Recurrent reversible mutations in the duskish allelomorphs of *Pharbitis Nil*

by

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Contents

Introduction

The gene duskish (IMAI 1931 a; HAGIWARA 1931), which is located in the duskish chromosome (IMAI 1933), manifests the so-called duskish flowers (IMAI 1931 a, Pl. V, Fig. 7). The pedigree culture of the duskish stock gave some self-coloured[1] and variegated variants. The variegated plants bear flowers showing various grades of variegation, from plain to self-coloured. The plain forms have duskish flowers, sometimes a few normal-coloured spots occurring on the duskish background. On the variegated flowers normal-coloured flecks or parts appear in mosaic with the original duskish parts. The production of self-coloured variants is due to simple mutations from recessive to dominant. The origin of the variegated or ruled variants is also due to mutation, the process, however, being greatly complicated by mutual transformations from recessive to dominant

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[1] In the present paper self-coloured means mono-coloured normally. The stock being purple magenta duskish, the self-coloured mutants bear 'red' flowers.

and *vice versa.* In a previous paper (IMAI 1931a), I wrote "we cannot draw a final conclusion as to the precise nature of the variability of duskish, especially in relation to the ruled variant". The present paper is an attempt to add data that may help to throw some light on this obscure subject. The behaviour of duskish is one of the most complicated problems in connection with this plant.

The unstable plain pedigrees

Summarizing the data given in a previous paper (IMAI 1931a), the duskish pedigrees gave 21 self-coloured, 104 ruled, and 1511 plain plants in their total offspring, corresponding to 1.3 percent self-coloured, 6.4 percent ruled, and 92.3 percent plain. The newly obtained results are given in Table 1.

Table 1

Pedigree number	Self-coloured		Highly ruled		Ordinary ruled		Plain		Total
	Num.	%	Num.	%	Num.	%	Num.	%	
2—6	0	0.0	1	2.0	17	24.5	50	73.5	68
2—7	2	3.8	1	2.4	9	16.4	41	77.4	53
2—8	1	1.9	2	4.5	6	10.6	44	83.0	53
Total	3	1.7	4	3.0	32	17.7	135	77.6	174

Here a high proportion of the ruled variants was obtained, amounting to an average of 20.7 percent. As stated before, the ruled variants bear flowers exhibiting various grades of variegation, almost continuously in a series. If, however, an artificial classification of the amount of variegation is admitted, we may group them into two classes, highly ruled and ordinary ruled; the former bears mostly self- or nearly self-coloured flowers, while the latter has variegated flowers of ordinary grades. In the data of Table 1, the contents of 20.7 percent of the ruled variants are 3.0 percent of the highly ruled and 17.7 percent of the ordinary ruled. Table 2 contains data obtained subsequently by selfing some plain individuals.

Table 2

Pedigree number	Self-coloured	Ruled	Plain	Total
2—1—2	1	2	11	14
2—1—3	0	6	10	16
2—6—1	0	0	27	27
2—6—2	0	6	15	21
2—7—1	0	1	16	17
2—8—1	0	0	21	21
2—8—2	0	7	16	23
Total	1	22	116	139
Percentage	0.7	15.8	83.5	100

In this generation the two ruled classes were not discriminated. Both self-coloured and ruled variants were again produced, though two pedigrees (Nos. 2—6—1 and 2—8—1) bred true to the plain flowers. Since the plain plants give rise almost invariably to self-coloured and ruled variants in their offspring, the stock is regarded as unstable duskish. The available data for the plain pedigrees bred so far are collected in Table 3.

Table 3

	Self-coloured	Ruled	Plain	Total
Observed	25	162	1762	1949
Percentage	1.3	8.3	90.4	100

The figures thus obtained may indicate the average percentages of the variants produced in the unstable plain pedigrees.

The ruled pedigrees

The ruled variants gave a higher proportion of self-coloured and ruled segregates in their progeny than the plain pedigrees (IMAI 1931 a), indicating the genetic difference of the ruled from the plain. The new data collected in 1931 are shown in Table 4.

Table 4

Pedigree number	Self-coloured		Ruled		Plain		Total
	Num.	%	Num.	%	Num.	%	
1	91	67.4	37	27.4	7	5.2	135
2	72	49.0	53	36.0	22	15.0	147
3	21	25.3	56	67.5	6	7.2	83
Total	184	50.4	146	40.0	35	9.6	365

Of three pedigrees, the mother plants of Nos. 1 and 2 were highly ruled and the other ordinary ruled, the former giving a higher ratio of self-coloured variants. In the next generation, the ruled variants which consequently appeared gave the results shown in Table 5 (page 245).

The highly-ruled variants gave a higher percentage of self-coloured mutants in the offspring compared with the ordinary ruled variants. This proves the genetic difference between the two types of variegation. The gene for the ordinary ruled character may be called ordinary-ruled, that for the highly ruled, highly-ruled; and that for the unstable plain, unstable-plain. Of the highly ruled pedigrees, group A gave a few plain segregates, whereas group B segregated a high proportion of them, amounting to 22.2 percent. The difference may be attributed to the different genotypes, the former being homozygous for highly-ruled and the latter heterozygous for highly-ruled and unstable-plain.

Table 5

Mother plant	Geno-typic group	Pedigree number	Self-coloured Num.	%	Highly ruled Num.	%	Ordinary ruled Num.	%	Plain Num.	%	Total
Highly ruled	A	1–2	25	64.1	6	15.4	7	17.9	1	2.6	39
		1–3	18	41.9	10	23.3	15	34.8	0	0.0	43
		1–4	33	64.7	10	19.6	8	15.7	0	0.0	51
		1–5	13	39.4	13	39.4	7	21.2	0	0.0	33
		Total	89	53.6	39	23.5	37	22 3	1	0.6	166
	B	2–1	17	25.8	10	15.2	21	31.8	18	27.2	66
		2–4	27	52.9	6	11.8	10	19.6	8	15.7	51
		Total	44	37.6	16	13.7	31	26.5	26	22.2	117
Ordinary ruled	A	2–2	4	10.5	4	10.5	28	73.7	2	5.3	38
	B	2–3	4	6.9	1	1.7	29	50.0	24	41.4	58
		2–5	5	8.1	0	0.0	15	24.2	42	67.7	62
		Total	9	7.5	1	0.8	44	36.7	66	55.0	120

Table 6

Mother plant	Genotypic group	Pedigree number	Self-coloured	Ruled	Plain	Total
Highly ruled	A	1–4–1	17	6	0	23
		1–2–1	15	0	2	17
		1–2–2	10	4	0	14
		1–2–3	18	3	0	21
		Total	60	13	2	75
		Percentage	80.0	17.3	2.7	100
	B	1–2–4	5	10	1	16
		Percentage	31.3	62.5	6.3	100
	C	2–1–5	16	16	12	44
		Percentage	36.4	36.4	27.2	100
Ordinary ruled	A	2–2–2	5	20	0	25
		Percentage	20.0	80.0	0.0	100
	B	2–1–1	5	10	8	23
		2–2–1	13	16	7	36
		2–2–3	3	15	13	31
		2–3–1	3	12	5	20
		2–1–6	12	12	10	34
		2–1–4	2	8	5	15
		Total	38	73	48	159
		Percentage	23.9	45.9	30.2	100

In the ordinary-ruled class, group A gave a higher ratio of self-coloured and highly-ruled variants, and a lower ratio of the plain duskish as compared with group B. This difference is supposed to be due to the different genotypes of their mothers, the former being homozygous for ordinary-ruled and the latter heterozygous for ordinary-ruled and unstable-plain.

Returning to the pedigrees listed in Table 4, No. 1 may be homozygous for highly-ruled, No. 2 heterozygous for highly-ruled and unstable-plain, and No. 3 homozygous for ordinary-ruled. Table 6 (pag. 245) contains data obtained last season.

Of these pedigrees, group A of the highly-ruled class may be homozygous for highly-ruled, group B heterozygous for highly-ruled and ordinary-ruled, and group C heterozygous for highly-ruled and unstable-plain; group A of the ordinary ruled class may be homozygous for ordinary-ruled and group B heterozygous for ordinary-ruled and unstable-plain. The respective results, however, were greatly disturbed by reversible mutations of the genes contained. Accepting the above assumption with reference to the genotypes of the ruled flowers, we have the final data shown in Table 7.

Table 7

Genotype	Number of pedigrees	Self-coloured		Ruled		Plain		Total
		Num.	%	Num.	%	Num.	%	
Homo. high.-rul.	9	240	63.8	126	33.5	10	2.7	376
High.-rul./ord.-rul. . . .	1	5	(31.3)	10	(62.5)	1	(6.3)	16
High.-rul./unst. pl. . . .	4	132	42.9	116	37.6	60	19.5	308
Homo. ord.-rul.	3	30	20.5	108	74.0	8	5.5	146
Ord.-rul./unst -pl. . . .	8	47	16.8	118	42.3	114	40.9	279

Excepting a heterozygous class, highly-ruled/ordinary-ruled, the respective cases contain a reliable number of progenies, although not adequate. The homozygous forms give a higher proportion of self-coloured variants and a lower ratio of plain ones compared with the heterozygous forms. A similar relation also holds between the highly-ruled and ordinary-ruled forms.

The self-coloured mutants

Though the highly-ruled variants bear many self-coloured or nearly self-coloured flowers, some plants bear self-coloured flowers throughout. Such self-coloured flowers appear in unstable-plain, ordinary-ruled, and highly-ruled pedigrees, although the proportions of these differed considerably. As stated in my previous paper (IMAI 1931 a), the progeny of three self-coloured variants were examined, when the data obtained showed their heterozygosity for plain. Since then only two self-coloured plants were tested, the results being shown in Table 8.

Table 8

Pedigree number	Self-coloured		Highly ruled		Ordinary ruled		Plain		Total
	Num.	%	Num.	%	Num.	%	Num.	%	
1—6	40	100.0	—	—	—	—	—	—	40
1—1	84	92.3	5	5.5	2	2.2	0	0.0	91

Both mother plants came from a grandmother homozygous for highly ruled. No. 1—6 showed its homozygosity for self-coloured, and No. 1—1 contained the gene highly-ruled heterozygously. The progeny of the homozygous self-coloured plants that were kept under examination for two generations bred true to type.

A near-stable plain stock RL

The culture of the unstable duskish pedigrees came from stock No. 361 a. Another duskish stock, known as RL in my culture, shows somewhat different behaviour as regards variability. The strain is characterized by rootletless (IMAI 1931 b), the pedigree culture for three years being shown by the data in Table 9.

Table 9

Yearage	Self-coloured	Ruled	Plain	Total
1931	0	0	58	58
1932	0	1	415	416
1933	0	0	86	86
Total	0	1	559	560
Percentage	0.0	0.2	99.8	100

Only one plant that was listed as ruled appeared as a variant in the pedigree culture of this strain. It was however a chimera, bearing plain and self-coloured flowers, the genetics of which will be dealt with later. The occurrence of a mosaic plant indicates the mutable tendency of stock RL, though the mutability is very low and the form is regarded as near-stable plain.

Crossing experiments

The different forms exhibited in the duskish variation are crossed with stock RL, which is nearly stable for the plain duskish. The results are collected in Table 10.

Reciprocal crossings gave nearly the same results. Hybridization generally resulted in a lower proportion of self-coloured variants and a higher proportion of plain, compared with cases of selfing. To ascertain this relation more clearly, a summary of data covering both pollinations are given in Table 11.

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Table 10

Hybridization		Self-coloured	Ruled	Plain	Total
♀♀ Unstable-plain ♂♂ Near-stable-plain	2–6–1 × RL	0	0	24	24
	2–6–2 × RL	0	3	10	13
	2–8–1 × RL	0	0	20	20
	2–8–2 × RL	0	2	19	21
	2–7–1 × RL	0	0	10	10
	Total	0	5	83	88
	Percentage	0.0	5.7	94.3	100
♀♀ Near-stable-plain ♂♂ Unstable-plain	RL × 2–6–1	0	0	36	36
	RL × 2–6–2	0	3	29	32
	RL × 2–8–1	1	0	38	39
	RL × 2–8–2	0	0	44	44
	Total	1	3	147	151
	Percentage	0.7	2.0	97.3	100
Total		1	8	230	239
Percentage		0.4	3.3	96.3	100

Group A; ordinary ruled parent homozygous

		Self-coloured	Ruled	Plain	Total
♀♀ Ordinary-ruled ♂♂ Near-stable-plain	2–2–2 × RL	3	7	0	10
	Percentage	30.0	70.0	0.0	100
♀♀ Near-stable-plain ♂♂ Ordinary-ruled	RL × 2–2–2	1	33	6	40
	Percentage	2.5	82.5	15.0	100
Total		4	40	6	50
Percentage		8.0	80.0	12.0	100

Group B; ordinary ruled parent heterozygous for unstable-plain

		Self-coloured	Ruled	Plain	Total
♀♀ Ordinary-ruled ♂♂ Near-stable-plain	2–1–1 × RL	4	7	7	18
	2–2–1 × RL	6	6	4	16
	2–2–3 × RL	0	3	8	11
	2–3–1 × RL	1	15	12	28
	Total	11	31	31	73
	Percentage	15.1	42.5	42.5	100
♀♀ Near-stable-plain ♂♂ Ordinary-ruled	RL × 2–1–1	1	12	15	28
	RL × 2–2–1	1	8	8	17
	RL × 2–2–3	3	15	27	45
	RL × 2–3–1	1	17	20	38
	Total	6	52	70	128
	Percentage	4.7	40.6	54.7	100
Total		17	83	101	201
Percentage		4.7	41.3	54.0	100

Table 10 (continued)

Hybridization		Self-coloured	Ruled	Plain	Total
Group A; highly ruled parent homozygous					
♀♀ Highly-ruled ♂♂ Near-stable-plain	1–4–1 × RL	16	2	0	18
	1–2–1 × RL	11	4	1	16
	1–2–3 × RL	10	4	0	14
	Total	37	10	1	48
	Percentage	77.1	20.8	2.1	100
♀♀ Near-stable-plain ♂♂ Highly-ruled	RL × 1–4–1	9	9	0	18
	RL × 1–2–1	5	9	5	19
	RL × 1–2–2	8	13	1	22
	RL × 1–2–3	5	8	1	14
	Total	27	39	7	73
	Percentage	37.0	46.6	9.6	100
Total		64	49	8	121
Percentage		52.9	40.5	6.6	100
Group B; highly ruled parent heterozygous for unstable-plain					
♀♀ Near-stable-plain ♂♂ Highly-ruled	RL × 1–2–4	1	14	5	20
	Percentage	5.0	70.0	25.0	100

Table 11

Genotype	Selfing			Crossing		
	Self-col. %	Ruled %	Plain %	Self-col. %	Ruled %	Plain %
Homo. unst.-pl.	1.3	8.3	90.4	0.4	3.3	96.3
Homo. high.-rul.	63.8	33.5	2.7	52.9	40.5	6.6
High.-rul./unst.-pl. . . .	42.9	37.6	19.5	(5.0)	(70.0)	(25.0)
Homo. ord.-rul.	20.5	74.0	5.5	(8.0)	(80.0)	(12.0)
Ord.-rul./unst.-pl, . . .	16.8	42.3	40.9	4.7	41.3	54.0

The percentages given in parenthesis being based on a rather small number of tests, too much importance should not be attached to it. In the respective cases, hybridization invariably diminished the proportion of the self-coloured variants and increased that of the plain. Plain stock RL therefore carries a different genotype from the ordinary unstable plain that were used to a considerable extent in my investigation. As already pointed out, stock RL is nearly stable with regard to flower colour. The gene carried by the stock may be called near-stable-plain. The heterozygosity for near-stable-plain therefore gives less chance for the production of self-coloured variants and a much greater one for the production of plain.

Variations of ruled flowers

Ruled plants bear flowers variegated in various grades, including mono-chromatic plain and self-coloured. Such variations exhibited in one and the same plant do not accompany any genic changes in the majority of cases. In Table 12 have been collected data obtained by selfing three selected plants which showed remarkable variation in the amount of variegation.

Table 12

Flower type		Self-coloured		Ruled		Plain		Total
		Num.	%	Num.	%	Num.	%	
1	Self- & near-self-col. .	17	77.3	4	18.2	1	4.5	22
	Highly-ruled	46	70.8	18	27.7	1	1.5	65
	Mixed	28	58.3	15	31.3	5	10.4	48
	Total	91	67.4	37	27.4	7	5.2	135
2	Highly-ruled	30	40.0	34	45.3	11	14.7	75
	Slightly-ruled	32	61.5	12	23.1	8	15.4	52
	Mixed.	10	50.0	7	35.0	3	15.0	20
	Total	72	49.0	53	36.0	22	15.0	147
3	Self- & near-self-col. .	8	57.1	5	35.7	1	7.2	14
	Highly-ruled	3	15.0	16	80.0	1	5.0	20
	Slightly-ruled	3	15.0	15	75.0	2	10.0	20
	Plain	7	24.1	20	69.0	2	6.9	29
	Total	21	25.3	56	67.5	6	7.2	83
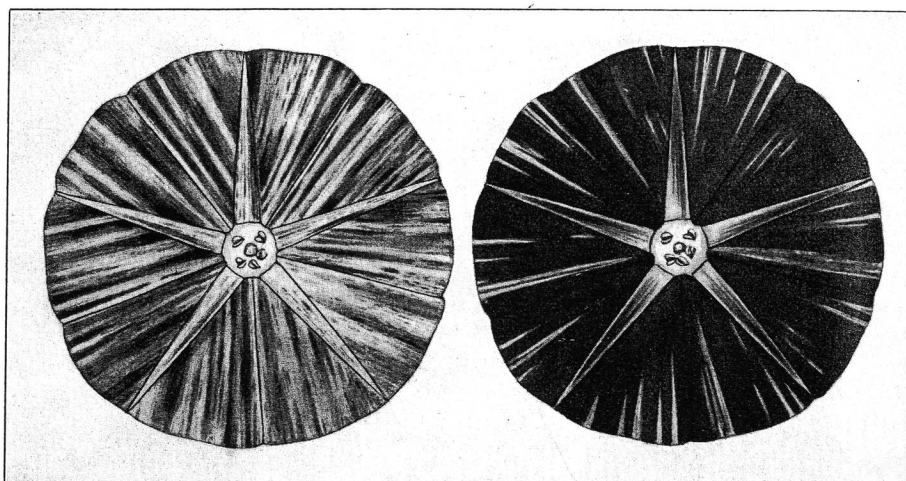
Fig. 1. Two ruled flowers with different amount of variegation. Dark parts represent normal-coloured areas and light parts the duskish background

The classification of the amount of variegation in the ruled flowers is arbitrary, there being no sharp distinction between the classes. The results in the offspring are practically the same in the different classes of the same mother plants. In the progeny of self- and nearly self-coloured flowers of No. 3, a high proportion of normal individuals made their appearance, but we cannot attach much importance to this owing to the small number that were examined. The difference, however, is rather conspicuous in the individual plant.

The variegation manifested in the duskish flowers is somewhat special in form, frequently showing fine dotted stripes or patches (Fig. 1), its variability in the same plants being accompanied generally by no genic changes.

Vegetative mutations

Rarely clear sectorial chimeras may occur in one plant, bearing plain flowers on some branches and self-coloured flowers on others. In such a case, mosaic flowers and branches are sometimes observed. Three mosaic plants attracted my attention during my field observations in 1932. Experimenting with them, I performed some self- and cross-pollinations, the data obtained being shown in Table 13.

Table 13

Pedigree number and flower type		Self-coloured	Ruled	Plain	Total
A; 2–6–3	Self-coloured . . .	20	2	11	33
	Plain	0	0	28	28
B; 2–7–2	Self-coloured . . .	21	0	10	31
	Plain	0	1	25	26
C; from RL	Self-coloured . .	1	0	16	17
	Plain	0	0	9	9
RL × A, self-coloured		11	1	12	24
RL × A, plain		0	0	15	15
RL × B, self-coloured		9	0	9	18
RL × B, plain		0	0	15	15
RL × C, self-coloured		0	0	18	18
RL × C, plain		0	1	11	12

Stock RL bears duskish flowers with a rather high constancy, for which reason it was used as a stable stock in the crossings. The two mosaic plants, Nos. A and B, were collected from ruled pedigrees. Both self- and cross-pollinations showed that the self-coloured variation transmitted their characters to the offspring, though they threw out some plain individuals as recessives. Consequently the vegetative variations that bore self-coloured flowers either contained at least two mutated, ecto- and meso-histogens (*Pharbitis* is considered to be developed from three histogens) or they consisted of homogeneous mutated

tissues. Only such forms of bud-variations should bear ordinary self-coloured flowers accompanying genic changes. In contrast to these, the self-coloured flowers of No. C did not inherit the character. This can be attributed to their special chimerical constitution, the mutated tissue being confined to the ecto-histogen, or epidermis. Such a form of periclinal chimera should bear similar self-coloured flowers. As was shown in the case of the other chimerical flowers of *Pharbitis* (IMAI 1931 a), these two periclinal types can be distinguished by their stem colours. In the present case, however, the stem colour of duskish flowers is also dark red as in the case of self-coloured flowers, so that their identification is possible only by inspecting their next generation. So far as my experiments are concerned, no other clear cases of vegetative mutations were observed in the duskish flowers.

The duskish allelomorphs and their reversible mutations

The data given in the preceding sections may lead to the inference that the five forms, self-coloured, highly-ruled, ordinary-ruled, unstable-plain, and near-stable-plain, constitute a set of multiple allelomorphs. In the ordinary cases of multiple allelomorphs, only two forms are segregated in the progeny propagated by selfing hybrids. As however the duskish allelomorphs frequently mutate from one to the other or *vice versa*, the other forms thus mutated are mixed together with segregates. Under such circumstances, the segregation is greatly complicated. The order of dominance is self-coloured, highly-ruled, ordinary-ruled, unstable-plain, and near-stable-plain. The lowest allelomorph, near-stable-plain, is nearly stable. The gene rarely mutated to the highest allelomorph, the self-coloured. In contrast to this, the gene unstable-plain mutates at times to its dominant allelomorphs, self-coloured, highly-ruled, and ordinary-ruled. In the pedigree culture of unstable plain stock, 1.3 percent self-coloured and 8.3 percent ruled were obtained, their occurrence being due to recurring mutations of unstable-plain to self-coloured and ruled respectively. The gametic contents of the unstable-plain are roughly estimated at 0.4 percent of the self-coloured, 3.3 percent of the ruled, and 96.3 percent of the plain (see Table 10). Table 1 contains 1.7 percent self-coloured, 3.0 percent highly-ruled, 17.7 percent ordinary-ruled, and 77.6 percent plain. This shows that a few highly-ruled individuals occur in the progeny of the unstable plain stock. From these figures, the gene unstable-plain seems to mutate most frequently to ordinary-ruled and next to highly-ruled and self-coloured. The production of highly-ruled in the plain pedigree may also be regarded as having been produced by the double mutations that successively occurred, thus unstable-plain → ordinary-ruled → highly-ruled, but this suggestion only complicates the case and diminishes the possibility of their occurrence. Since frequency of mutations, however, varies greatly according to pedigree culture, these figures may be regarded as rough indications of their mutability. It is not yet clear from our data whether mutation from unstable-plain to near-stable-plain occurs or not, but the former is probably the case. Since the homozygous ordinary-ruled plants gave 20.5 percent of self-coloured, 74·0 percent of ruled, and 5.5 percent of plain, the gene
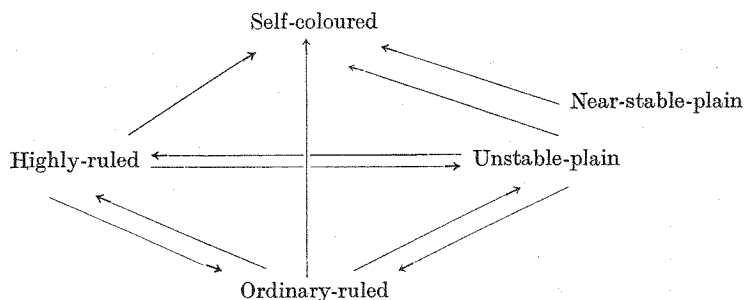
ordinary-ruled frequently mutates to self-coloured and to plain. In this case the self-coloured variants are due to dominant mutations, and the plain ones to recessive mutations, a proportion of 5.5 percent of the latter indicating a high mutation rate, owing to its recessiveness. Fragmental data so far examined showed that these mutated plain carry the gene unstable-plain. In crossing the homozygous ordinary-ruled with the near-stable-plain, 8.0 percent self-coloured, 80.0 percent ruled, and 12.0 percent plain were obtained, roughly indicating the contents of the gametes produced by the homozygous ordinary-ruled. The production of the highly-ruled roughly equalled that of the self-coloured in their frequency. The ordinary-ruled heterozygous for unstable-plain gave 16.8 percent of self-coloured, 42.3 percent of ruled, and 40.9 percent of plain. The crossing of the heterozygous ordinary-ruled with the near-stable-plain resulted in 4.7 percent self-coloured, 41.3 percent ruled, and 54.0 percent plain, the figures themselves indicating the contents of the segregated and mutated gametes produced by the heterozygous ordinary-ruled. In this case, the expected percentages of the three forms are 4.2 self-coloured, 41.65 ruled, and 54.15 plain. The figures, which closely agreed with those observed, were calculated by averaging the percentages of the corresponding cases of homozygous ordinary ruled and unstable plain.

The homozygous highly-ruled gave 63.8 percent self-coloured, 33.5 percent ruled, and 2.7 percent plain. The contents of the gametes are 52.9 percent, 40.5 percent, and 6.6 percent respectively, the figures having been obtained from crossing experiments. The gene highly-ruled therefore mutates very frequently to self-coloured and at times to plain (probably unstable-plain at least in the majority of cases), this being the most inconstant of the duskish allelomorphs. The highly-ruled and ordinary-ruled forms appeared nearly with the same percentage in the culture of the highly-ruled. Under such circumstances, only about 20 percent of the gametes produced by the homozygous highly-ruled are the original gametes carrying highly-ruled, the others being mutated gametes. In the ordinary-ruled the original gametes constitute about 70 percent, while in the unstable plain it remains at 96.3 percent. The highly-ruled heterozygous for ordinary-ruled gave 31.3 percent self-coloured, 62.5 percent ruled, and 6.3 percent plain; these figures were however calculated on the basis of only a small number of tests. The third form of the highly-ruled, which is heterozygous for unstable-plain, resulted in 42.9 percent self-coloured, 37.6 percent ruled, and 19.5 percent plain. The gametic contents are 5.0 percent, 70.0 percent, and 6.6 percent respectively, which estimation however is also based on only a small number of tests. Of these figures, the percentage of self-coloured is much lower than that expected from data obtained by culture of highly-ruled heterozygous for unstable-plain. As the distribution of self-coloured gametes in the homozygous highly-ruled amounted to 52.9 percent, the expectable percentage in this case is 26.45.

The highest self-coloured allelomorph may be mutated from its recessive allelomorphs with different frequency; very rarely from the near-stable plain, to the extent of about 0.4 percent from the unstable-plain, about 8.0 percent

from the ordinary-ruled, and about 52.9 percent from the highly-ruled. The gene itself however is quite constant and does not mutate at all.

The directions of the recurring mutations observed in the duskish allelo-morphs may be graphed as follows:

The recurring mutations in the three allelomorphs, highly-ruled, ordinary-ruled, and unstable-plain, are reversible; the frequency however, is different. The self-coloured allelomorph has only one way of mutating, it being mutated from, but not to, its recessive allelomorphs. The prototype of the allelomorphs is self-coloured, from which the recessive allelomorphs are derived directly or indirectly in the course of evolution under cultivation. The mutations, however, are sporadic in their occurrence. So far as examined, near-stable-plain mutated only to self-coloured, but I believe that when fully studied and observed on a large scale, it may be found that the gene mutates also to the other allelo-morphs.

The mutations generally appeared seminally; the vegetative ones were rather rare under my observation. Only those cases in which vegetative muta-tions occurred both from near-stable-plain and from unstable-plain to self-coloured are proved. So far as my examination goes, the variations exhibited in the flowers borne by the ruled, however, do not accompany any genic changes, though somatic mutations are still expected in these cases.

Conclusion and discussion

Since DE VRIES (1905) published his work on the variegated *Antirrhinum*, anthocyanin variegation has become useful in genetic analyses. General attention was called to it by the researches of CORRENS (1910) on *Mirabilis* and by EMERSON (1914) on *Zea*. A large quantity of published data on anthocyanin variegation has accumulated, the principal studies being *Antirrhinum* studied by BAUR (1914, 1930); *Zea* by EMERSON (1917), HAYES (1917), and EYSTER (1924, 1925, 1928); *Raphanus* by SÔ, IMAI, and TERASAWA (1919); *Celosia* by TERASAWA (1922), KANNA (1929), KOJIMA (1930), and KIHARA (1932); *Lathyrus* by PUNNETT (1922); *Pharbitis* by IMAI (1925, 1927, 1931a), and TERAO and U (1930); *Im-patiens* by KANNA (1926); *Amaranthus* by IMAI and KANNA (1927); *Portulaca*

by IKENO (1929); *Delphinium* by DEMEREC (1931); *Pisum* by DE HAAN (1931); *Mirabilis* by KANNA (1933); *Chrysanthemum* by MIYAKE and IMAI (in press); and others. Generally the labile genes are recessive to self-coloured, so that the recurrent mutations occur merely from recessive to dominant. In a few cases the mutations occur in the reverse way only; namely, from dominant to recessive (*Raphanus* and *Chrysanthemum*). The direction of the recurring mutation in these and other cases is one way, but sometimes it takes place in two directions, from the labile gene to its dominant self-coloured allelomorph and to its recessive plain allelomorph, the mutated genes generally being·constant (*Mirabilis*, *Zea*, *Lathyrus*, and *Impatiens*). In certain cases of *Zea* and *Celosia*, the mutated self-coloured genes are mutable, altering into the mutable variegated allelomorph, from which the self-coloured is mutated. Since in these cases, the mutable self-coloured gene (inconstant self-coloured) differs from the constant self-coloured, the mutation from variegated to inconstant self-coloured is not a reversion in the strict sense.

The anthocyanin variegation in general is well elucidated by the mutable genes with given behaviour and mutability. The anthocyanin flecks being due to recurrent mutations, the times when it mutated may be inferred from their size. If mutation occurs at an early stage of plant ontogeny, a larger self-coloured part will appear on the sporophyte, sometimes putting out bud-variations, but should it occur at a late stage, a smaller fleck is exhibited. Although the mechanism of bud-variation is now made clear, a full account of it is deferred till another occasion. CHITTENDEN (1927) attempted to explain anthocyanin variegation by plastid inheritance, but his suggestion is fundamentally irrational, anthocyanin and chlorophyll variegations being manifested by different substances.

The results of duskish have been examined and its general behaviour explained in the foregoing, which however may not yet be thoroughly satisfactory because of the fact that the variegation was by nearly continuous differences in amount and because the variants produced in the plain and ruled pedigrees vary considerably in their rate of occurrence in each case. When strictly viewed, the variegation seems to be manifested in a series graded from near-stable plain to highly ruled or to near-self-coloured, the matter being presented as follows:

Near-stable-plain   Unstable-plain   Ordinary-ruled   Highly-ruled   Self-coloured

$$dk^{ns}, \quad dk^{ns\prime}, \qquad dk^{us}, \quad dk^{us\prime}, \qquad dk^{or}, \quad dk^{or\prime}, \qquad dk^{hr}, \quad dk^{hr\prime}, \qquad Dk \ (or +)$$

Tentatively two gradations are presented in each form, a dash indicating a higher grade of variegation than the standard. These grouping genes constitute together a set of multiple allelomorphs with the normal. The grouping genes dk^{ns} ... $dk^{hr\prime}$ are mutable, changing one to another reversibly, and to, but not from, the normal. The theoretical substance in regard to mutual changes in the duskish allelomorphs can then be roughly denoted by a general formula as follows:

$$a^1, \ a^2, \ a^3, \ a^4, \ \ldots\ldots\ldots\ldots\ldots \ a^n, \ A^c \ (+)$$

The respective genes are arranged in a graded series according to the diffe-
rent average extent of variegation from a^1 (near-stable) to a^n (near-self-coloured),
including the constant form (A^c). In the duskish allelomorphs, we have not
yet positively found a constant plain duskish (a^c) and inconstant self-coloured
(A^i). The recurring mutations may occur reversibly in the grouping genes from
dk^1 to dk^n, step by step to the next grades or at a bound to the others. The
mutations generally made their appearance seminally in the duskish complex.

Studying the variegated pericarp of maize, EYSTER (1925, 1928) formulated
his genomere theory, which rests on the random assortment of contrasting geno-
meres at somatic mitosis. Though the genomere theory seemingly accounts
for the complicated inheritance of variegation, certain objections arise, as have
been pointed out by DEMEREC (1931) and DE HAAN (1931). The variegated maize
however can be completely accounted for by the theory presented in connection
with the duskish *Pharbitis*. The white (or variegated) allelomorphs of maize
are composed of some series of grouping genes from white to self-coloured. If it
is admissible to collect data from different sources, as published by EMERSON,
HAYES, EYSTER, and other workers, and to try to represent it collectively, the
grouping genes may be expressed by the following scheme:

$$a^c, \; a^1, \; a^2, \; a^3, \; a^4, \; \ldots \ldots \ldots a^n, \; A^i, \; A^c \; (+)$$

The gene a^c is constant white, $a^1 \ldots a^n$ are responsible for the graded
series to the amount of variegation or different frequency of mutation, A^i re-
presents inconstant self-red and A^c (+) the constant self-red. EMERSON (1917)
reported a case in which the reverse mutations occurred from self-red to varie-
gated. In this case, however, the self-red, which had appeared by a mutation
from the variegated, is regarded as an inconstant self-red (A^i), though the pheno-
type may be ordinary self-coloured. These grouping genes constitute together a
set of multiple allelomorphs. The variegation is exhibited by the grouping genes
from a^1 to a^n, the recurring mutations from one to the other occurring reversibly.
When the recurrent mutations mostly occur step by step from one to the next
grade in the allelomorphic series, the 'segregation' in the progeny of the variegated
maize will be almost continuous, with the larger frequency in the average classes
and smaller frequency in the deviated classes. EMERSON (1913, 1917) and HAYES
(1917) also considered that the variegated complex is composed of some graded
allelomorphs.

After presenting his genetic data of the *albovariabilis* form of *Capsella
Bursa pastoris*, CORRENS (1919) summed up the results as follows: „Die *albo-
variabilis*-Sippe vererbt ihre Weißbuntheit nach den MENDELschen Gesetzen,
ist aber nicht konstant, sondern veränderlich. Durch Auswahl mehr weißer oder
mehr grüner Pflanzen oder entsprechender Äste einer Pflanze als Samenträger
läßt sich eine Verschiebung der durchschnittlichen Färbung der Nachkommen-
schaft erzielen, die auf der einen Seite bis konstantem Grün geht, auf der andern
Seite, vielleicht nur aus technischen Gründen, nur bis zu einer stark weißen

Durchschnittsfärbung, die durch gleichgerichtete Auswahl auf derselben Höhe gehalten werden kann. Solange noch keine Konstanz (homogenes Grün) erreicht ist, kann die Selektion hin und her betrieben werden; die Zwischenstufen sind nicht fixiert worden". The case seems also to be fully explained by my idea. If we represent the most whitish form (least mutable white) of *albovariabilis* by a gene a^1, the near-green (most mutable white) by a^n, the inconstant green by $A\,i$, and the constant green by A^c (+), with certain intermediate grades, the general formula may be expressed by

$$a^1,\ a^2,\ a^3,\ a^4, \dots\dots\dots\dots\dots\dots\ a^n,\ A^i,\ A^c\ (+)$$

The main feature of the variable proportions of the recessive *albovariabilis* segregates in the hybrid progeny are regarded as due to different rates in the mutations from *albovariabilis* to green. In the heterozygotes for *typica* (constant green or A^c) and *albovariabilis*, the *albovariabilis* complex seems to mutate more frequently. In this case however the grouping genes manifest chlorophyll variegation.

In his experiments with the variegated form of *Celosia*, KIHARA (1932) took the view that his variegated form had a tendency to 'Stabilisierung' to the constant yellow, passing through certain gradations. His idea, when substantiated with more data, seems to come under some such general expression as follows:

$$a^c,\quad a^1,\quad a^2,\quad a^3,\quad a^4, \dots\dots\dots\dots\dots\dots\dots\dots\ a^n,\ A^c\ (+)$$

In the above formula the multiple allelomorphs are arranged in a series according to the rate of mutability, from constant (a^c) to the most inconstant (a^n), including constant self-coloured (A^n). His 'Stabilisierung' from variegated to yellow is graphed by the upper arrow, and the recurring mutations of the variegated grouping genes are greatly affected by a^c (his a_k) in its heterozygous state. The lower broken arrow under the formula indicates the reverse mutations toward self-red, but it is not clear whether or not the transitional mutations repeatedly occur from higher mutability to lower.

A painstaking work on *Malva parviflora* completed by LILIENFELD (1929) is cited here in connection with these cases. According to her experiments, the *laciniata* form of *Malva* frequently makes 'Zustandsänderung' toward *hypernormal* (no²). The changes are more frequent and rapid in the hybrids heterozygous for no². The substance of the graded series from *laciniata* (a^1) to *hypernormal* (A^c) may be represented by a general formula as follows:

$$a^1,\ a^2,\ a^3,\ a^4, \dots\dots\dots\dots\dots\dots\ a^n,\ A^c\ (\mathrm{no}^2)$$

The graded genes (Zustände) constitute together a set of multiple allelomorphs with *hypernormal* and *normal*, and they are mutable, changing towards *hypernormal*, generally step by step but sometimes at a bound (an arrow under

the above formula shows this). The mutations towards the stable *hypernormal* are so frequent that the 'segregation' is apparently 'non-Mendelian'.

ANDERSSON (1930) published the results of her laborious investigation on the variegated fern, *Polystichum angulare*. Summing up the main results, she states that "The changes (mutations) from green to pale green in different cells are considered to be due to changes in a factor determining chlorophyll development, this factor being assumed to exist in seven different states (C, c_1—c_6). The factor in each state is either stable or unstable. The instability consists in change (mutation) from one state to another at various stages of the life cycle, the factor in each state having its characteristic mode of activity". In this plant it is possible to investigate "the effect and behaviour of factors in their single state in the haploid somatic cells of the gametophyte", and since "the mode of development of the prothallium is extremely regular and simple", it is possible to "determine precisely in what cell and at what stage of development mutation from green to white or *vice versa* occurred" by inspecting the variegation on a prothallium. Her seven 'states' are translated to seven grouping genes consisting of a set of multiple allelomorphs. Of these genes, two are stable and five unstable, each of the latter having a definite mode of mutability.

In the above statements I have, to simplify matters, arranged several grouping genes in a series. The substance of the genes being a complicated organic unit, variegation may occur in various ways but not in single series (for instance, *Zea* by ANDERSON 1924). The exact number of the grouping genes is not clearly determined in these cases, except in *Polystichum*. The simplest cases involve only two allelomorphs, one mutable and the other self-coloured. The next cases involve three genes, constant-plain, inconstant-plain (or variegated), and self-coloured, the three constituting triple allelomorphs. Further complicated cases are those above discussed. In such cases, some authors called the grouping genes 'Zustände' or 'states'. If these terms are more adequate, all grouping genes or at least those unstable should be expressed in the same way. When all the grouping genes are constant (not mutable), the graded series of allelomorphs are inherited simply and segregated typically, as for instance in the white eye-colour allelomorphs of *Drosophila melanogaster*. According to DEMEREC (1928), the yellow body-colour allelomorphs of *Drosophila virilis* are composed of four genes, including mutable magenta-alpha. The 'Pal-Serie' for the flower colour of *Antirrhinum* consists of nine allelomorphs, of which one is mutable and the others constant (BAUR 1930). These instances are associated with the complicated cases in which some or several mutable genes occur in a compound set of multiple allelomorphs. KIHARA (1932) analyzed four genes, forming quadruple allelomorphs, one of them being mutable yellow or variegated, possibly composed of some grouping genes. In *Zea*, ANDERSON (1924) found nine allelomorphs for the colour of the pericarp and cob, of which two (composed of many grouping genes) are mutable and the others constant. The total number of the allelomorphic genes is considered to be much greater than this.

The variegation exhibited in duskish flowers requires an additional explanation for its 'fluctuating' variability. Before discussing the problem, however, I shall have to criticise DE HAAN's hypothesis (1931) formulated in connection with his experiments with the variegated flowers of *Pisum*. His purple-dotted stock gives rise to purple and purple-dotted variants as well as purple-patched in its progeny. The purple variants are due to recurring mutations from recessive to dominant in their occurrence. Since the purple-dotted variants breed true to type in the subsequent generation, the character is regarded as a pattern in its manifestation. On selfing, the purple-patched repeatedly produced the variants in various proportions. In crossing the patched with the white, which is recessive to the former and constitutes together triple allelomorphs with their dominant purple, he obtained different results from both reciprocal matings. The crossing, patched ♀ × white ♂, gave similar results to the case of selfing the patched, whereas its reciprocal hybridization, white ♀ × patched ♂, gave purple and purple-dotted, no ordinary purple-patched being observed. To account for the results, DE HAAN wrote that "The colourless cells of the patched form have the constitution A_2A_2, the plasm of these cells being labile. The purple cells have the constitution AA_2, and the purple dotted parts the constitution A_2A_2, the plasm being normal. From this hypothesis it follows that if the plasm of an AA_2 plant continues labile and no change occurs in the factor A_2, the flowers will be colourless, that is white. Such plants have repeatedly been observed: they could, however, be distinguished from white aa form by their patched leaf axils. Most plants with labile plasm showed purple patches as a result of the factor mutation $A_2 \to A$. Moreover dotted parts appeared as a result of the transition of the labile plasm to normal plasm. Purple-dotted and purple-patched are fundamentally different. Purple-dotted is a pattern of genetically equal parts, purple-patched on the other hand consists of a mosaic of genetically different parts. The labile plasm furthers the mutation of $A^2 \to A$." According to his hypothesis, the respective parts of the mosaic flowers which is originally 'A_2A_2 with labile plasm' are

Genetic complex	Flower colour
A_2A_2 + labile plasm	Colourless
A_2A_2 + normal plasm	Purple-dotted
AA_2 + labile plasm	Purple
AA_2 + normal plasm	Purple

In my opinion, his hypothesis is not adequate to account for all his results. His Table 13 contains data of 26 pedigrees of the purple-dotted peas, the proportion of the 'segregation' forms being very variable. In this case, the purples are mutants and they are produced by alternation of the patched. Therefore, they may be added to the number of the patched in comparing it with the purple-dotted to know the proportion of occurrence of purple-dotted variants in the respective pedigrees. Thus the percentage of the dotted is calculated in the pedigrees and are arranged according to their percentages.

Class (%)	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
Frequency	1	1	3	3	2	2	4	3	0	0	1	2	0	1	1	1	0	1

The frequency covers a wide range, from 7 percent to 90 percent. A close inspection, however, reveals the fact that the pedigrees are crowded in classes 4—40 %, while the others are scattered between classes 55 % and higher. This seems to call for some special explanation. I take this opportunity of submitting my hypothesis for his patched peas. The white allelomorphs of the peas consist of white (a), dotted-constant (a^c), dotted-inconstant (a^i), and purple $(A$ or $+)$, the former being recessive to the latter. Of these genes, a^i is auto-mutable, frequently changing to two directions a^c and A. Owing to this, the inbred patched peas may contain some individuals heterozygous for dotted-constant, the homozygotes giving small proportions (5—40 %) of the mutated purple-dotted in the progeny, and the heterozygotes high proportions (55—90 %), which include segregates and mutants. The property of the plasm is considered to be different in the patched and white peas. The plasm contained in the patched stock greatly stimulates the mutability of the gene a^i, whereas that of the white is less stimulating. The gene dotted-inconstant that is working in the less stimulating plasm may give slightly purple-patched individuals as well as the purple-dotted with purple bud-variations. Therefore the reciprocal matings of the purple-patched and white give different results. So far as his data are concerned, the above view amply covers all the facts presented.

The mosaic ears of *Amaranthus paniculatus* (IMAI and KANNA 1927) gave nearly similar progeny with the 'white' ears, the population being a mixture of 'white', mosaic, and red, with the 'white' predominating. The red ears, which appeared as seminal variants from the 'white' or mosaic pedigrees, also breed in the subsequent generation in much the same way. A recent experiment seems to indicate that the red (not the false red cited above), the variegated (or 'white'), and the green (without red colour) constitute a set of multiple allelomorphs. Therefore the mosaic or 'white' character is due to a gene manifesting the variability. The gene seems to set the plasm into a labile condition, manifesting the 'white' ears which are liable to change to red. Should the plasmic changes occur in the somatic cells, then the mosaic ears will be exhibited, whereas changes in gametogenesis result in red-eared individuals as seminal variants. These forms, both red and mosaic, are the same in their genic constitution as the 'white' ears, therefore in the main, their progeny is the same as in the type of population. The gene responsible for the 'white' makes the plasm labile, which, under the control of the gene, changes the ability of anthocyanin formation in the cell-sap. The gene itself, however, does not change, unlike the cases of common variegated. The potency hypothesis presented in our previous paper, therefore, is replaced by the above conception. Full details will not be given here until further investigations on the variegated *Amaranthus* are completed and published.

I shall now return to the duskish *Pharbitis*. In the respective duskish individuals, the considerable variation in the amount of variegation does not generally accompany a heritable change. It seems that the variable expression of variegation on the flowers of a given ruled individual is effected by the plasm under the control of the genes carried by the stock, generally without any changes

in the genes themselves.   The changed plasm is distributed in the sporophyte through cell-division, exhibiting mosaic flowers with different degrees of variegation.   In *Amaranthus*, only one gene that controls the changing manifestation of the plasm is found at present, whereas in *Pharbitis* a series of such genes are detected.   The changed plasmic manifestation seems to be renewed, possibly, during the gametogenesis in the duskish *Pharbitis*, as well as in the variegated *Amaranthus*.   As stated before, the plasm affects the mutability of the gene for the dotted-inconstant character in *Pisum*, giving a somewhat different case to *Pharbitis* and *Amaranthus* in the relation of the gene and plasm.   The variegation in the duskish flowers appears frequently as a finely dotted pattern, which seems to be due to the discontinuous expression of the plasm in the successive cells. In some self-coloured flowers of other plants, some colourless cells occur in the red epidermis of corollas.

A mutant character male-sterile-2

In observations of my own cultures of the Japanese morning glory, several different forms of male sterility have appeared through sporadic mutations. One of them, named male-sterile-1, is transmitted as recessive to the normal and considered to be located in the variegated chromosome (IMAI 1933).   In a ruled duskish pedigree, another form, male-sterile-2 (ms 2), occurred, in 1932, by mutation in the manner as shown in Table 14.

Table 14

Pedigree number	Normal	Male-sterile-2	Total
2–1	53	13	66

The male-sterile-2 character segregated in a recessive ratio.   The mutants have somewhat small leaves and bear small flowers with abortive anthers.   The anthers at times contain good pollen.   Last summer an observation of the subsequent generation was made, the recorded data being given in Table 15.

Table 15

Pedigree number	Normal	Male-sterile-2	Total
2–1–1	23	—	23
2–1–2	12	2	14
2–1–3	14	2	16
2–1–4	11	4	15
2–1–5	35	9	44
2–1–6	27	7	34
Total	99	24	123

On account of the sterility of the staminate organs, the table contains only the progeny of normals. The data prove the simple recessiveness of male-sterile-2, though a deficit of segregates was observed.

Summary

1. The duskish allelomorphs are composed of at least five genes, according to the order of their dominance, being arranged as self-coloured (normal or prototype), highly-ruled, ordinary-ruled, unstable-plain (ordinary-duskish), and near-stable-plain. Excepting the normal allelomorph, they are mutable, the rate of mutability however being different.

2. The unstable plain gives 1.3 percent self-coloured, 8.3 percent ruled, and 90.4 percent plain in the progeny, the appearance of the first two forms being due to recurring mutations. The ruled mutants are predominantly ordinary ruled, but include a few highly ruled.

3. The near-stable plain, which however is nearly constant, rarely mutates.

4. The homozygous ordinary-ruled results in 20.5 percent self-coloured, 74.0 percent ruled, and 5.5 percent plain in the offspring, the occurrence of the self-coloured and plain being due to the mutable nature of the gene ordinary-ruled. The heterozygous ordinary-ruled throw out a smaller proportion of self-coloured mutants than the homozygous ones.

5. The homozygous highly ruled gives rise to a larger proportion of self-coloured mutants, reaching 63.8 percent, and a smaller ratio of plain variants reaching 2.7 percent. The heterozygous highly-ruled gives rise to a smaller percentage of self-coloured offspring.

6. The self-coloured mutants, when they become homozygous, breed true to type; or in other words, the gene self-coloured is perfectly constant.

7. Three forms, highly-ruled, ordinary-ruled, and unstable-plain, were crossed with near-stable-plain, when nearly the same results in both reciprocal matings were obtained. In the respective cases, compared with the selfing, hybridization invariably diminishes the proportion of the self-coloured variants and increases that of the plain ones.

8. Examination proved that the variation exhibited in the ruled flowers of one and the same plant does not generally accompany any genic changes.

9. Rarely the plain duskish put out bud-variations with self-coloured flowers, the appearance of which is due to vegetative mutations from near-stable-plain or unstable-plain to normal.

10. The gametic contents of the unstable-plain are estimated to be 0.4 percent of the self-coloured, 3.3 percent of the ruled, and 96.3 percent of the plain. The majority of the ruled gametes carries the gene ordinary-ruled and some have the gene highly-ruled. The percentages are 52.9, 40.5 and 6.6 respectively in the homozygous highly-ruled. In the homozygous ordinary ruled, the frequency of the self-coloured diminishes and that of the plain increases, as compared with the ordinary ruled.

11. So far as the three genes, unstable-plain, ordinary-ruled, and highly-ruled are concerned, the recurring mutations are reversible.

12. Strictly viewed, however, the graded series of variegation in the duskish flowers seems to be due to many more grouping genes. The theoretical substance of the duskish allelomorphs therefore is roughly expressed by the following general formula:

$$a^1, \; a^2, \; a^3, \; a^4, \; \ldots\ldots\ldots\ldots\ldots\ldots \; a^n, \; A^c \; (+)$$

13. The complexity found in *Zea, Capsella, Malva, Polystichum,* and *Celosia* may be elucidated by applying the view above-proposed.

14. The rôle of the plasm in the manifestation of the anthocyanin variegation is considered in connection with the 'fluctuating' expression of the ruled flowers.

15. A recessive mutant character, male-sterile-2, is described.

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