ON A MONSTROUS FLOWER AND ITS LINKAGE IN THE JAPANESE MORNING GLORY[1].

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(With Four Text-figures and One Plate.)

Introduction.

The Japanese morning glory (*Pharbitis Nil*) is very commonly cultivated in Japan as an ornamental flower; it contains exceedingly numerous forms. The attention of our cultivators has been called to two points, the size of the flowers and their abnormality. As to the latter, quite a number of monstrous types are found in our morning glory. In the present paper we shall describe the hereditary behaviour of one peculiar type of the flower, called by our gardeners "Shishi," and discuss its linkage with a leaf form.

Genetical studies on the abnormal flowers of this plant have already been undertaken by several investigators. According to Toyama (1916) and Imai (1920) the five-lobed flower acts as a simple recessive to the normal, funnel-shaped flower. This abnormal flower always accompanies the so-called maple leaf, which is usually five-lobed, the normal leaf being three-lobed. Two types of the so-called cup flower were studied by Miyake and Imai (1920) and Imai (1920, 1924 *b*); the one always accompanies a crapy leaf, while the other does not. Both cup flowers act as recessives to the normal. The papers by Imai (1920, 1924 *a*, 1924 *c*) and Hagiwara (1921) also dealt with other abnormal flowers. As to the doubling of this plant several forms were reported from the genetical point of view. According to Takezaki (1918) a form of doubling with peculiar leaves having a long petiole, called "Tenaga-Botan," is segregated from the heterozygous single flower by the Mendelian rule. Miyake and Imai (1920, 1921) showed two types of genetically different recessive doubles, both due to petalody; the one accompanies the "peacock" leaf, but the other does not. They also investigated a duplicated double

[1] The results of the study on coupling were published in the *Botanical Magazine*, Vol. xxxv. pp. 101–115, 1921, in Japanese.

with no accompanying traits (1921). This duplicated form is segregated as a recessive from the heterozygous single flower.

The double flowers of the Japanese morning glory may be divided into two groups artificially, the one is the double proper, containing several forms due either to petalody, petalomany, or duplication of flowers, and the other the "Shishi" flower, which will be discussed in the latter part of this paper. Two papers which dealt with the "Shishi" flower were published by Sô and Nishimura (1919) and Imai (1924 *b*). Our "Shishi" form having a "grasp" leaf seems to be the same as that studied by the former authors, and the factors concerned may also be common.

Origin of Pedigrees.

From a packet of seeds furnished by a nursery firm we raised 15 plants all bearing the variegated leaves. According to the differences in the other traits they may be grouped in the following three classes:

Class I. Normal-formed and punched leaf, single flower (counted 4 individuals).

Class II. Normal leaf with roundish lobes, the surface of leaf punched and rolled up, single flower (counted 10 individuals).

Class III. Heart-shaped, and strongly rolled, forming the "grasp" leaf, flower blooms into "Shishi" (counted 1 individual) (Fig. 1).

These plants were bagged and their progeny traced, with the exception of the "Shishi" plant which gives no seeds. In raising the next generation we found that four plants of class I all bred true to the parental form, while ten plants of class II each formed a segregating family. The actual data of such segregating families are shown in Table I.

TABLE I.

	Normal			Roundish normal			Heart			
Pedigree number	Punched single	Rolled single	Grasped "Shishi"	Punched single	Rolled single	Grasped "Shishi"	Punched single	Rolled single	Grasped "Shishi"	Total
D 56	8	—	—	—	3	—	—	1	1	13
D 57	22	—	—	—	33	—	—	—	13	68
D 58	7	—	—	—	25	—	—	—	21	53
D 59	6	—	—	—	10	—	—	—	8	24
D 60	5	1	—	—	10	—	—	—	8	24
D 61	13	—	—	2	19	—	—	—	16	50
D 62	11	—	—	—	17	—	—	1	10	39
D 63	15	—	—	2	23	—	—	—	15	55
D 64	10	—	—	1	17	—	—	1	5	34
D 65	29	1	—	3	56	—	—	—	27	116
Total	126	2	0	8	213	0	0	3	124	476
Expected	116·150	2·833	0·017	2·833	232·334	2·833	0·017	2·833	116·150	476

A glance at the table shows that such an abnormal segregation might be due to the result of the linkage which takes place between the heart

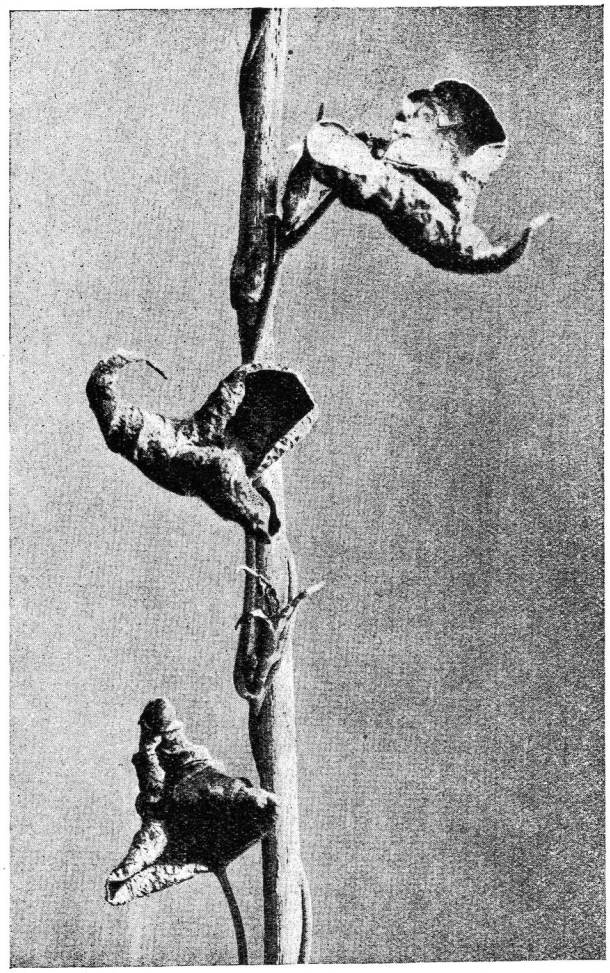

Fig. 1. Portion of stem with grasped heart leaves ("Shishi").

leaf and the "Shishi." Before going on to examine this special relation it may be necessary to consider what sorts of allelomorphs are concerned in this cross.

HEART LEAF.

As was stated before, the 15 original plants were composed of four normals, ten roundish-lobed normals and one heart leaf. With the exception of the last one, they all produced progeny; the first type each propagated a pure family, while the second one segregated into three phenotypes of normal (Fig. 2 *c*), roundish normal (Fig. 2 *b*) and heart (Fig. 2 *a*) as follows:

TABLE II.

	Normal	Roundish normal	Heart	Total
Observed	128	221	127	476
Expected	119	238	119	476

Thus the segregation occurred about in a 1 : 2 : 1 ratio, showing that the parental plants bearing roundish-normal leaves are heterozygous for

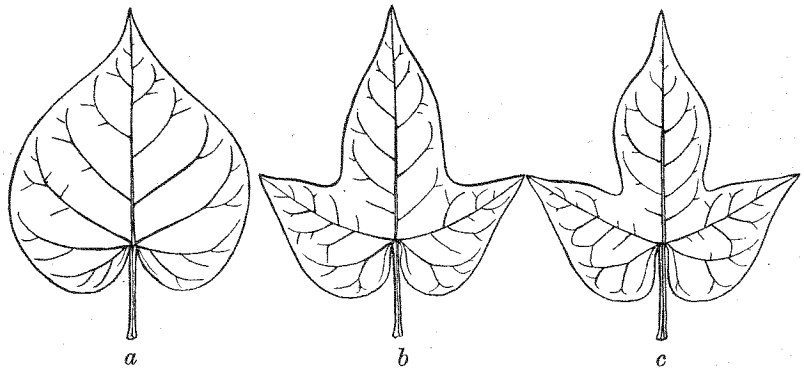

Fig. 2. (*a*) Heart, (*b*) Rounded, (*c*) Normal.

the leaf form. The hereditary relationship of the heart leaf to the normal has been studied out by several authors, of whom we cite Tanaka (1915), Sô and Nishimura (1919), Imai (1920) and Hagiwara (1921).

In raising a further generation we had the following facts: 91 plants bearing normal leaves gave pure families containing a total of 2449 individuals, while 164 roundish-normal leaves segregated into three forms of normal, roundish-normal and heart leaves. The summarisation of the data of the latter is given in the next table:

TABLE III.

	Normal	Roundish normal	Heart	Total
Observed	874	1849	642	3365
Expected	841·25	1682·50	841·25	3365

A marked deficiency is apparent in the heart leaf class, but this may be due to the mortality of the "Shishi" plants, of which the main part of the members of this class consisted. The record of the individuals of this generation was made when the plants had recovered their growth after being transplanted in the field. It is possible, therefore, that we may have failed to note certain plants which died early after transplantation, without their traits being recorded. On account of long-continued dry and hot days in this season, many weak seedlings were damaged, especially those of the "Shishi" strain, which were especially weak. As the observation of the first segregating generation was made just at the time of transplantation, such a discrepancy of ratio may not have been noted. Actually there was a fair accordance between observed numbers and those calculated from a 1 : 2 : 1 ratio, as was shown before. So that the deviation in question may be attributed readily to the result of the high death-rate among the "Shishi" strain. Those families giving no "Shishi" flowers, but all singles even among the heart leaves themselves, then, might be expected to segregate fairly into a 1 : 2 : 1 ratio, because there is no reason for the occurrence of such an unequal mortality. The actual segregation of eight such families went as follows:

TABLE IV.

	Normal	Roundish normal	Heart	Total
Observed	47	125	56	228
Expected	57	114	57	228

Thus the deficiency of the third class in this table did not appear, proving the above consideration. In the next raising of the heart leaves we obtained only three families giving 57 hearts, as a result of the fact that the majority of them are accompanied by the "Shishi" flower.

With these experimental results we can fairly conclude that the normal leaf is transmitted as an incomplete dominant character to the heart leaf, giving a 1 : 2 : 1 ratio in the segregation of the hybrids. The possibility, thus, of inferring the heterozygous genotype from the phenotype will be of great convenience in our linkage study, as may be seen in the later pages.

THE "SHISHI" FORM.

Four original plants bearing punched leaves and single flowers each gave uniform offspring, while the other ten single-flowered plants with rolled leaves segregated into three classes as represented in the next table:

TABLE V.

	Punched single	Rolled single	Grasped "Shishi"	Total
Observed	134	218	124	476
Expected	119	238	119	476

The observed number appeared clearly in a 1 : 2 : 1 ratio, showing a monohybrid segregation. Thus the plants of the first and the third classes respectively may be expected to breed true to the parental type, while those of the middle class will again yield segregating families. The experimental test proved the case to our satisfaction with the exception of the "Shishi" flowers, which could not be examined on account of their sterility. The normal flowers with punched leaves propagated invariably a uniform offspring; 97 plants gave 2662 as the total in the next generation. 161 plants of the middle class, however, all gave segregated families as shown in the following table:

TABLE VI.

	Punched single	Rolled single	Grasped "Shishi"	Total
Observed	847	1781	581	3209
Expected	802·25	1604·50	802·25	3209

The deviation was conspicuous, but as we have suggested in the former section, it may have been caused by the unequal mortality which occurred after the time the seedlings were transplanted in the field. The segregation would have occurred in the proportion of 1 : 2 : 1, had the record been taken earlier.

The "Shishi" flower thus behaves as a simple recessive to the normal, and it is always accompanied by the rolled leaf, by which we can conveniently, without failure, detect the strain even in the cotyledonous stage of the seedling.

A word may be added at this point as to the behaviour of the grasped leaves of the "Shishi" flower. The common type of the "Shishi" flowers carries the rolled leaf, but the rolling state is not so pronounced as to form the so-called grasped leaf. The question therefore naturally arises as to why in our present study we had in the "Shishi" plants all grasped leaves. According to Imai (1924 *d*) there are two types of the so-called punched leaves, in which the margin of the lamina is somewhat rolled up and the surface is uneven. From the fact that our homozygous normal flowers carried the punched leaves we may conclude that the grasped leaf is a characteristic produced by the combined effect of the factors of the "Shishi" flower and the punched leaf. With only our results as a basis, we cannot say that the grasped condition of the leaf is due to

the direct effect of the "Shishi" factor. Strictly speaking, the representation of the "Shishi" factor in the leaf condition is a moderate "rolledness" (Plate VIII, fig. 8 *c*).

COUPLING DATA.

Notwithstanding the fact that the segregating mode of each allelomorphic pair was quite simple we obtained, as was shown in Table I, rather complicated results, when we considered their segregations together. This complication is partly due to the incomplete dominancy of each one of the allelomorphic characters of the two pairs, but it must be mainly attributed to the result of linkage. By the incomplete dominance of the characters the fate of each plant may be predicted without making further experiments, namely, a phenotype predicts a genotype. And, further, we can directly estimate the percentage of crossover from the data on self-propagation without making back-cross experiments. If we represent the factor for a heart leaf by **h** and that for the "Shishi" form by **si** the following hypothesis may be made. Because the segregation is a coupling we may consider that a given chromosome in the germ-cells of the original hybrid parents carries **h** and **si** factors, while its homologous one contains both dominant factors. The genetical varieties of germ-cells produced in such plants should be **hsi** and **HSi** of the non-crossover gametes, and **Hsi** and **hSi** of the crossover gametes. By combination of these four sorts of gamete we should expect the following result:

Origin	Genetical composition	Characters		
		Leaf form	Leaf surface	Flower type
Non-crossover g. × non-crossover g.	**HHSiSi**	Normal	Punched	Normal
	HhSisi	Roundish n.	Rolled	Normal
	hhsisi	Heart	Grasped	"Shishi"
Non-crossover g. × crossover g.	**HHSisi**	Normal	Rolled	Normal
	HhSiSi	Roundish n.	Punched	Normal
	hhSisi	Heart	Rolled	Normal
	Hhsisi	Roundish n.	Grasped	"Shishi"
Crossover g. × crossover g.	**HHsisi**	Normal	Grasped	"Shishi"
	HhSisi	Roundish n.	Rolled	Normal
	hhSiSi	Heart	Punched	Normal

In the first segregating generation, as the following discussion will show, we do not find any individuals which might be expected to be produced by the union of two crossover gametes. The respective origin of the doubly heterozygous individuals, however, can be theoretically considered to be either a case of non-crossover gamete × non-crossover gamete or of crossover gamete × crossover gamete. But, as will be shown

later, the percentage of crossover is very low in this case, and so it is impossible to suppose that the **Hsi** + **hSi** individuals would be produced with such a limited number in the experiment; theoretically only one such individual is expected in about every 6700 double heterozygotes. Actually the **HhSisi** individuals, so far as our experiment went, all segregated into coupling data. If the plants are produced by the fertilisation of two crossover gametes, **Hsi** and **hSi**, they must result in repulsion segregations in their offspring. So the doubly heterozygous plants obtained in our experiments may practically all be regarded as produced by the union of two normal gametes, **HSi** and **hsi**. To continue the representation of the actual results, in our experiment the number of individuals produced by the union of non-crossover gamete and crossover gamete was 13 in all, while of those having the origin of non-crossover gamete × non-crossover gamete there was a total of 463. For the production of the zygotes in these quantities there would be needed just double the number of gametes. The number of gametes thus concerned should be, then, theoretically 13 crossovers and 939 non-crossovers; consequently the gametic ratio is 72·23 : 1. From this, the value of crossover is calculated as 1·37 per cent.

By means of 259 plants obtained in the first segregating generation, with the exception of those of the family D 58, we traced the next generation to see to what extent the above expectation agreed with the further data. Of these, 89 plants bearing three-lobed punched leaves and single flowers may be considered as carrying the genetical composition of **HHSiSi**, and be expected to breed true to the parental characteristics. Actually 2432 individuals of the expected form were produced as the next progeny. The other 156 plants having the doubly heterozygous traits, however, all segregated into several phenotypes, as is represented in Table VII. These plants being doubly heterozygous, the mode of their

TABLE VII.

The data of the doubly heterozygous families in the second segregating generation.

	Normal			Roundish normal			Heart			
	Punched single	Rolled single	Grasped "Shishi"	Punched single	Rolled single	Grasped "Shishi"	Punched single	Rolled single	Grasped "Shishi"	Total
Total	806	19	0	18	1698	8	0	29	557	3135
Expected	764·978	18·658	0·114	18·658	1530·184	18·658	0·114	18·658	764·978	3135

segregation was complicated and particular, as was observed in the foregoing generation. With the total number as a basis we calculate 1·18 per cent. of crossover (non-crossover gamete : crossover gamete :: 83·57 : 1).

This figure approximates that of the foregoing generation, showing clearly that the results were the same. If an estimate is made on the grand total throughout the two generations the average value of crossover is 1·21 per cent. (gametic ratio is 81·87 : 1). As to the origin of these two forms of genotype they must be considered to be derived from two normal gametes. Let us next describe the offspring of the plants derived from the union of a crossover gamete and a non-crossover gamete. By the combination of a non-crossover gamete carrying **HSi** and a crossover gamete containing **Hsi**, three-lobed and rolled leaves may be produced which would be expected to segregate in the next generation with respect to the factor for the "Shishi" only. The results obtained by two such plants are:

TABLE VIII.

Pedigree number	Normal punched single	Normal rolled single	Normal grasped "Shishi"	Total
D 60–14	5	6	2	13
D 65–63	1	2	1	4
Total	6	8	3	17
Expected	4·25	8·50	4·25	17

Thus the segregation occurred in a monohybrid scheme of the 1 : 2 : 1 ratio. The "Shishi" plants with three-lobed and grasped leaves are a new form which had never appeared in the doubly heterozygous families throughout two generations, as the result of high linkage. Theoretically only one such form in 27,000 individuals would be expected in our hybrid segregation. The single-flowered plants bearing punched and roundish-lobed leaves being regarded as having the **HhSiSi** composition, may be expected to produce offspring of the three leaf forms in the proportion of 1 : 2 : 1. The actual segregation went as follows:

TABLE IX.

Pedigree number	Normal punched single	Roundish normal punched single	Heart punched single	Total
D 61–30	1	12	4	17
–31	2	10	5	17
D 63– 5	29	62	29	120
–22	4	13	5	22
D 64–19	1	2	1	4
D 65– 2	1	0	1	2
–56	2	10	4	16
–70	9	16	7	32
Total	49	125	56	230
Expected	57·5	115	57·5	230

The parental plants of these families might be synthesised by the union of a non-crossover gamete carrying **HSi** and a crossover gamete

having **hSi**. Single-flowered plants with three-lobed and rolled leaves, however, may be regarded as being produced by an **hsi**-carrying non-crossover gamete and an **hSi**-containing crossover gamete, and they will give the following generation, where the segregation occurs only for "Shishi" form. Actually three plants gave the expected results as follows:

TABLE X.

Pedigree number	Heart punched single	Heart rolled single	Heart grasped "Shishi"	Total
D 56– 5	5	5	3	13
D 62–20	10	19	9	38
D 64–25	2	3	1	6
Total	17	27	13	57
Expected	14·25	28·50	14·25	57

The single flowers with heart and punched leaves, which appeared in about one-fourth of the above total number, are another type never obtained in our doubly heterozygous segregation throughout two generations, where it might be expected theoretically to have the same chance of yielding the "Shishi" flower with the normally formed leaf.

From the above breeding experiments it may be clearly stated that two factors, **H** and **Si**, represent a linkage segregation of 1·2 per cent. of crossover. Owing to the fact that the dominance in each allelomorphic pair is so incomplete that the heterozygotes can be separated phenotypically from their respective pure form, the value was calculated directly by the data of the self-propagated generation, without making a back-cross to the double recessive.

A linkage case between the "Shishi," with the grasped leaf, and the heart leaf reported by Sô and Nishimura (1919) seems to be the same one as ours, the only differing feature being that the segregation is either coupling or repulsion. On account of the repulsion state of segregation they had no double recessives in the segregating families. To calculate on the basis of our hypothesis, there might theoretically be only one double recessive in about every 27,000 individuals. And so, they[1] have concluded that the repulsion must be either complete or very high.

Repulsion Data.

In the progeny propagated by a plant (D 324) of unknown origin we recorded the segregation that involves repulsion in the characters under discussion. The original plant had little rolled and roundish-normal

[1] They did not make note of the heterozygous forms separately from their respective pure normal forms.

leaves, but it bloomed quite normally. On selfing this plant we had the following results:

TABLE XI.

	Normal			Roundish normal			Heart			
Pedigree number	Even single	Weakly rolled single	Rolled "Shishi"	Even single	Weakly rolled single	Rolled "Shishi"	Even single	Weakly rolled single	Rolled "Shishi"	Total
D 324	0	1	19	0	45	1	25	0	0	91
Expected	0·003	0·495	22·252	0·495	44·510	0·495	22·252	0·495	0·003	91

Thus the segregation appeared in the repulsion state, giving no double recessives. The original plant, then, may be considered to have the **Hsi**-carrying and the **hSi**-carrying chromosomes. On sexual maturity it will produce two sorts of gamete, **Hsi** and **hSi**, by the normal procedure and the other two sorts of gamete, **HSi** and **hsi**, by the crossover mechanism. In the above table we count 89 plants which are considered to be produced by the union of two non-crossovers, and two plants which are expected to be synthesised by the result of non-crossover × crossover, while no plants thought to be obtained by two crossovers appeared. On the basis of these data the frequency of crossover is estimated to be 1·10 per cent. (gametic ratio is 1 : 90). As this value is not far from that obtained in the coupling data we may be considered to have had the same results in both coupling and repulsion cases. The "Shishi" form invariably accompanies the moderately rolled leaves in this case, while in the former case the grasped leaf was the accompanying character. The difference of this plant is, as already stated, due to the effect of a factor (**u**) which has the influence of producing the punched appearance on the surface of the leaves.

MANIFOLD EFFECTS OF THE **Si** FACTOR.

In the common double flowers the modification appears toward the inner part of the corolla, but in the "Shishi" strain some special malformations occur on the outside of the flower (Fig. 3). Though the sexual organs in the "Shishi" flower are present without marked degeneration morphologically, their function is much reduced. Consequently this strain usually produces no seeds. The flower has some fragmentary pieces on the outside of the corolla, thus forming a "feathering." The development of the feathers is varied in the different plants; this is also true even of the different flowers on the same plant. In the offspring of D 56–65 the variation in the "Shishi" flowers rarely went further in the direction of the extreme form in which the corolla was split into

Fig. 3. Two "Shishi" flowers.

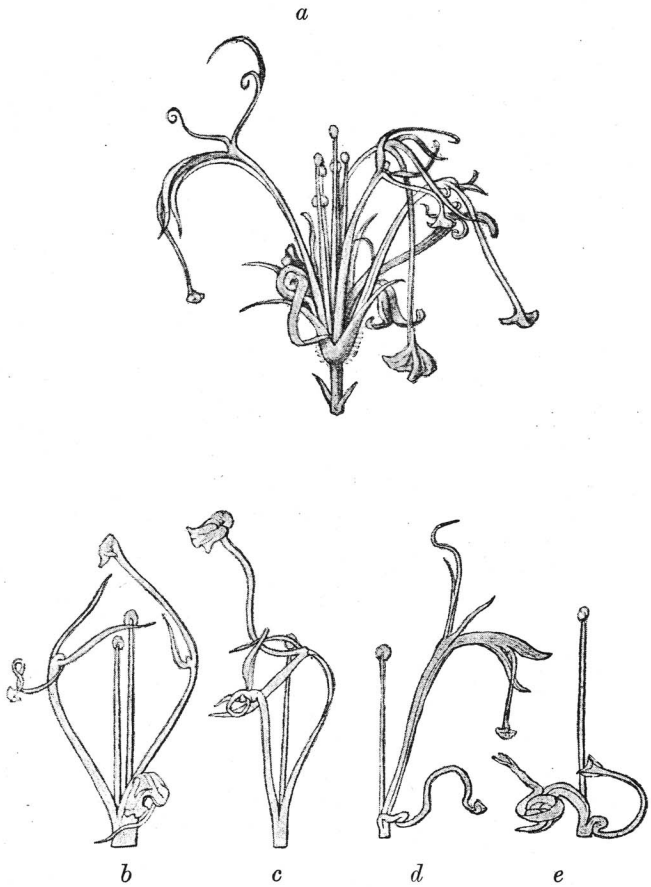

Fig. 4. (*a*) An extreme form of "Shishi" flower in shape of a "crown." (*b–e*) Dissected parts of the same.

five slender petals, and they again feathered and branched in shape of a "crown" flower (Fig. 4). On account of the sterility of the "Shishi" flowers, in practice they must be sought for among the offspring of the heterozygous normal plants. It is a well-known fact among our cultivators that the lineage of the "Shishi" may frequently depart from the ordinary culture in the course of raising further generations. The heterozygotes for the **Si** factor, however, can be picked out phenotypically by the weakly rolled state of leaves as was shown. If we keep this special feature in mind we need never lose the lineage of the "Shishi" flower. The rolled leaf and the monstrous flower are the manifold representations of a single "Shishi" factor. The rolling effect of this factor appears very early, even on the extended cotyledonous leaves of the seedling, the cotyledons being rolled up in a special manner.

The phenomena of manifold representations of a single factor are not rare in the Japanese Morning Glory; among them, the following examples may be cited. According to Takezaki (1918) the factor for a sort of double flower represents, beside the flower characteristic, also a long petioled leaf of a particular form. The **m** factor given by Imai (1920), and studied early by Toyama (1916), results in a split flower and the maple leaf. The **i** factor studied by the former author (1920) and Hagiwara (1921) is responsible for a "creased" flower and the "Rangiku" leaf. Imai (1920) further showed **d** and **t** factors which represent manifold characteristics respectively, the former for contraction of whole parts over the plant body, and the latter for the crapy leaf, cup flower and hairs on the outside of the corolla. His recent papers (1924 *a*, 1924 *c*) dealt with some other cases of similar phenomena in this plant.

SUMMARY.

1. The heart leaf (**h**) and the "Shishi" form (**si**) are respectively transmitted as recessives to the normal.

2. Owing to the incomplete dominance of the **H** and **Si** factors the segregating ratios are each a 1 : 2 : 1.

3. About 1·2 per cent. of crossover occurs in a linkage between these two factors. By the convenient nature of incomplete dominance calculation of linkage was directly made with the self-propagated specimens in the hybrid progeny.

4. The percentage of crossover is almost equal in the case both of coupling and repulsion.

5. The **Si** factor represents multiple effects on flower and leaf as well as cotyledon.

6. The grasped leaf found in the "Shishi" strain is due to the result of the additional effect of a punched factor (**u**).

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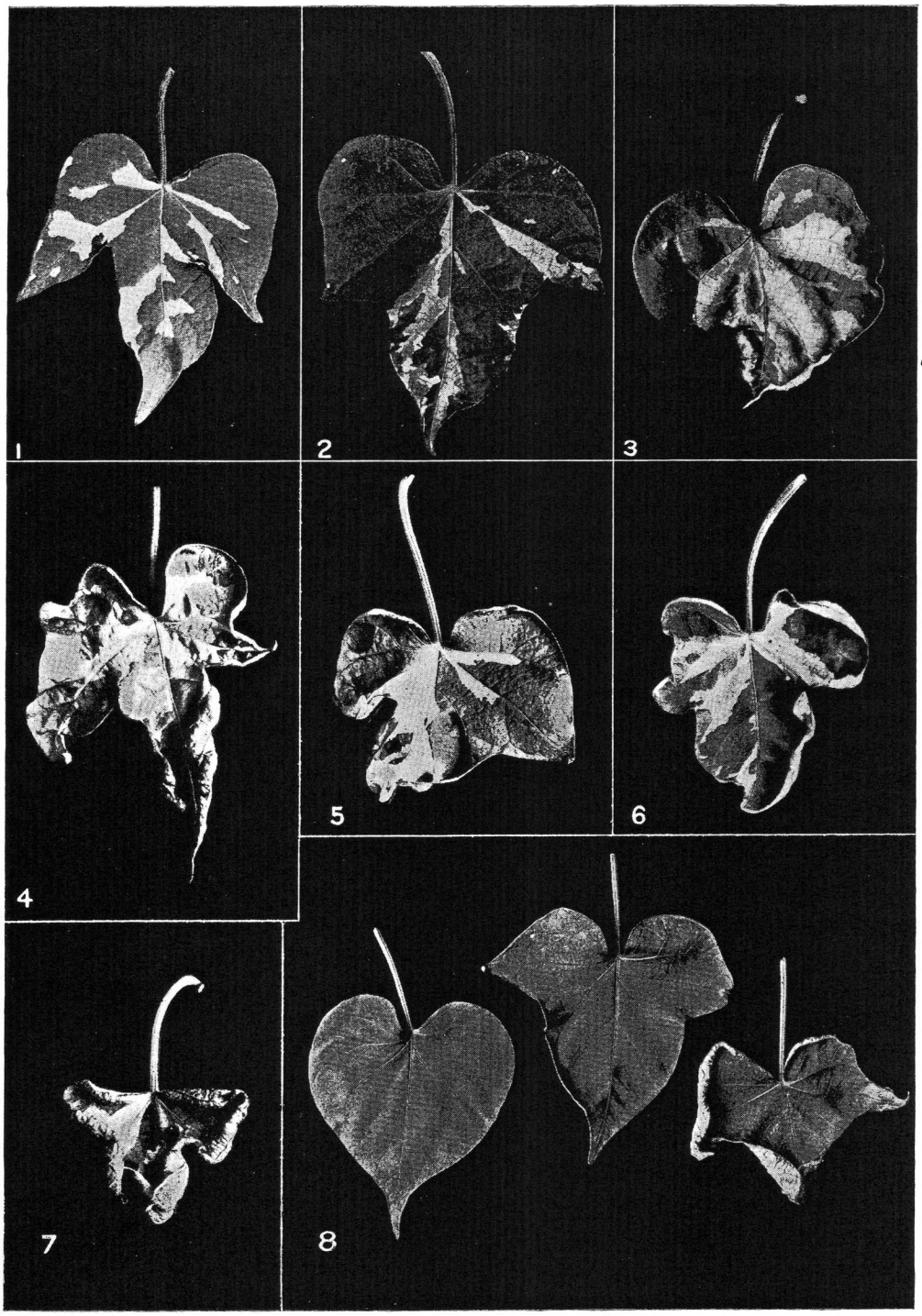
EXPLANATION OF PLATE VIII.

With the exception of Fig. 8, which was obtained from the progeny of D 324, all the figures in this plate were taken from specimens of the progeny of D 56-65.

Fig. 1. Punched normal.
Fig. 2. Punched roundish-normal.
Fig. 3. Rolled heart.
Fig. 4. Rolled normal.
Figs. 5 and 6. Rolled roundish-normals.
Fig. 7. Grasped roundish-normal ("Shishi").
Fig. 8. (*a*) even heart; (*b*) weakly rolled roundish-normal; (*c*) rolled normal ("Shishi").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