd	6.25	Intense-red	11.25	
SsUUdd	5.00			
SSUuDD	2.00	Dilute-red	73.50	
SSUuDd	10.00			
SSUuDd	10.00			
SsUuDd	29.00			
SSUudd	12.50			
SsUudd	10.00			
SSuuDD	1.00	Spotted	36.75	
SsuuDD	5.00			
SSuuDd	5.00			
SsuuDd	14.50			
SSuudd	6.25			
Ssuudd	5.00			
ssUUDD	6.25	Pink	11.25	Dilute-colored series (Faintly colored stem)
ssUUDd	5.00			
ssUUdd	1.00	Intense-pink	1.00	
ssUuDD	12.50	Shaded	24.50	
ssUuDd	10.00			
ssUudd	2.00			
ssuuDD	6.25	White	12.25	
ssuuDd	5.00			
ssuudd	1.00			

The expected number shown in Table XVI is calculated on the basis of the theoretical ratio above represented, but the value of P is very low.

The breeding aspect of these segregating flowers was partly described in the former pages and we will take up those of which results are not yet stated. As will be seen from Table XVII, the dilute-red flowers invariably carry the factor *S* in the simplex or duplex constitution and the simplex *U*, but cannot say without breeding examination whether the flowers have the factor *D* or *d*. So the F_3 results of the intense-red F_2 flowers are not simple in the segregating forms owing to their various composition. In Table XVIII I collected these data.

TABLE XVIII.

The F_3 data of the dilute-red F_2 flowers.

Pedigree number	Intense-colored series (Colored stem)				Dilute-colored series (Faintly colored stem)				Total	Genetic composition
	Red flower	Intense-red flower	Dilute-red flower	Spotted flower	Pink flower	Intense-pink flower	Shaded flower	White flower		
69	16	—	30	13	—	—	—	—	58	*SSUuDD* (or *SSUuDd*)
93	2	—	18	3	—	—	—	—	23	
96	1	—	5	1	—	—	—	—	7	
112	1	—	3	4	—	—	—	—	8	
Total	20	—	56	20	—	—	—	—	96	
Expected	24	—	48	24	—	—	—	—	96	
		$\chi^2=2.667$		P=0.271						
5	6	—	11	6	2	—	2	2	29	*SsUuDD* (or *SsUuDd*)
20	4	—	9	2	1	—	4	1	21	
26	1	—	1	2	1	—	0	0	5	
40	12	—	37	18	2	—	5	4	78	
59	4	—	7	5	2	—	3	5	26	
78	0	—	4	6	1	—	1	1	13	
83	5	—	6	4	2	—	4	0	21	
100	2	—	1	2	0	—	2	1	8	
103	2	—	9	5	1	—	4	0	21	
Total	36	—	85	50	12	—	25	14	222	
Expected	41.625	—	83.25	41.625	13.875	—	27.75	13.875	222	
		$\chi^2=3.009$		P=0.698						
6	—	4	8	5	—	—	—	—	17	*SSUudd*
42	—	19	33	15	—	—	—	—	67	
77	—	17	53	27	—	—	—	—	97	
101	—	4	7	3	—	—	—	—	14	
Total	—	44	101	50	—	—	—	—	195	
Expected	—	48.75	97.50	48.75	—	—	—	—	195	
		$\chi^2=0.650$		P=0.744						
3	—	1	6	3	—	0	2	0	12	*SsUudd*
9	—	8	17	14	—	1 ?	3	3	46	
17	—	9	18	6	—	2 ?	6	3	44	
Total	—	18	41	23	—	3 ?	11	6	102	
Expected	—	19.125	38.25	19.125	—	6.375	12.75	6.375	102	
		$\chi^2=3.096$		P=0.686						
36	17	3	32	10	—	—	—	—	62	*SSUuDd*
50	20	6	43	21	—	—	—	—	90	
68	15	4	34	11	—	—	—	—	64	
70	7	1	14	3	—	—	—	—	25	
Total	59	14	123	45	—	—	—	—	241	
Expected	45.19	15.09	120.50	60.25	—	—	—	—	241	
		$\chi^2=8.206$		P=0.043						

TABLE XVIII. (continued)

Pedigree number	Intense-colored series (Colored stem)				Dilute-colored series (Faintly colored stem)				Total	Genetic composition
	Red flower	Intense-red flower	Dilute-red flower	Spotted flower	Pink flower	Intense-pink flower	Shaded flower	White flower		
10	9	1	21	7	4	0	8	4	54	*SsUuDd*
18	14	6	36	23	5	0	9	4	97	
34	9	6	32	7	1	1	8	7	71	
35	18	6	20	23	8	1	8	5	89	
38	4	1	11	8	1	0	1	1	27	
39	2	2	11	6	2	0	4	3	30	
47	6	2	26	10	5	0	5	4	58	
54	32	9	107	33	14	3	32	22	252	
61	12	3	13	11	5	1	10	2	57	
62	2	1	6	2	1	0	1	0	13	
63	11	5	25	11	11	1	8	7	79	
94	1	1	11	3	0	0	5	2	23	
98	2	2	9	3	2	0	4	0	22	
109	2	2	6	2	1	0	2	1	16	
Total	124	47	334	149	60	7	105	62	888	
Expected	115.53	50.97	333.00	166.50	50.97	4.53	111.00	55.50	888	
	$\chi^2=6.683$			$P=0.464$						
81	2	0	4	2	0	2	3	2	15	*SsUuDd*

The triply heterozygous F_3 pedigrees displayed linkage segregation between the factors, *s* and *d*, as will be seen in the last group of segregating forms. To obtain ample data for linkage in question I collected all the results available in my crossing experiments in Table XIX.

TABLE XIX.

The available data for the examination of linkage between the factors *s* and *d*.

Generation	*SD*	*Sd*	*sD*	*sd*	Total
F_2	47	10	17	0	74*
F_3	124	47	60	7	238*
	106	48	47	4	205
F_4	30	15	14	0	59
Total	307	120	138	11	576
Expected	299.755	132.245	132.245	11.755	576

$\chi^2=1.608$ $P=0.662$

* These pedigrees made segregation as to the *Uu*-allelomorphs, but I omitted the segregating numbers of the dilute-red, spotted, shaded and white flowers from this table.

With this table we can obtain about a 1 : 2.5 gametic ratio, or, in other words the crossing over between the factors *s* and *d* is 28.57 per cent, or nearly 30 per cent.

In Table XVIII, fifteen pedigrees making trifactorial segregation comprise repulsion data with one exception. No. 81 is this pedigree, and probably it may be the one making coupling segregation, though the observed number is not sufficient to convince us. As the linkage is not very strong, we should naturally expect some occurrences of coupling segregation, contrasted phenomenon of repulsion.

The spotted flowers appearing in the hybrid progeny were composed of those having intense spots on the rays and those having dilute spots, their intensity varying to some extent, including the very faintly colored ones with almost white flowers together, but I have observed no plants bearing only white flowers which carry the factor *S*. Roughly speaking, the dilute spotted flowers act as dominant over the intense ones, but their exact nature cannot be detected owing to their considerable variation.

Now let us describe the F_3 results of the shaded F_2 flowers. On selfing fifteen plants I recorded their F_3, which are indicated in Table XX.

TABLE XX.

The F_3 data of the shaded F_2 flowers.

Pedigree number	Pink flower	Intense-pink flower	Shaded flower	White flower	Total	Genetic composition
15	1	—	1	3	5	*ssUuDD* (or *ssUuDd*)
23	19	—	26	9	54	
28	12	—	26	21	59	
37	1	—	9	1	11	
45	3	—	14	6	23	
46	8	—	27	10	45	
90	2	—	6	1	9	
107	1	—	8	3	12	
Total	47	—	117	54	218	
Expected	54.5	—	109	54.5	218	
	$\chi^2=1.624$		P=0.458			
8	7	2	32	16	57	*ssUuDd*
49	13	2	27	14	56	
53	13	4	32	17	66	
72	4	1	4	5	14	
80	5	1	10	12	28	
84	8	1	11	6	26	
108	4	5	18	18	45	
Total	54	16	134	88	292	
Expected	54.75	18.25	146	73	292	
	$\chi^2=4.356$		P=0.230			

Thus progenies of fifteen plants came under two grouping segregations, the one in which pink, shaded and white flowers appeared in the ratio of 1 : 2 : 1, the other in which pink, intense-pink, shaded and white flowers occurred in 3 : 1 : 8 : 4, a modified dihybrid ratio. Theoretically speaking, the shaded F_2 flowers should be composed of three genotypes, *ssUuDD*, *ssUuDd* and *ssUudd*, as will be seen in Table XVII. Among them, I examined no cases last-cited, in which we should expect the segregation of three flowers, intense-pink, shaded and white, in the ratio of 1 : 2 : 1. Owing to linkage between the factors *s* and *d* the numerical contents among the shaded F_2 flowers are much influenced and theoretically we should have infrequent chances of obtaining the shaded flowers carrying such a genotype.

Similar results were repeatedly obtained from the F_4 data, as indicated in Table XXI, though its contents are meagre.

TABLE XXI.

The F_4 data of the shaded F_3 flowers.

Pedigree number of F_3	Number of pedigree	Pink flower	Intense-pink flower	Shaded flower	White flower	Total	Genetic composition
72	1 Expected	11 7.69	3 2.56	22 20.50	5 10.25	41 41	} *ssUuDd*
		$\chi^2=4.299$		P=0.235			
	1 Expected	4 3.75	— —	8 7.50	3 3.75	15 15	} *ssUuDD*?
		$\chi^2=0.200$		P=0.921			

The factor hypothesis above postulated fairly accords with the observed results, as will be seen by the above statements. In Table XXII, the linked segregation is confirmed by the numerical comparison of the genotypical contents of F_2.

TABLE XXII.

A comparison between the theoretical and actual F_2 genotypes, confirming linkage between *s* and *d*.

Genotype	Observed	Expected
SSDD *SSDd*	3 11 } 3*	1.67 8 37
SSdd	5	10.46
SsDD *SsDd*	5 23 } 5*	8.37 24.27
Ssdd	4	8.37
ssDD *ssDd*	8 10 } 5*	10.46 8.37
ssdd	0	1.67
Total	82	82.01

* The genotypes are obscure owing to their insufficient number in F_3

TABLE XXIII.

The theoretical F_2 segregation in the cross W. S. (*rrSSUUdd*) × W. D. (*RRssuuDD*).

Intense-colored series (colored stem)				Dilute-colored series (Faintly colored stem)				White flowers with green stem
Intense-red flower	Red flower	Dilute-red flower	Spotted flower	Intense-pink flower	Pink flower	Shaded flower	White flower	White flower
6.25 *RRSSUUdd*	1.00 *RRSSUUDD*	2.00 *RRSSUuDD*	1.00 *RRSSuuDD*	1.00 *RRssUUdd*	6.25 *RRssUUDD*	12 50 *RRssUuDD*	6.25 *RRssuuDD*	6.25 *rrSSUUdd*
▭	▭	4.00 *RrSSUuDD*	2.00 *RrSSuuDD*	▭	▭	25.00 *RrssUuDD*	12.50 *RrssuuDD*	5.00 *rrSsUUdd*
5.00 *RRSsUUdd*	5.00 *RRSsUUDD*	10.00 *RRSsUuDD*	5.00 *RRSsuuDD*		5.00 *RRssUUDd*	10.00 *RRssUuDd*	5.00 *RRssuuDd*	1.00 *rrSSUUDD*
▭	▭	20.00 *RrSsUuDD*	10.00 *RrSsuuDD*		▭	20.00 *RrssUuDd*	10.00 *Rrssuudd*	5.00 *rrSsUUDD*
	5.00 *RRSSUUDd*	10.00 *RRSSUuDd*	5.00 *RRSSuuDd*		→2.00 *RrssUUdd*	2.00 *RRssUudd*	1.00 *RRssuudd*	5.00 *rrSSUUDd*
	▭	20.00 *RrSSUuDd*	10.00 *RrSSuuDd*			4.00 *RrssUudd*	2.00 *Rrssuudd*	14.50 *rrSsUUDd*
	14.50 *RRSsUUDd*	29.00 *RRSsUuDd*	14.50 *RRSsuuDd*			→12.50 *RrssUUDD*		2.00 *rrSSUuDD*
	▭	58.00 *RrSsUuDd*	29.00 *RrSsuuDd*			→10.00 *RrssUUDd*		10.00 *rrSsUuDD*
	→12 50 *RrSSUUdd*	12.50 *RRSSUudd*	6.25 *RRSSuudd*					10.00 *rrSSUuDd*
	→10.00 *RrSsUUdd*	25.00 *RrSSUudd*	12.50 *RrSSuudd*					29.00 *rrSsUuDd*
		10.00 *RRSsUudd*	5.00 *RRSsuudd*					12.50 *rrSSUudd*
		20.00 *RrSsUudd*	10.00 *RrSsuudd*					10.00 *rrSsUudd*
		→2.00 *RrSSUUDD*						1.00 *rrSSuuDD*
		→10.00 *RrSsUUDD*						5.00 *rrSsuuDD*
		→10.00 *RrSSUUDd*						5.00 *rrSSrrDd*
		→20.00 *RrSsUUDd*						14.50 *rrSsuuDd*
								6.25 *rrSSuudd*
								5.00 *rrSsuudd*
								1.00 *rrssUUdd*
								6.25 *rrssUUDD*
								5.00 *rrssUUDd*
								12.50 *rrssUuDD*
								10.00 *rrssUuDd*
								2.00 *rrssUudd*
								6.25 *rrssuuDD*
								5.00 *rrssuuDd*
								1.00 *rrssuudd*
11.25	48.00	271.50	110 25	1.00	13.25	96.00	36.75	196.00

The one indicated with an arrow changes the flower color by its heterozygous *Rr*-constitution.

The F_2 plants, the subsequent generation of which was examined, were 112 in number, but I have shown the genotypes of 85 plants with the omission of those which bore spotted and white flowers, because of the fact that we could not know their constitution as to the *D*, *d* allelomorphs with inbreeding experiments. In the table the numerals asterisked show the ones of which the segregating types are not clear owing to their insufficient number in F_3. Under such circumstances, we cannot make exact comparison between observed and theoretical numbers, but a glance at the table will show considerable agreement.

THE RESULT OF W. S. × W. D. From the knowledge gained by the hybridization experiments above shown we can consider the genetic composition of the parental flowers of this crossing; namely, W. S.·········*rrSSUUdd*, and W. D.·········*RRssuuDD*. If this is the case the F_1 flowers should be dilute red in color by their quadruple heterozygous constitution, and in F_2 we will have the segregates as shown in Table XXIII.

In consideration of Table XXIII, the linked assortment occuring between the factors *s* and *d* and the intermediate expression of the factor *r* in its heterozygosity made it somewhat complex in giving an unfamiliar ratio. I postulate the effect of heterozygotic *r* to reduce the intensity of the flower color in such a way; namely, intense-red, red, intense-pink and pink into red, dilute-red, pink and shaded, respectively. Actually the theoretical number calculated on the basis of this expectation is nearly in accordance with observation, as will be found in Table XXIV.

TABLE XXIV.

The F_2 data of the cross W. S. × W. D., showing the segregation of flower color.

	Red flower	Intense-red flower	Dilute-red flower	Spotted flower	Pink flower	Intense-pink flower	Shaded flower	White flower (f.c.s.)	White flower (g. s.)	Total
Observed	24	2	108	41	10	0	31	12	81	309
Expected	18.92	4.43	107.01	43.45	5.22	0.39	37.84	14.49	77.25	309

$\chi^2=9.461$ $P=0.307$

Although the final decision may require the examination of F_3 we can say that the above hypothesis is probably correct.

Feathered Corolla.

The double flower of *Pharbitis purpurea* is due to the feathering of the corolla (v. Pl. VIII). The doubling of the flower produces an irregularly split corolla with some petalous filaments, which resembles the "Shishi" flower of the Japanses morimg glory. The "Shishi" flower usually contains abortive sexual organs and produces no seeds, but the feathered flower of *Ph. purpurea* bears normal pistil and stamens, and produces good seeds. The degree of feathering, however, is very fluctuating, and even on one and the same individual it varies considerably, frequently flowers with apparently single corollas can be found amongst them. The extremely developed flowers have many petaloid "skirts" and are irregularly split. Generally speaking, the stems showing vigorous growth bear less-feathered flowers compared with those on languishing stems, so from the observation of young plants one cannot always predict with certainty that they will produce double flowers. In the following, I will mention the genetic behavior of the feathered doubles[1] with the data gained in my crossing experiments.

The F_1 plants obtained by the hybridization of the double flowers with the singles bore invariably flowers with feathered tubes,[2] and in F_2 they gave the data indicated in Table XXV.

TABLE XXV.

The F_2 data showing the segregation of double and single flowers.

Cross	Double flower	Single flower	Total
R′. S. × W. D.	103	50	153
W. D. × R′. S.	39	14	53
W. D. × R. S.	58	17	75
W. S. × W. D.	129	57	186
W. D. × W. S.	98	25	123
Total	427	163	590
Expected	442.5	147.5	590

The segregation occurred in a 3 : 1 ratio, indicating one-factor difference between two flower forms in their genotypes.[3] Of these F_2 segregates, I made the F_3 examination in raising the progenies of 112 F_2 plants which consisted of 69 double and 43 single flowers. Table XXVI summarizes their F_3 data.

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[1] BARKER's conclusion was "feathering of the corolla is a Mendelian character dominant over its absence", but his segregating data are not sufficient.

[2] The degree of feathering is generally imperfect compared with that exhibited by the parental double.

[3] In some crosses, extremely developed double flowers of somewhat complicated types appeared, but I leaved their study for a future opportunity.

TABLE XXVI.

The F_3 data of the cross R'. S. × W. D., showing the inheritance of double flower.

Character of F_2	Number of pedigree	Double flower	Single flower	Total
Double flower	1	14	—	14
	13	142	47	189
	Expected	141.75	47.25	189
Single flower	43	—	1398	1398

The breeding aspect of 55 double-flowered pedigrees, which are not contained here, will be mentioned in the text.

Single flowers bred always true to the type, while the doubles gave both true-breeding and segregating progenies. The main part of the F_3 offspring was left in the field without the later management in twinning about the vines after their early record was taken, so I could not obtain their precise data on the segregation of double flowers. Table XXVI does not include the results of 55 double-flowered pedigrees because of insufficient discrimination. In spite of this their record is not useless when we collect the data as to the numerical contents of homozygotic and heterozygotic F_2 doubles. Of 69 F_2 doubles those which gave progenies consisting all of double flowers were 17 in number, while the others, 52, produced segregating pedigrees as to the flower type, where we expect 23 of the former and 46 of the latter. Table XXVII includes the F_4 data in regard to the flower type.

TABLE XXVII.

The F_4 data of the cross R'. S. × W. D., showing the inheritance of flower type.

Character of F_3	Pedigree number of F_2	Number of pedigree	Double flower	Single flower	Total
Double flower	9, 72	7	141	—	141
	9, 14	3	23	12	35
	Expected		26.25	8.75	35
Single flower	14, 30, 34, 35	18	—	331	331

The figures contained in the above table confirm the results gained in the previous generation, indicating the simple dominancy of the feathered corolla to the single condition. In the Japanese morning glory, there are several forms of double flowers, but no dominant ones[1] are found, even the "Shishi" flower[2] itself, which is due to feathering of the corolla.

* * *

As stated before I found a case of linkage between the factors *s* and *d*, but no remarkable dependent relation seems to exist between the doubleness and flower color in their segregation, as will be seen in Table XXVIII, in which I collect the F_2 data obtained from the cross R′. S. x W. D. and the like.

TABLE XXVIII.

The F_2 data indicating the segregating aspect of the doubleness and flower color.

Cross	Character	Colored stem				Faintly colored stem				Green stem	Total
		Red flower	Intense-red flower	Dilute-red flower	Spotted flower	Pink flower	Intense-pink flower	Shaded flower	White flower	White flower	
R′.S. x W.D.	Double	14	3	35	17	8	0	14	12	—	103
	Single	11	1	22	2	3	0	4	7	—	50
W.D, x R′.S.	Double	3	3	16	2	4	0	8	3	—	39
	Single	2	1	7	0	1	0	2	1	—	14
W.D. x R.S.	Double	8	3	24	9	1	0	8	5	—	58
	Single	1	1	12	1	0	0	1	1	—	17
Total	Double	25	9	75	28	13	0	30	20	—	200
	Single	14	3	41	3	4	0	7	9	—	81
W.S. x W.D.	Double	6	2	44	21	2	0	14	5	35	129
	Single	7	0	19	6	2	0	7	2	11	57
W.D. x W.S.	Double	9	0	37	9	6	0	7	5	25	98
	Single	2	0	8	5	0	0	3	0	7	25
Total	Double	15	2	81	30	8	0	21	10	60	227
	Single	9	0	27	11	2	0	10	2	21	82

Seed Color.

The seed color of the common strains is black, but W. D., a white-flowered double, produces whitish or tan seeds. The F_1 plants obtained by the cross of black-seeded with tan-seeded produce black seeds, showing the recessiveness of the tan color.[3] In F_2 the segregation occurs in a simple ratio

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[1] cf. MIYAKE, K. and IMAI, Y.—On the double flowers of the Japanese morning glory. Journ. Genetics. In press.

[2] cf. MIYAKE, K. and IMAI, Y.—On a monstrous flower and its linkage in the Japanese morning glory. Journ. Genetics. 16 : 63–76. 1925.

[3] BARKER also gained the result showing "black is the dominant color" in his experiments with black and tan seeds.

and in the subsequent generations the inheritance of seed color follows quite simple Mendelian expectations. So the diversity of the seed color of black and tan lies in one factor difference. The seed color, however, is accompanied by the stem color, or, more particularly, the SS- or Ss-plants always produce black seeds, while ss-ones tan seeds. Although I did not examine the seed color of all the hybrid progeny it is evident that the black and tan color is due to the pleiotrophic expression of the S, s allelomorphs. With the Japanese morning glory some investigators[1] made their genetic experiments on the seed color, among which we can cite striped and white seeds,[2] which are due to pleiotrophy of the respective factors for the variegated leaf and a certain white flower.

Opportunity is taken at this point to express my hearty thanks to Professor K. Miyake for his helpful suggestions, and also to Mr. K. Hashimoto for his encouraging interest in the progress of my investigation.

Summary.

1. The three types of stem color are manifested by different combinations of the S, s and R, r pairs of allelomorphs, which, however, also affect the flower color. The respective genotypes of three stem varieties are:

Colored stem	RS
Faintly colored stem	Rs
Green stem	rS, rs

2. The factors determining the flower color in my crossing experiments are:

S, s—The allelomorphs give pleiotrophic manifestation in the color of stem and flower. The factor S makes the flower color more intense and its recessive gives a contrary result, producing two series of flower color groups, intense and dilute.

R, r—The recessive factor r results in a green-stemmed white flower in its double doses. In the heterozygous state the flower color is affected when the plants carry the UU-factors, displaying a somewhat intermediate condition.

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[1] Miyake, K. and Imai, Y.—Genetic experiments with morning glories. I. Bot. Magazine, Tokyo. 34 : 1–26. 1920. (In Japanese.) Miyazawa, B.—Genetic studies on the seed color of the Japanese Convolvulus. Jap. Journ. Genetics. 2–1 : 1–11. 1923. (In Japanese.) Imai, Y.—A genetic analysis of white-margined flowers in the Japanese morning glory. Genetics. In press.

[2] In the consideration of the genetic composition of the white-flowered strain bearing white seeds, Miyazawa, however, postulated two different factors, one for white flower and the other for white seed, and concluded that these two factors completely or highly link together in inheritance.

U, u—*U* is a factor for color extension of the corolla. The heterozygous condition exhibits approximately an intermediate expression between the *UU*- and *uu*-conditions.

D, d—*D* is a diluting factor. The detection of the factor, however, can be made outwardly in the *UU*-plants only.

These four pairs of allelomorphs result in following flower color series by their various combinations :

Colored stem	(1) Intense-red	*SSRRUUdd, SsRRUUdd*
	(2) Red	*SSRRUUDD, SsRRUUDD, SSRRUUDd, SsRRUUDd,* *SSRrUUdd, SsRrUUdd*
	(3) Dilute-red	*SSRRuuDD, SsRRUudd, SSRRUuDd, SsRRUuDd,* *SSRRUudd, SsRRUudd, SSRrUUDD, SsRrUUDD,* *SSRrUUDd, SsRrUUDd, SSRrUuDD, SsRrUuDD,* *SSRrUuDd, SsRrUuDd, SSRrUudd, SsRrUudd*
	(4) Spotted	*SSRRuuDD, SsRRuuDD, SSRRuuDd, SsRRuuDd,* *SSRRuudd, SsRRuudd, SSRruuDD, SsRruuDD,* *SSRruuDd, SsRruuDd, SSRruudd, SsRruudd*
Faintly colored stem	(5) Intense-pink	*ssRRUUdd*
	(6) Pink	*ssRRUUDD, ssRRUUDd, ssRrUUdd*
	(7) Shaded	*ssRRUuDD, ssRRUuDd, ssRRUudd, ssRrUUDD,* *ssRrUUDd, ssRrUuDD, ssRrUuDd, ssRrUudd*
	(8) White	*ssRRuuDD, ssRRuuDd, ssRruudd, ssRruuDD,* *ssRruuDd, ssRruudd*
		(The white flower with faintly colored stem is produced by the factor interaction of two recessive factors, *s* and *u*, in their double doses)
Green stem	(9) White	All combinations above cited with no dominant factor as to the *R, r* allelomorphs.

3. Linkage with 1 : 2.5 gametic ratio occurs between *s* and *d*.

4. Feathered double behaves as a simple dominant over the singleness.

5. Almost free combinations take place between flower color and doubleness.

6. Tan seed is transmitted as a simple recessive to the black, and these characters are due to pleiotrophic manifestation of the *S, s* allelomorphs.

EXPLANATION OF PLATE VIII.

Fig. 1. White flower with faintly colored stem (W. D.).
Fig. 2. Intense-red flower (R'. S.).
Fig. 3. Dilute-red F_1 flower obtained by the cross of W. D. with R'. S.
Fig. 4. Intense-red flower. Figs. 4–12 are the representatives of various F_2 segregates.
Fig. 5. Red flower.
Fig. 6. Dilute-red flower.
Fig. 7. Intense-pink flower.
Fig. 8. Pink flower.
Fig. 9. Shaded flower.
Fig. 10. Spotted flower.
Fig. 11. Faintly spotted flower.
Fig. 12 White flower.

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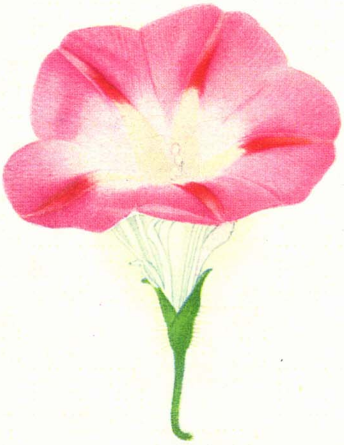

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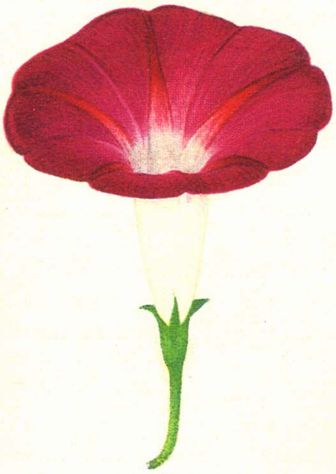

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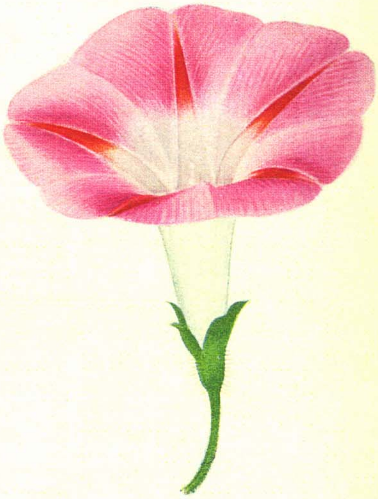

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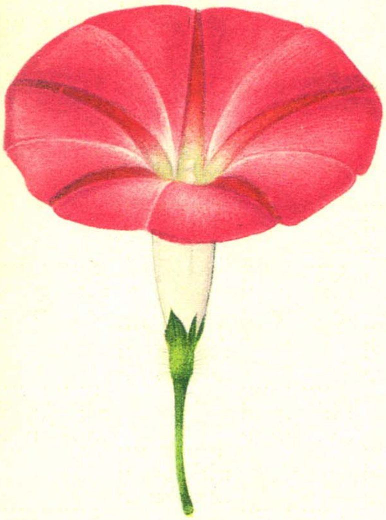
Plate VIII.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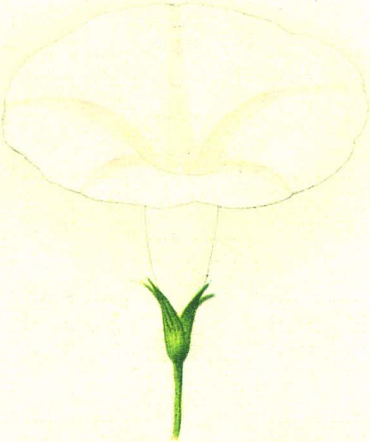
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