THE PIPY FLOWER OF *PHARBITIS NIL* AS A MUTABLE CHARACTER.

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(With Plates V and VI and One Text-figure.)

Up to the present twenty genes with various degrees of lability have been discovered in the Japanese morning glory, *Pharbitis Nil* (Imai, 1934). These genes, contained in seventeen loci in certain chromosomes, are called contracted, cream, delicate, dotted, near-stable duskish, unstable duskish, ordinary ruled duskish, highly ruled duskish, flecked, lobeless, miniature-inconstant, pine-inconstant, pipy, purple, speckled, willow, wrinkled, xanthic, yellow-inconstant, and yellowy. The mutable behaviour of these genes has been made clear by the following investigators: willow by Imai (1925) and Tabuchi (under preparation), delicate by Imai (1927*a*) and Tabuchi (under preparation), pine-inconstant by Imai (1927*a*) and U (1930), yellow-inconstant by Imai (1927*b*, 1930, 1934) and Miyazawa (1929, 1932), flecked by Imai (1931, 1934), duskish by Imai (in press), and others by Imai (1927*a*, 1934), Terao and U (1930), etc. Some of the mutable genes operate in connection with the anthocyanin and chlorophyll distributions, and others with the morphological characters that affect the leaves and flowers. Of the latter, contracted, delicate, miniature-inconstant, pine-inconstant, and willow affect the foliage and floral parts, pipy and wrinkled the flower only, while lobeless, according to Terao and U (1930), affects the leaves.

The origin of the pipy flower.

In 1931 pipy flowers appeared *en masse* by spontaneous mutation in an F_2 pedigree as a simple recessive, the data being shown in Table I.

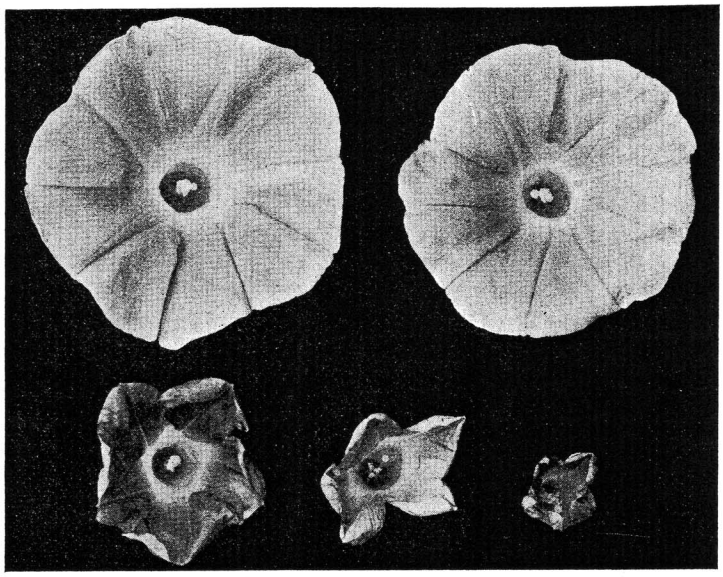
TABLE I.

Mutation record of the pipy flower: F_2 from cross, RL × A 50.

Number of pedigrees	Normal	Pipy	Mosaic pipy	Total
4	624	—	—	624
1	117	21	2	140

The F_2 tests resulted in the sporadic segregation of the pipy flower which has a tubular corolla of small size (Plate V, fig. 2 and Text-fig. 1). The growth of the corolla is stunted through defective growth of the

sutural parts of the petals, crumpling the corolla, which curves inward and forms a tubular flower. The fertility of the pipy flower is very low. Out of twenty-three pipy plants, two mutated vegetatively to crinkled normal, the result being mosaic. As will appear in more detail later, pipy, which is recessive to normal, is automutable, and at times changes to normal in the course of somatogenesis of the pipy sporophytes. These two mosaics are evidently due to the unstable nature of pipy.



Text-fig. 1. Normal (upper left), heterozygous, crinkled normal (upper right), enlarged pipy (lower left), less-enlarged pipy (lower middle), and pipy (lower right).

From the fact that the pipy character did not segregate in the parental stocks of the cross, and that only one out of the five F_2 pedigrees segregated this character, it is believed that the pipy flower appeared by spontaneous mutation, most probably by the union of a mutated gamete furnished, by one of parents, with a normal gamete, so that an F_1 plant heterozygous for pipy was produced.

Experimental results.

In 1932 some F_3 offspring from the mutated pedigree were raised with the object of examining the genetic behaviour of the pipy flowers. Table II shows the results obtained.

Although the simple recessiveness of the pipy character to the normal is apparent, a marked deficit in the pipy segregates was generally noted. The pipy flowers, instead of breeding true to type in the subsequent generation, produced also some crinkled normals. The occurrence of the crinkled normal and mosaic plants in the pipy pedigrees is attributed to the seminal and vegetative mutations that occurred from pipy to normal. In the Japanese morning glory, the recurrent seminal mutation

TABLE II.

F_3 from the mutated pedigree.

Mother plant	Pedigree No.	Normal	Pipy	Mosaic pipy	Total
Normal	9 pedigrees	338	—	—	338
	1	14	3	—	17
	5	45	7	1	53
	10	39	3	—	42
	14	8	2	—	10
	15	38	10	—	48
	Total	144	25	1	170
Pipy	12	2	8	3	13
	16	1	3	—	4
	Total	3	11	3	17
Mosaic pipy—crinkled normal	17	10	1	—	11

TABLE III.

F_4 data for pipy.

Mother plant	Pedigree No.	Normal	Pipy	Mosaic pipy	Total
Crinkled normal	1–1	25	8	1	34
	1–2	17	1	—	18
	5–1	13	5	2	20
	12–1	6	2	—	8
	12–2	14	7	1	22
	Total	75	23	4	102
Mosaic pipy—crinkled normal	5–2	20	1	2	23
	12–3	21	3	—	24
	12–4	24	5	—	29
	Total	65	9	2	76
Mosaic pipy—enlarged pipy	12–5	14	1	3	18

accompanies vegetative mutation which affects certain parts of the sporophytes, generally in their early ontogeny. The two mosaics that appeared in 1931 were selfed, but offspring were raised only from the normal branches of a mosaic plant, the data showing the heterozygous constitution of the mutated, normal flowers.

In 1933 flowers of the F_4 generation were placed under observation with results shown in Table III.

The normal flowers that are heterozygous for pipy (Plate V, fig. 3 and Text-fig. 1) have somewhat crinkled corollas on account of the slight

cramping that occurs at the sutural parts of the petals—a characteristic that distinguishes them from the homozygous normal flowers (Plate V, fig. 1 and Text-fig. 1), the identification of which however is not always easy. The progenies of five crinkled normals that were tested resulted in simple monogenic segregation for pipy. Two (Nos. 12–1 and 12–2) of

TABLE IV.

F_5 data for pipy.

Mother plant	Pedigree No.	Normal	Crinkled normal	Mosaic crinkled normal	Pipy	Mosaic pipy	Total
Normal	4 pedigrees	129	—	—	—	—	129
Crinkled normal	1–1–1	14	29	—	11	3	57
	1–1–2	14	26	1	7	3	51
	1–2–1	10	12	2	4	1	29
	5–2–1	13	19	—	2	2	36
	12–4–1	7	11	—	8	1	27
	12–4–2	2	5	—	1	1	9
	12–4–3	4	13	—	0	1	18
	12–4–4	16	42	—	7	1	66
	12–2–1	10	20	—	6	1	37
	12–5–1	13	22	2	9	2	48
	Total	103	199	5	55	16	378
Pipy	1–1–3	—	—	—	3	—	3
	1–1–4	—	—	—	2	2	4
	1–2–2	—	—	—	2	—	2
	5–1–1	—	—	1	23	1	25
	5–1–2	—	4	—	1	—	5
	5–2–2	—	2	—	46	7	55
	5–2–3	—	—	—	8	6	14
	5–2–4	—	—	—	2	—	2
	12–3–1		—	—	5	1	6
	12–4–5	—	—	—	3	—	3
	12–1–1	—	—	—	5	—	5
	12–2–2	—	—	—	3	2	5
	12–2–3	—	—	—	22	2	24
	Total	—	6	1	125	21	153
Mosaic pipy— enlarged pipy	12–5–2	6	16	2	6	3	33
	12–5–3	2	8	—	3	3	16
	Total	8	24	2	9	6	49
Mosaic pipy— less-enlarged pipy	5–1–3	—	—	—	5	1	6
	12–5–4	—	—	1	4	1	6
	Total	—	—	1	9	2	12

these five were seminal mutants that occurred in a pipy pedigree. Four mosaics that appeared in F_3 were

No. 5–2. Pipy resulted in bud-variation to crinkled normal.

No. 12–3. The same.

No. 12–4. Excepting a few pipy flowers, nearly every flower bloomed into crinkled normal.

No. 12–5. Almost all the flowers bloomed into enlarged pipy.

Examination showed that the crinkled normal sports that occurred

on the pipy plants were heterozygous for pipy, segregating normal and pipy in a monogenic ratio. The enlarged pipy (Plate VI, fig. 7 and Text-fig. 1) also gave the same results, so far as the progeny test was concerned. Owing probably to unfavourable conditions during that season, bagging the pipy plants and the pipy flowers of the mosaic plants gave no seeds in F_3.

Continued cultivation of pipy in 1934 gave the data of Table IV.

While the general results substantiate the former data, some explanation is necessary in regard to the tests of mosaic plants. This season, two types of sports, an enlarged pipy and a less-enlarged pipy, were placed under observation. The results in the case of the enlarged were identical with those of previous tests: pipy segregates were thrown out as recessives. The less-enlarged pipy, which blooms into somewhat opened, tubular corollas (Plate VI, fig. 5 and Text-fig. 1), bred just like the pipy.

THE MUTABILITY OF PIPY.

As already mentioned, the pipy flowers have low fertility: fifteen plants gave in all only 170 offspring, as follows:

	Crinkled normal	Pipy	Mosaic pipy	Total
Observed	10	136	24	170
Percentage	5·9	80·0	14·1	100

The progeny includes 5·9 per cent. crinkled normals heterozygous for pipy, so that about 2·9 per cent. of the gametes produced by the pipy flowers carried the mutant, normal allelomorph. The pipy plants frequently exhibit vegetative mutation to normal, becoming themselves mosaic in various chimerical forms. Seeing that the occurrence of mosaic pipy amounted to 15 per cent. of the total pipy, the pipy gene is very labile, changing frequently to the normal allelomorph.

THE SEGREGATING RATIO.

Owing to the mutable nature of the gene, the proportion of pipy segregates in the heterozygous pedigrees should be below normal expectation. In four generations, the pipy segregates occurred as follows:

Year	Number of pedigrees	Normal	Pipy	Total	Pipy %
1931	1	117	23	140	16·4
1932	5	144	26	170	15·3
1933	5	75	27	102	26·5
1934	10	307	71	378	18·8
Total	21	643	147	790	18·6

Except in the 1933 data, proportionally speaking, the pipy segregates showed a remarkable deficit, averaging only 18·6 per cent., instead of the expected 25 per cent. To give such a percentage, it is calculated that 13·8 per cent. of the pipy gametes were mutant normals. This figure however is much larger than that calculated in the case of the pipy pedigrees.

In the 1934 observation, crinkled normals were recorded separately from normals, resulting in 199 and 103, respectively, a ratio of nearly 2 : 1.

Vegetative mutation and chimeras.

The tests of vegetative mutation are shown in Tables II–IV. The sports occurred in three ways on the pipy plants, and in one way on the crinkled normals. The former three were crinkled normal (Plate VI, fig. 6), enlarged pipy (Plate VI, fig. 7 and Text-fig. 1), and less-enlarged pipy (Plate VI, fig. 5 and Text-fig. 1). These types sometimes occurred as apparently seminal mutants—almost, if not all, the flowers bloomed into monotype. Such plants, however, are regarded as mosaics, in which vegetative mutation arose early during embryonic ontogeny, and the mutated parts overpowered the original tissues. Sometimes mosaic flowers (Plate VI, fig. 8) bloomed on a mosaic plant. The enlarged pipy flowers, when selfed, gave rise to normal and pipy segregates according to a monogenic ratio (see Tables III and IV), whereas the less-enlarged pipy bred like the pipy (see Table IV). The crinkled normal sports, in their progeny tests, behaved like heterozygous normals (see Tables II and III). It is clear from these results that the enlarged pipy is the pipy with mutated, normal meso-histogen, and that the less-enlarged pipy is the pipy with normal ecto-histogen, whereas the crinkled normal has normal ecto- and meso-histogens or homogeneous normal tissues, the normal components in every case being generally heterozygous. The flower shape, such as that of the pipy and its chimeras, is strongly influenced by the genic constitution of the meso-histogen. In some cases the mosaic pipy plants bore more than two flower types, showing the complicated position held by the mutated tissues in the sporophytes (Plate VI, fig. 6). The average percentage of occurrence of mosaic pipy in the total pipy through four generations is 17·2, a more reliable figure than the previously calculated 15 per cent., and which indicates a high tendency to vegetative reversion in pipy plants.

The effect of the normal endo-histogen on the pipy stock is not clear. The influence is probably so slight as to render it impossible to distinguish the flower from the ordinary pipy. After studying the periclinal forms

of delicate and willow, Mr K. Tabuchi also was unable to detect a flower with normal endo-histogen. In the structural chimeras, the identification of this type seems to be very difficult, although it is clearly recognized in the flecked, yellow-inconstant, and other colour chimeras.

Heterozygotes, or crinkled normals, at times bore perfectly normal flowers (see Table IV; Plate V, fig. 4), the vegetative mutation being regarded as forming homozygous normal parts on the heterozygous sporophytes. This fact indicates that a mutable nature also resides in the heterozygotes, in which the stable normal allelomorph incompletely dominates the unstable pipy in the manifestation of the pipy character.

SUMMARY.

1. The pipy flower, which has a small tubular corolla, appeared spontaneously by mutation in an F_2 pedigree. The character is due to a recessive gene, which is automutable, frequently changing into normal.

2. The pipy plant produces about 2·9 per cent. of mutated, normal gametes, resulting in 5·9 per cent. heterozygous normal individuals. The lability of pipy causes a marked deficit in the pipy segregates in the heterozygous pedigrees. In addition to this, pipy plants exhibit vegetative mutation to normal, becoming themselves mosaic. The occurrence of mosaics in the pipy plants reaches 17·2 per cent. Vegetative mutation occurs also in the heterozygous normal sporophytes, bearing normal flowers in otherwise heterozygous crinkled flowers.

3. Bud-variation on the pipy stock appears in three forms, namely, crinkled normal, enlarged pipy, and less-enlarged pipy. The crinkled normal sport has either mutated, normal ecto- and meso-histogens or all normal tissues, the enlarged pipy has normal meso-histogen, and the less-enlarged pipy normal ecto-histogen, the last two at least being periclinal chimeras with heterogeneous tissues.

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EXPLANATION OF PLATES V AND VI.

PLATE V.

Fig. 1. Normal.

Fig. 2. Pipy.

Fig. 3. Crinkled, heterozygous normal.

Fig. 4. Crinkled normal mutating vegetatively to normal. The upper three flowers are normal, including the mosaic one in the centre of the photo, while the lower two are crinkled normal.

PLATE VI.

Fig. 5. Pipy mutating vegetatively to bloom less-enlarged pipy. The upper flower is pipy and the lower less-enlarged pipy.

Fig. 6. Pipy bearing also sported enlarged (lower two) and crinkled normal (upper one) flowers.

Fig. 7. Enlarged pipy.

Fig. 8. Mosaic flower, half pipy and half enlarged pipy.

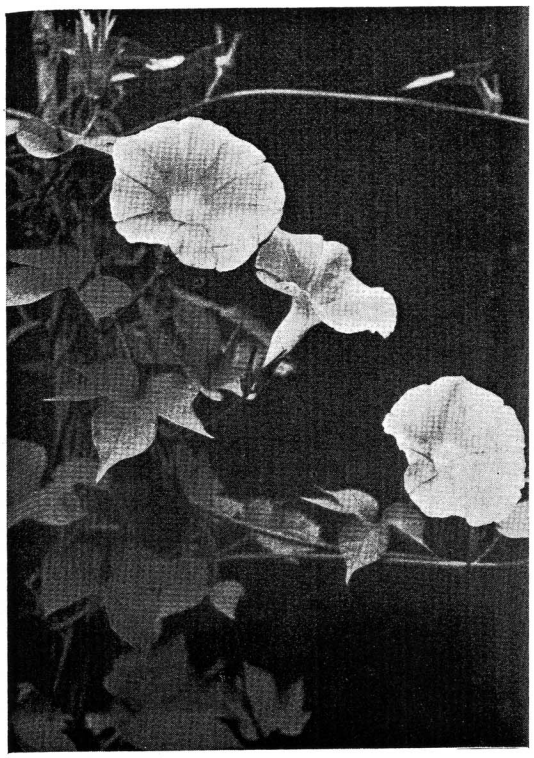

Fig. 1.

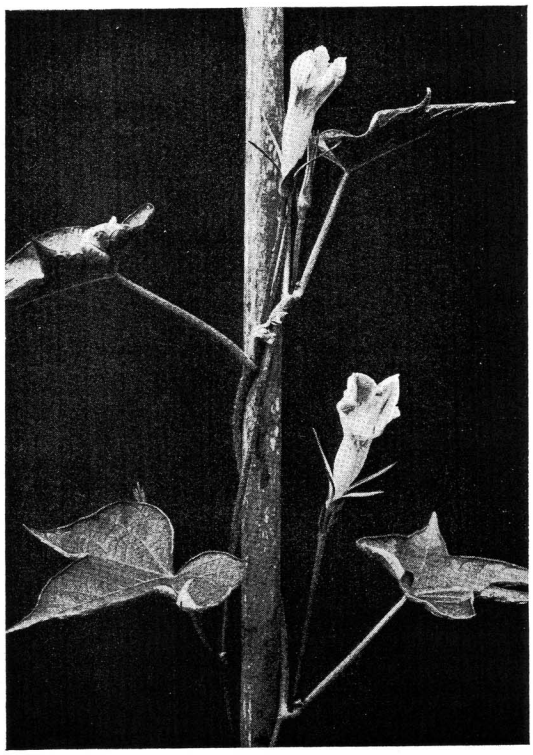

Fig. 2.

Fig. 3.

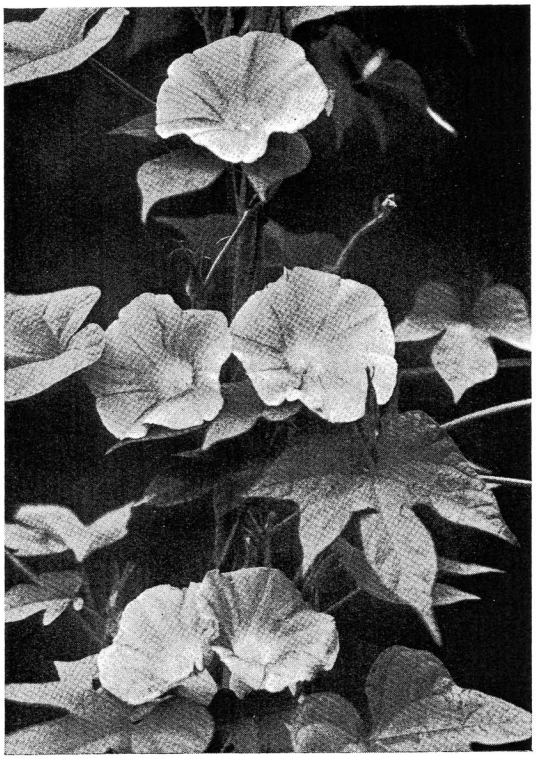

Fig. 4.

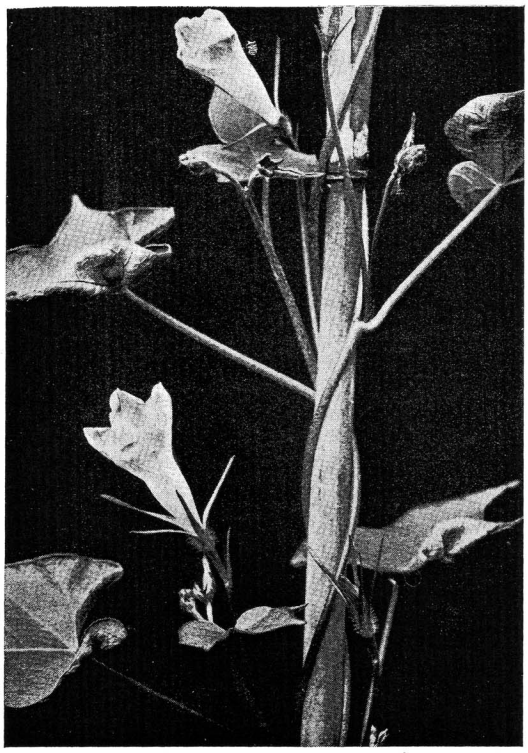

Fig. 5.

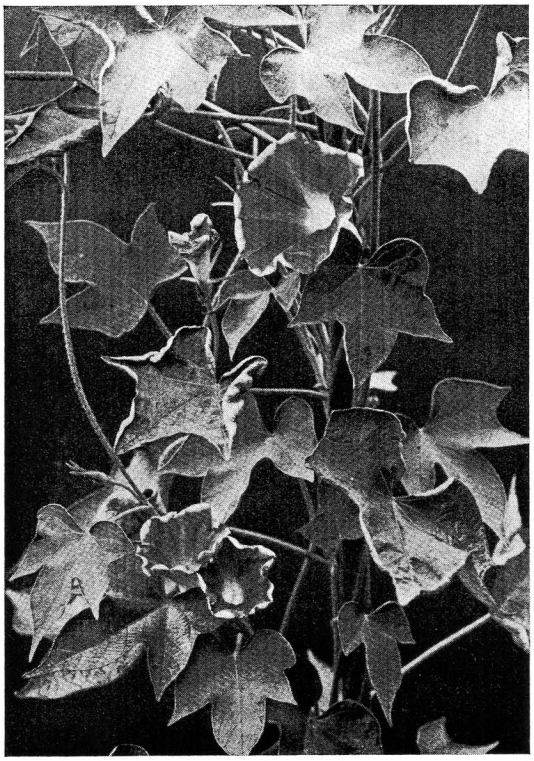

Fig. 6.

Fig. 7.

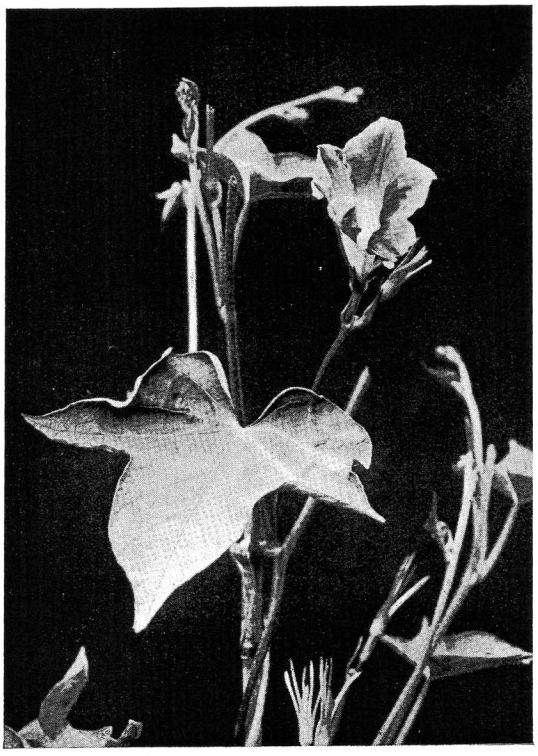

Fig. 8.