GENETIC BEHAVIOUR OF THE WILLOW LEAF IN THE JAPANESE MORNING GLORY[1].

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(With Two Plates and Two Text-figures.)

CONTENTS.

INTRODUCTION.

IN my previous papers[2] I have dealt with some leaf forms of the Japanese morning glory, *Pharbitis Nil.* The willow leaf, which I am now going to discuss, is another form found in this plant. The leaves are narrow and elongated just like those of the willow, so that the form is known as the willow leaf. The outside of the shoulder parts of the lamina are more or less protruded (Pl. IX, fig. 1), varying sometimes into real winged lobes, thus making a slender three-lobed leaf (Pl. IX, fig. 4). The flower of the willow leaf is invariably split into five narrow parts (Pl. IX, figs. 3 and 5); the type of the divided corolla is somewhat different from those of the other races, such as the maple and the "Sasa." The petals are more slender than those of the two above strains, being divided near the base of the flower tube. With the slender foliage and flowers the strain gives an impression of delicacy (Pl. IX, fig. 3). Introducing the double flower factor to this form our excellent cultivators produce one of the most admirable flowers, the flower being

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[1] The substance of this paper was published in the *Botanical Magazine*, Tôkyô, vol. XXXVIII, 1924, in Japanese.

[2] Imai, Y., "Genetic studies in Morning Glories. II, XI, XII and XIII," *Botanical Magazine*, Tôkyô, vols. XXXIV–XXXVIII, 1920–1924, in Japanese.

divided into numerous narrow lobes to form a cluster of petals. The cotyledonous leaves of the willow are slender in form (Pl. IX, fig. 2), and the thigh of the two lobes is wider than that of the normal, these traits being more conspicuous in the "contracta" variety. The characteristics represented in such diverse parts of the plant body are transmitted together as a unit. Consequently the strain may be distinguished even in the seedling stage when the cotyledons are extended. Such a seedling selection is the method used widely in practice by our cultivators.

Inheritance of the Willow Leaf.

The willow form which was used widely as a maple parent in my breeding experiments bore the willow leaves, but the shoulders were not protruded like those above described. In the F_2 generation of the cross of this strain and the normal leaf there was dihybrid segregation of willow and heart leaves. From this experiment we are able to say that the willow strain now used is a willow carrying the heart leaf factor. So I may represent here the data obtained from the hybrids of unknown origin for the demonstration of the hereditary relationship between the willow and the normal leaves.

In 1919, I sowed a quantity of seeds bought from a seedsman, and reared six seedlings, all of which, with the exception of one which had the willow cotyledons, grew up with the normal leaves of the "contracta" variety. The exception was transplanted as a seedling into a pot, and allowed to grow there. The leaves of the seedling grew into the willow shape and it formed slender split flowers, but they produced no seeds. Thus my first willow plant died without giving progeny; luckily, however, some willow leaves reappeared in the offspring of the sister plants. Out of five normal plants, two gave a constant progeny of 52 and 32 normals respectively, whereas the remaining three threw out some willow leaves. The segregating numbers obtained are:

TABLE I.

Pedigree No.	Normal leaf	Willow leaf	Maple leaf	Total
Y 120	93	34	2	129
Y 122	38	9	0	47
Y 123	210	71(1)	0	281
Total	341	114(1)	2	457
Expected	342·75	114·25	0	457

The numeral in brackets denotes the number of the plants which made bud-variation.

Obviously the segregation occurred in a monohybrid fashion; the willow is thus a simple recessive to the normal. Quite unexpectedly, however, I obtained two rogues which bore neither the normal nor the willow leaf, but the maple. How were these plants produced? Encouraged by the occurrence of such rogues I carefully re-examined the whole progeny in the field, and my labour was rewarded by the recognition of an abnormal individual. The plant was originally a willow, while later in the course of its growth it put out a branch bearing quite different leaves and flowers. I was able to identify this bud-sport as a maple. This occurrence of the maple branch on the willow plant seemed to give a clue to the cause of the appearance of the maple rogues. In the course of my experiment such abnormal occurrences, however, were found to be an habitual feature of the willow leaf. The sporting phenomena will be fully discussed in the later pages, so we may leave this subject for the present.

The examination of the next generation was made through the use of five normals, which gave the following results: One yielded 12 normal individuals, while the remaining four produced offspring comprising normals and willows in the proportion of three to one. The actual segregation was as follows:

TABLE II.

Pedigree No.	Normal leaf	Willow leaf	Maple leaf	Total
Y 120–1	8	2	0	10
–2	18	5	0	23
–3	12	3	0	15
–4	7	3	0	10
Total	45	13	0	58
Expected	43·5	14·5	0	58

From these, the willow-throwing families have been cultivated for many generations, but have yielded no new results beyond the expectation of Mendelian segregation and the rare appearance of the maple sports.

THE RELATION BETWEEN THE WILLOW AND HEART LEAVES.

With the pollen of a willow leaf (non-contracta) obtained from the segregating family of the heart leaf, a different line to that cited in the former section, I crossed with the normal leaf, and attempted systematically to trace the hereditary behaviour of the willow leaf in the hybrid progeny. As the willow leaf, however, is derived from the heart leaf it must be supposed to carry the heart leaf factor[1]. The only visible

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[1] Tanaka, C., *A text-book of genetics*, Tôkyô, 1915, in Japanese. So, M., and Nishimura, T., "Linkage in Morning Glory," *Journal of the Scientific Agricultural Society*, No. 208, 1919, in Japanese. Imai, Y., "Genetic studies in Morning Glories. II," *Botanical Magazine*, Tôkyô, vol. XXXIV, 1920, in Japanese. Miyake, K. and Imai, Y., "Genetic experiments with Morning Glories. III," *Ibid.* vol. XXXV, 1921, in Japanese. Hagiwara, T., "On the inheritance of linked genes in the leaf of the Japanese Morning Glory. II," *Journal of the Scientific Agricultural Society*, No. 224, 1921, in Japanese.

representation of the heart leaf factor on the willow leaf is the roundish shoulder of the lamina (Pl. IX, figs. 2, 3 and 5). Actually the parental willow, numbered as 505, bore willow leaves with roundish shoulders; consequently the winged lobes never develop in this willow strain. The F_1 plants obtained from the cross of the normal (65) and the willow (505) bore normal leaves, their main lobe being invariably roundish on account of the hybrids carrying the heart leaf factor in a heterozygous state. In the F_2 generation we obtained the following results:

TABLE III.

Pedigree No.	Normal leaf	Heart leaf	Willow leaf	Roundish willow leaf	Maple leaf	Heart-shaped maple leaf	Total
65 × 505–1	71	18	14	3	2	0	108
–2	31	10	10	2	0	0	53
–3	32	6	6	2	0	0	46
–4	58	15	14	5	1	0	93
–5	51	17	13	4	1	0	86
Total	243	66	57	16	4	0	386
Expected	217·12	72·38	72·38	24·12	0	0	386

In the above table the roundish normal leaves were counted together with the pure normals, since the identification of the former form might be accompanied by mistakes in this generation. As was stated above, segregation may be expected in both allelomorphic pairs, non-willow *v.* willow and non-heart *v.* heart, and this was actually the case. By free combination of the factors the willow leaf may be endowed either with the non-heart factor or with the heart one; those having the heart leaf factor should be the willow with roundish shoulders, while those carrying the non-heart leaf factor should be the so-called normal willow, the shoulders of the lamina being protruded. The willow leaves in the hybrid progeny cited in the former section invariably had protruded shoulders, showing that all specimens carry the non-heart leaf factor (**H**) in duplex, the segregation consequently occurring in a single pair of allelomorphs. The present segregation, however, should yield four forms, viz. normal, heart, willow and roundish willow leaves in the proportion of 9 : 3 : 3 : 1. Actually the observed numbers showed some deviation from the theoretical ones calculated on the basis of this dihybrid ratio. The comparatively low value of P (= 0·11) may be, however, due largely to the small number of specimens found in the willow class. Summing up, the non-willow is to the willow as 309 : 77, where we expected 289·5 and 96·5 respectively. The difference between the non-willow and willow is due to a single factor, so such a deviation from a 3 : 1 ratio cannot be considered to be the result of any disturbance in the factorial relation. Consequently we can correct the actual data on the basis of a 3 : 1 ratio of non-willow to willow, and this may also be equally admitted in the segregation of non-heart and heart leaves. As the result of double treatment of correction the observed numbers will be changed into 216·72 normals, 72·825 hearts, 72·825 willows and 23·63 roundish willows, where we expected 217·12, 72·38, 72·38 and 24·12 respectively. Here $\chi^2 = 0{\cdot}02$, consequently $P \fallingdotseq 1$. The goodness of fit is very high, demonstrating free assortments of two factor-pairs. The data of the F_3 rearing are represented in Table IV. The results came quite according to expectation, *i.e.*, normal leaves being pure for the **H** factor either bred true or segregated into normal and willow leaves in the ratio of 3 : 1 according to their genetic compositions, and the roundish normal leaves invariably segregated into either normal, roundish normal and heart leaves in the proportion of 1 : 2 : 1, or normal, roundish normal, heart, willow and roundish willow leaves in the ratio of 3 : 6 : 3 : 3 : 1, while the progeny of the heart leaves resulted in pure breeding and segregating. In the data of the offspring of the roundish normals, however, we had again some discrepancies in both segregating ratios, but these seem to be only a superficial deviation like that previously discussed. So the mathematical treatment on this point will not be repeated here. With the exception of the sporting phenomena, therefore, the segregating data obtained throughout two generations can easily be explained by assuming two factors, **h**, a heart leaf factor, and **w**, a willow leaf factor.

TABLE IV.

The F_3 *data of the cross* 65 × 505.
Offspring of the normal leafed F_2.

Pedigree No.	Normal leaf	Willow leaf	Maple leaf	Total
Total of 6 pedigrees	539	—	—	539
10	10	5	—	15
19	2	1	—	3
24	73	11	1	85
25	256	83	2	341
27	98	30	1	129
29	165	55	—	220
30	160	50	1	211
36	36	13	—	49
51	60	14	—	74
54	11	2	—	13
Total	871	264	5	1140
Expected	855	285	—	1140
47	48	—	15	63
Expected	47·25	—	15·75	63

TABLE IV (*continued*).

Offspring of the roundish normal leafed F_2.

Pedigree No.	Normal leaf	Roundish normal leaf	Heart leaf	Willow leaf	Roundish willow leaf	Maple leaf	Heart-shaped maple leaf	Total
5	2	4	2	—	—	—	—	8
18	33	99	36	—	—	—	—	168
28	5	10	3	—	—	—	—	18
41	5	37	6	—	—	—	—	58
42	11	16	12	—	—	—	—	39
43	4	8	1	—	—	—	—	13
46	17	55	20	—	—	—	—	92
Total	77	229	90	—	—	—	—	396
Expected	99	198	99	—	—	—	—	396
1	21	39	22	18	5	1	—	105
2	8	5	2	6	0	—	—	21
4	3	26	11	9	0	—	—	49
6	11	47	16	9(1)	2	1	—	86
7	9	19	3	2	0	—	—	33
8	11	37	15	18	8	—	—	89
11	5	11	9	12	4	—	—	41
14	7	4	5	3	2	—	—	21
15	29	32	15	24	5	—	—	105
17	17	46	18	18	10	—	—	109
21	9	28	16	13	2	—	—	68
33	4	10	8	4	1	—	—	27
34	19	51	29	18(1)	8	1	—	126
35	13	45	16	11	5	2	—	92
37	6	25	7	11	2	—	—	51
39	8	12	11	9	3	—	—	43
45	7	11	10	3	2	—	—	33
53	10	47	15	11	5	—	—	88
55	14	21	15	12	3	—	—	65
57	6	23	7	10	2	—	—	48
Total	217	538	250	221(2)	69	5	0	1300
Expected	243·75	487·50	243·75	243·75	81·25	—	—	1300

Offspring of the heart leafed F_2.

Pedigree No.	Heart leaf	Roundish willow leaf	Heart-shaped maple leaf	Total
Total of 4 pedigrees	270	—	—	270
3	21	2	—	23
12	90	19	—	109
13	49	18	—	67
20	101	39	1	141
38	28	4	—	32
40	43	19	—	62
44	93	21	—	114
48	26	6	—	32
56	96	32	1	129
58	58	13	—	71
Total	605	173	2	780
Expected	585	195	—	780

The numeral in brackets denotes the number of the plants which made bud-variation.

APPEARANCE OF THE FILAMENTOUS WILLOW LEAF.

From the seeds obtained of 326, a pure strain bearing the heart-shaped "Sasa" leaf[1], with the pollen of 505 I obtained F_2 plants bearing heart leaves. Both parents bloomed with split flowers, but not of quite the same type, the flower of the willow being split into lobes so slender that a tubular corolla might be obtained when five lobes are united edge to edge, while the lobes of the flower of the "Sasa" were much broader, though not so broad as those in the maple flower, and if we combine the edges of lobes the so-called "gentian" flower would be obtained. The heart leafed F_1, however, bore normal, funnel-shaped flowers. The result thus shows us that both parental split flowers differ in their factorial pair, and working in a complementary way they produce the normal flower.

Speaking of the generation in F_2 (see Table V), there were produced besides the heart, the willow and the heart-shaped "Sasa" leaves, a few leaves having the filamentous lamina (Pl. IX, fig. 6). This novel form may be called the filamentous willow leaf from its appearance in my *Pharbitis*-study. It blooms into quite a slender flower split into five filamentous lobes. We can therefore conclude that both parental plants carried the heart leaf factor, and so, we had no normal leaves in the descendants of the cross. Strictly speaking, therefore, the filamentous willow leaves which appeared in F_2 should be those of the heart leaf variety. As was stated, F_1 assumed the funnel-shaped flower, but this reversion is due to the recovery of two dominant factors for non-willow and non-"Sasa" in the hybrid. Consequently segregation of the flower type in the F_2 offspring occurred in a 9 : 7 ratio. In the above table the heart leaves all flowered normally, while the others bloomed with split flowers. Such complete correlations between the leaf form and the flower

TABLE V.

Pedigree No.	Heart leaf	Roundish willow leaf	Heart-shaped "Sasa" leaf	Filamentous willow leaf	Maple mutants	Total
326 × 505–1	35	8	6	2	—	51
–2	20	4	5	1	—	30
–3	37	12	9	1	—	59
–4	70	23	22	5	—	120
Total	162	47	42	9	0	260
Expected	146·25	48·75	48·75	16·25	—	260

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[1] Imai, Y., "Genetic studies in Morning Glories. XIII. On the behavior of the 'Sasa' leaf and the phenomena of mutation in *Pharbitis Nil*," *Botanical Magazine*, Tôkyô, vol. XXXVIII, 1924, in Japanese.

type are due to the result of the manifold representations of each factor. The inheritance of the flower type can also be learned incidentally from the segregating data of the leaf form. We shall not attempt therefore to discuss again the subject of segregation of the flower type in the later generation.

The leaves of the parental 326 are of the heart-shaped "Sasa," but the margin of the lamina is much protruded. Such a protruded margin is not the subordinate characteristic of the heart-shaped "Sasa" leaf, but a modified form of it. I observed the entire-margined "Sasa" leaves in the other strains. And further, even in the present cross I met with the segregation of the entire and the protruded margins in the heart (Fig. 1), the heart-shaped "Sasa" and even in the roundish willow leaves, though the distinction between them cannot be clearly drawn. Such a fact may prove the above suggestion that the protruded margin is an additional characteristic of the heart-shaped leaves. And if I may be allowed a further suggestion I would say that the protruding margin may be due to the influence of a modifier or modifiers, and it seems to have a special relation to the "Sasa" leaf in segregation (linkage?). The extracted willow leaves in the F_2 generation were thus either entire-

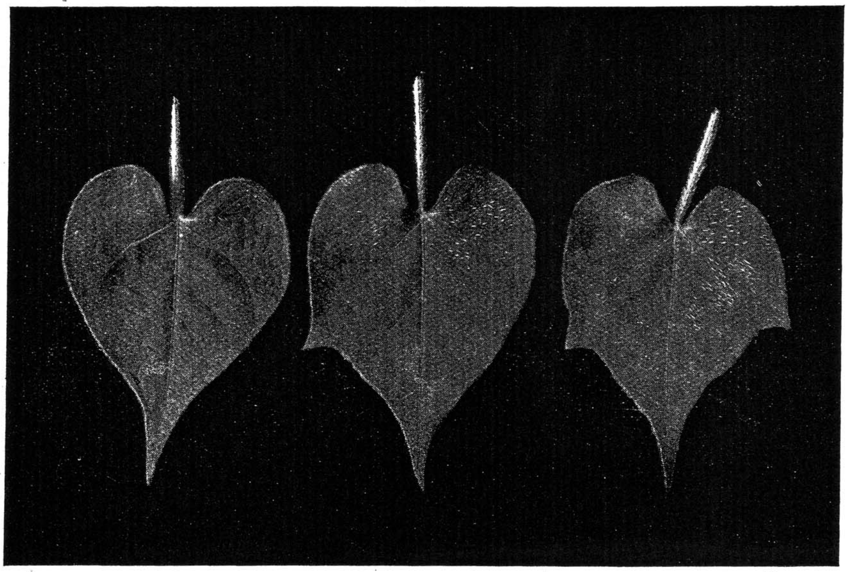

Fig. 1. One ordinary heart leaf and two protruded heart leaves.

margined or with protruding margin (Fig. 2). The latter may be mistaken for the normal willow leaves, if we do not know from which crosses they were derived. A large part of the filamentous leaves have the single lamina, but frequently they were mixed with some branched ones. All such protruding or branched laminae may serve to remind us of the modifying factor affecting the margin of the leaves. The hereditary behaviour of such a modifier will be one of the subjects of my future study. As was seen in Table V the segregating ratio of the four forms, heart, roundish willow, heart-shaped "Sasa," and filamentous willow leaves, was near 9 : 3 : 3 : 1. The factors segregated in this cross must be those of the willow and the "Sasa" leaves. So that the filamentous willow leaf is a double recessive form resulting from the combination of these two factors. On raising the F_3 generation, the examination was much limited on account of the sterility of some segregated forms; the willow and the filamentous leaves invariably produced no seeds, and many "Sasa" proved to be sterile. The actual results are shown in Table VI. With the exception of three "Sasa" families the table contains only the data of the progenies of double dominant F_2. A glance at the

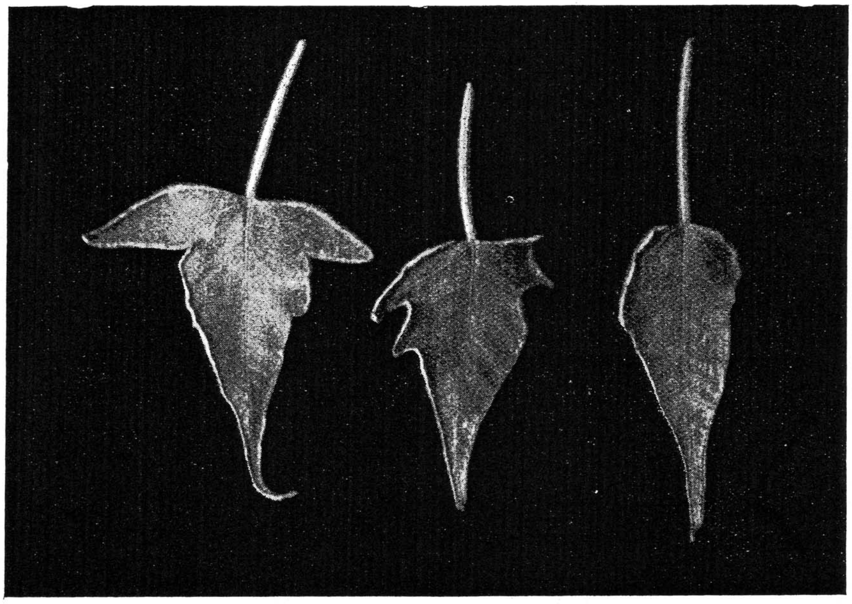

Fig. 2. Protruded poundish willow leaves.

TABLE VI.

The F_3 *data of the cross* 326 × 505.
Offspring of the heart leafed F_2.

Pedigree No.	Heart leaf	Heart-shaped "Sasa" leaf	Roundish willow leaf	Filamentous willow leaf	Heart-shaped maple leaf	Heart-shaped maple "Sasa" leaf	Total
Total of 8 pedigrees	272	—	—	—	—	—	272
2	19	2	—	—	—	—	21
9	11	2	—	—	—	—	13
14	41	8(1)	—	—	—	—	49
16	51	17	—	—	—	—	68
22	3	3	—	—	—	—	6
24	8	1	—	—	—	—	9
35	35	8	—	—	—	—	43
37	23	8(1)	—	—	—	—	31
48	26	12	—	—	—	—	38
49	8	6(1)	—	—	—	—	14
51	10	4	—	—	—	—	14
64	50	17	—	—	—	—	67
66	36	4	—	—	—	—	40
69	59	22(1)	—	—	—	—	81
70	9	5(1)	—	—	—	—	14
71	26	7	—	—	—	—	33
75	3	2	—	—	—	—	5
79	63	16	—	—	—	—	79
81	25	8	—	—	—	—	33
94	51	11	—	—	—	—	62
Total	557	163(5)	—	—	—	—	720
Expected	540	180	—	—	—	—	720
15	66	—	26	—	1	—	93
23	2	—	1	—	—	—	3
31	5	—	2	—	—	—	7
34	37	—	6	—	—	—	43
36	28	—	4	—	—	—	32
43	60	—	17	—	—	—	77
62	34	—	13	—	—	—	47
65	57	—	15	—	—	—	72
67	49	—	14	—	—	—	63
74	38	—	13	—	—	—	51
82	45	—	15	—	—	—	60
85	50	—	9	—	—	—	59
90	15	—	9	—	—	—	24
92	21	—	5	—	—	—	26
Total	507	—	149	—	1	—	657
Expected	492·75	—	164·25	—	—	—	657
1	40	4	7	1	—	—	52
3	21	7	4	1	—	—	33
4	13	4	1	0	—	—	18
5	37	2	8	0	—	—	47
6	9	3	4	1	—	—	17
8	4	1	1	1	—	—	7
10	43	11	10	1	—	—	65
11	24	9	6	4	—	—	43
12	27	12	9	2	—	—	50

The numeral in brackets denotes the number of the plants which made bud-variation.

TABLE VI (*continued*).

Pedigree No.	Heart leaf	Heart-shaped "Sasa" leaf	Roundish willow leaf	Filamentous willow leaf	Heart-shaped maple leaf	Heart-shaped maple "Sasa" leaf	Total
13	15	4	2	0	—	—	21
17	42	16	13	9	—	—	80
18	39	9	10	1	—	—	59
19	7	2	1	1	—	—	11
20	40	5	12	2	—	—	59
25	11	3	1	0	—	—	15
26	27	6	5	1	—	—	39
27	29	7	5	1	—	—	42
28	72	13	12	3(1)	—	—	100
30	5	0	0	1	—	—	6
32	20	11(1)	5	3	—	—	39
33	27	8	7	3	—	—	45
38	13	2	1	0	—	—	16
40	40	16(1)	4	1	—	—	61
42	16	8(1)	2	1	—	—	27
44	41	16(1)	21	4	—	—	82
45	17	2	10	3	—	—	32
46	7	1	2	0	—	—	10
47	12	3	4	1	—	—	20
50	16	6(1)	7	2	—	—	31
52	37	7	15	2	—	—	61
53	56	19	15	3	—	—	93
54	34	15	13	6	—	—	68
55	40	11	9	1	—	—	61
57	58	12	23	5	—	—	98
58	23	9	9	0	—	—	41
59	25	6	2	0	—	—	33
60	33	10	13	0	—	—	56
61	55	21	21	4	—	—	101
63	53	11	11	4	—	—	79
68	33	12	11	3	—	—	59
72	57	8	11	2	—	—	78
77	30	6	10	2	—	—	48
83	26	15	9	4	—	—	54
84	28	6	7	0	—	—	41
87	19	4	2	0	—	—	25
88	20	7	5	1	—	—	33
89	15	4	4	0	—	—	23
91	22	3	4	2	—	—	31
93	16	1	0	1	—	—	18
Total	1384	378(1)	378	88(1)	—	—	2228
Expected	1253·25	417·75	417·75	139·25	—	—	2228

Offspring of the heart-shaped "Sasa" F_2.

Pedigree No.	Heart-shaped "Sasa" leaf	Filamentous willow leaf	Heart-shaped maple "Sasa" leaf	Total
7	4	—	—	4
29	2	—	—	2
80	1	—	—	1
Total	7	—	—	7

The numeral in brackets denotes the number of the plants which made bud-variation.

table shows no new results beyond our expectation, so that no further discussion is necessary on the segregation of the factors in question. But a word will be added on the considerable discrepancy of the ratio observed in the result of the dihybrid segregation. Here the mathematical treatment shows that χ^2 is very high, numerically 37·91, so the value of P is almost zero. But this discrepancy in the ratio may be mainly due to the death of the recessive forms as a result of their weakness. If we correct the data on the assumption that the segregating ratio of each alternative character-pair must be 3 : 1, the numbers are 1243·08 hearts, 429·85 heart-shaped "Sasas," 429·285 roundish willows and 126·35 filamentous willows, where we expected 1253·25, 417·75, 417·75 and 139·25 respectively. Here χ^2 equal 1·91, so the goodness of fit is fairly high, numerically 0·59, showing about one chance of such an occurrence in every two trials.

THE PRODUCTION OF THE SPLIT WILLOW LEAF.

The type of leaves in a given strain is usually almost uniform in one individual, while it varies to a considerable extent in the leaves of the so-called "Rangiku," the sharp-pointed leaves irregularly being shaped and lobed. This strain blooms into a "creased" flower of funnel shape; the corolla consists of numerous petals and is frequently cut in one or two places. The cotyledons are shortened in the length of their lobes just like those of the radish, and sometimes are split in an irregular manner. These features are the multiple representations of a single "Rangiku" factor.

The experiments made by Hagiwara[1] and myself[2] showed that the characteristics are transmitted together as a recessive unit to the normal. The Japanese word "Rangiku" means "creased chrysanthemun," the name coming from its elegant flowering.

As the result of pollination with the pollen-grains of a willow leaf (505) on the stigma of a "Rangiku" flower (M 3) I obtained some F_1 plants bearing the roundish normal leaves and normal funnel-shaped flowers. These aspects as represented on the hybrid plants are entirely different from those of both parents, and the form is not that of any intermediate state. Such plants gave the F_2 offspring segregated as follows:

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[1] Hagiwara, T., "On the inheritance of linked genes in the leaf of the Japanese Morning Glory. II," *Journal of the Scientific Agricultural Society*, No. 224, 1921, in Japanese.

[2] Imai, Y., "Genetic studies in Morning Glories. II," *Botanical Magazine*, Tôkyô, vol. XXXIV, 1920, in Japanese.

TABLE VII.

Pedigree number	Normal leaf	Roundish normal leaf	Heart leaf	"Rangi-ku" leaf	Willow leaf	Roundish willow leaf	Split willow leaf	Maple leaf	Total
M 3 × 505–1	3	4	9	9	6	1	0	1	33
–2	20		8	9	10	3	3	0	35
Total	27		17	18	16	4	3	1	86
Expected	36·28		12·09	16·13	12·09	4·03	5·38	0	86

TABLE VIII.

The F_3 *data of the cross* M 3 × 505.

Offspring of the normal leafed F_2.

Pedigree No.	Normal leaf	"Rangiku" leaf	Willow leaf	Split willow leaf	Maple leaf	"Mitsuo" leaf	Total
6	40	—	—	—	—	—	40
4	38	9	—	—	—	—	47
9	18	2	—	—	—	—	20
10	60	21	—	—	—	—	81
19	9	3	—	—	—	—	12
Total	125	35	—	—	—	—	160
Expected	120	40	—	—	—	—	160
2	8	—	5	—	—	—	13
15	61	—	19	—	—	—	80
16	32	—	8	—	—	—	40
18	61	—	18	—	—	—	79
23	4	—	1	—	2	—	7
24	50	—	10	—	—	—	60
Total	216	—	61	—	2	—	279
Expected	209·25	—	69·75	—	—	—	279
1	105	33	33	8	2	—	181
5	7	2	4	0	—	—	13
11	61	28	20	1	—	—	110
13	52	12	18	9	—	—	91
17	25	5	6	3	—	—	39
Total	250	80	81	21	2	0	434
Expected	244·125	81·375	81·375	27·125	—	—	434

Offspring of the "Rangiku" leafed F_2.

Pedigree No.	"Rangiku" leaf	Split "Rangiku" leaf	"Mitsuo" leaf	Total
Total of 3 pedigrees	17	—	—	17
3	30	7	—	37
8	14	2	—	16
12	9	1	—	10
20	9	1	—	10
22	0	1	—	1
Total	62	12	0	74
Expected	55·5	18·5	—	74

The forms produced were normal, roundish normal, heart, "Rangiku," willow, roundish willow and split willow leaves (Pl. X, fig. 7); among them, the last form was a novelty to me. The split willow leaf as it might be called, is a variety of the willow, but the margin of the lamina is serrated and sometimes split into two or three lobes. The flower of this strain is divided and creased, or in other words it represents both characteristics of the willow and the "Rangiku" flowers. The cotyledons are small in size and irregularly formed in various shapes and sizes (Pl. X, fig. 7), the extreme variation going to form tiny spatula (Pl. X, fig. 8). Even in one seedling both cotyledons frequently differ conspicuously in size as well as in shape.

On account of sterility of some F_2 forms the F_3 raising was successful only in the normal, the heart and the "Rangiku" leaves. After transplantation in the field, the majority of the F_3 seedlings were, however, damaged by continuous rain, so the records made after that time do not contain an adequate number of specimens. For this reason the data based on the records made at the time of transplantation will be shown in Table VIII. On account of the fact that the records were taken on the examination of the seedlings, which extended to only two or three leaves, I failed to note the heart leaves as distinguished from the normals. So the normal class may contain heart leaves in the families segregated for their factor. The F_2 results prove the occurrence of segregation of two recessive factors, the "Rangiku" and the willow, as may be seen in the F_2 data. The genetic composition of the parental willow and "Rangiku" plants are considered to be $\mathbf{w_w w_w hhII}$ and $\mathbf{W_w W_w HHii}$ respectively, where $\mathbf{w_w}$ denotes the willow, **h** the heart and **i** the "Rangiku." On the triple combination of such factors the F_2 generation may be expected to be composed of:

Genotype	Its ratio	Phenotype	Its ratio
$\mathbf{W_wW_wHHII}$	1	Normal leaf	9
$\mathbf{W_ww_wHHII}$	2		
$\mathbf{W_wW_wHHIi}$	2		
$\mathbf{W_ww_wHHIi}$	4		
$\mathbf{W_wW_wHhII}$	2	Roundish normal leaf	18
$\mathbf{W_ww_wHhII}$	4		
$\mathbf{W_wW_wHhIi}$	4		
$\mathbf{W_ww_wHhIi}$	8		
$\mathbf{W_wW_whhII}$	1	Heart leaf	9
$\mathbf{W_ww_whhII}$	2		
$\mathbf{W_wW_whhIi}$	2		
$\mathbf{W_ww_whhIi}$	4		
$\mathbf{W_wW_wHHii}$	1	"Rangiku" leaf	12
$\mathbf{W_ww_wHHii}$	2		
$\mathbf{W_wW_wHhii}$	2		
$\mathbf{W_ww_wHhii}$	4		
$\mathbf{W_wW_whhii}$	1		
$\mathbf{W_ww_whhii}$	2		

Genotype	Its ratio	Phenotype	Its ratio
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{HHII}$	1	Willow leaf	9
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{HhII}$	2		
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{HHIi}$	2		
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{HhIi}$	4		
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{hhII}$	1	Roundish willow leaf	3
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{hhIi}$	2		
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{HHii}$	1	Split willow leaf	4
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{Hhii}$	2		
$\mathbf{w}_{\mathbf{w}}\mathbf{w}_{\mathbf{w}}\mathbf{hhii}$	1		

The hypothesis offered above is made on the basis of the results, so no further discussion on the subject is necessary.

TRIPLE SYSTEM OF ALLELOMORPHS.

As was fully stated in the foregoing pages the willow leaf behaves as a recessive to the normal, three-lobed leaf. But curiously enough, it gives almost habitually, though rarely in frequency, the maple bud-sports (Pl. X, figs. 10 and 13). Why has the willow leaf a tendency to change towards the maple? Is the willow leaf allelomorphic to the maple? Also, what relation is there among the normal, the maple and the willow leaves? Both leaf forms, maple[1] and willow, act as recessive characters to the normal. If we assume tentatively two recessive factors denoted by **a** and **b** respectively, the genetic composition of the normal leaf should be **AABB**, while both maple and willow leaves, each of which constitutes a monohybrid in hybridization with the normal, may have **aaBB** and **AAbb** compositions respectively. If this were the case, what sort of transformation of the willow leaf factor might occur in the continuously sporting phenomena? It is out of the question to think that **AAbb** might have changed at one step into **aaBB** or **aaBb**. So there is no other conclusion but that the genetic composition of the maple sport on the willow strain is **aabb**. Such a constitution may be considered as the result of transformation of the two **A** factors to the **aa**-condition. The sport maple branches and individuals, however, produce no seeds, so we could not examine the genotype by their descendants. When the willow leaf, however, is crossed with the maple the F_1 should revert to the normal as the result of recovery of both dominant factors, **A** from the willow parent and **B** from the maple partner. Such F_1 may produce offspring composed of 9 normals (1**AABB** + 2**AaBB** +2**AABb** + 4**AaBb**): 3 willows (1**AAbb** + 2**Aabb**): 4 maples (1**aaBB** + 2**aaBb** + 1**aabb**) in every 16 individuals. To see whether this is the case or

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[1] Toyama, K., "On one or two Mendelian characters," *Journal of the Japanese Breeders' Association*, vol. I, No. 1, 1916, in Japanese. Imai, Y., "Genetic studies in Morning Glories. II," *Botanical Magazine*, Tôkyô, vol. XXXIV, 1920, in Japanese.

not, I attempted to fertilise the common maple flowers by the pollen of the willow flower, and five individuals were raised from the seeds thus crossed. The F_1 plants, contrary to expectation, all bore maple leaves and bloomed with five-split flowers. Among them, three plants were allowed to grow for the purpose of obtaining seeds, but they proved to be sterile. The leaf form of the F_1 plants was maple, but the figure was somewhat more slender than the common maple. The narrow lobed maple was also a characteristic of the maple sport on the willow specimens. From these facts we may conclude that the normal, maple and willow leaves make up a triple system of allelomorphs. The order of dominancy is normal → maple → willow, and the last has a tendency to mutate into the middle form. Let us now attempt to represent the factors for these three leaves in one series of allelomorphs, namely, **M**, **m** and **m′** respectively. The occurrence of the maple sport on the willow strain should be, then, due to the result of the factor mutation from the willow, **m′m′**, to the heterozygous maple, **mm′**, and the slender figure of the sporting maple leaves may be understood to be the result of the recessive factor. The phenomena of multiple allelomorphs are not rare in the Japanese Morning Glory. I have detected five cases of a triple system of allelomorphs in this plant, viz.:

1. Normal, maple and willow leaves.
2. Normal, cup flower with crapy leaf and cup flower with normal leaf[1].
3. Fully coloured, "Shedding Tears" and "Circular Cloud" (colour patterns of corolla).
4. Normal, common contracta and contracta with "platicodon" flower.
5. Black, brown and tan seeds (?).

MUTABILITY OF THE WILLOW FACTOR TO THE MAPLE.

In the various crosses of the willow leaf as was shown in the previous tables we had almost invariably a few maples (Pl. X, figs. 9, 11 and 12) among the expected segregates, besides the rare occurrences of the maple bud-variation in the willow plants. So the spontaneous occurrence of the maple leaf may be considered a common phenomenon in the segregating families of the willow leaf. In Table X (p. 95) the available

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[1] Imai, Y., "Genetic studies in Morning Glories. XI. On the variegated and the heart leaf linkage groups in *Pharbitis Nil*," *Botanical Magazine*, Tôkyô, vol. XXXVIII, 1924, in Japanese.

data, which I now have on hand, will be found collected and summarised. Among them, the F_3 data of the cross, 65 × 505, were obtained from two sources, the one from Table IV, and the other from Table IX which consists of the records made at the seedling stage of the other families besides those given in the former table.

Thus the numerical proportion of the willow and non-willow leaves is nearly 1 : 3, but it contains about 0·4 per cent. of the maple individuals and approximately 0·12 per cent. of the maple bud-sports among the willows. The fact that the spontaneous appearance of the maple rogues and bud-sports is limited to the willow crosses tells us of an intimate relationship between the maple sports and the willow leaf. On a consideration of the spontaneous appearance of the maple, the occurrence of the bud-sports seems to give us a clue to the solution of the problem. The sport branch bears the maple leaves and blooms into five broad petals like that known as the "maple flowering" (Pl. X, fig. 10), while the willow parts of the same individual remain quite normal for the willow leaf and the five narrow lobed petals. Such bud-sports were detected on three plants among 1796 willows. The total comprises all the available specimens except that a part of the F_3 data given in Table IX is omitted on account of the inadequate conditions obtaining for our purpose, in that the record was taken from a bed of seedlings not fully grown, though even with such a handicap I observed one bud-sporting specimen. As was shown in the previous section the maple leaf acts as the second member of the triple allelomorphs of the willow series, so that its genetic difference to the willow must be in one factor. So the bud-sport may be considered to be the result of vegetative mutation of **m′** to **m**. Actually the willow leaf carries the **m′m′**-composition and as the result of its transformation to the **mm′**-composition the maple branch may be produced. Such sporting individuals being in the proportion of 0·17 per cent. among the total willows, the frequency of the vegetative transformations of the willow to the maple must be rare, though the phenomenon is habitual. As to the individual sports 61 maple mutants are formed among 15,200 observed individuals, the frequency of the occurrence being 0·40 per cent. The ever-sporting nature of the willow factor to the maple in the vegetative tissues may indicate the possibility that these mutants are at least partly due to the result of the vegetative sport occurring on the mother plant. If this were the case, the seeds collected from the non-willow plant which looks quite normal, but contains mutated tissue of the **Mm**-composition, should give some maples among the expected segregatives. The proportion of

TABLE IX.

The F_3 *data of the cross* 65 × 505.
Offspring of the non-willow leafed F_2.

Pedigree No.	Non-willow leaf	Willow leaf	Maple leaf	Total
Total of 35 pedigrees	3461	—	—	3461
59	43	19	2	64
60	5	4	—	9
61	30	9	—	39
62	84	24	1	109
63	27	8(1)	2	37
64	45	21	—	66
65	100	27	—	127
66	59	19	1	79
67	13	6	—	19
68	201	55	—	256
71	73	31	—	104
72	21	4	—	25
73	32	6	—	38
74	124	44	1	169
75	48	23	—	71
76	66	22	—	88
77	98	42	—	140
78	128	39	—	167
79	27	5	—	32
80	62	13	2	77
82	51	18	—	69
83	75	28	1	104
84	34	7	—	41
85	27	13	—	40
86	144	31	—	175
94	25	6	1	32
95	137	38	—	175
97	60	17	—	77
100	71	24	—	95
103	101	45	—	146
106	16	9	2	27
107	165	44	2	211
109	284	91	3	378
110	43	11	—	54
111	3	2	1	6
117	194	50	1	245
119	89	22	2	113
120	54	25	1	80
121	59	14	—	73
122	44	8	—	52
124	4	1	—	5
125	80	29	1	110
126	131	39	—	170
127	17	7	—	24
128	25	11	—	36
130	29	16	—	45
131	73	29	1	103
133	84	29	—	113
136	17	5	—	22
138	160	43	—	203
142	297	75	3	375
144	73	20	—	93
145	104	19	1	124

TABLE IX (*continued*).

Pedigree No.	Non-willow leaf	Willow leaf	Maple leaf	Total
146	55	21	—	76
147	37	12	—	49
148	30	8	—	38
149	68	24	—	92
150	67	18	—	85
151	240	64	—	304
152	97	20	—	117
153	33	9	—	42
154	140	37	—	177
155	49	13	—	62
156	112	29	1	142
157	17	4	—	21
158	75	26	—	101
159	175	41	4	220
160	106	37	3	146
162	46	11	—	57
Total	5403	1621(1)	37	7061
Expected	5295·75	1765·25	—	7061

The numeral in brackets denotes the number of the plants which made bud-variation.

TABLE X.

Cross	Non-willow	Willow	Bud-Sporting willow	Maple	Total
Y 120	93	34	—	2	129
Y 122	38	9	—	—	47
Y 123	210	70	1	—	281
Y 120—(1–4)	45	13	—	—	58
65 × 505—F_2	309	73	—	4	386
—F_3 (from Table IV)	2481	725	2	12	3220
—F_3 (from Table IX)	5403	1620	1	37	7061
326 × 505—F_2	204	56	—	—	260
—F_3	2269	615	—	1	2885
M 3 × 505—F_2	62	23	—	1	86
—F_3	608	175	—	4	787
Total	11722	3413	4	61	15200
		3417			
			3478		
Expected	11400		3800		15200

the appearance of the maple mutants may vary according to the degree of the extent of the area of the mutated tissue. Generally speaking, the result of such a vegetative mutation is to cause the mutants to occur more or less in a mass. Actually we observed no adequate positive evidence in the segregating families of the divergent crosses. Examining carefully the actual numbers of the tables we see that the mutants generally occur one by one in each family. For this reason the possibility that the mutants are due to the result of somatic variation in the tissue of the parental plant seems to be small. So we may recognise that the origin of maple mutants, at least in the majority of cases, lies in the gametogenesis[1] of the willow plants. But even if we can hardly recognise the possibility of the somatic occurrence of the mutation as a cause of the appearance of the maple mutants, this does not mean that we altogether abandon the expectation of such an actual occurrence. As was stated before, we had 0·17 per cent. occurrence of bud-sports among the willow leaves. So it is not impossible to expect such a somatic variation also on the $\mathbf{Mm}'$-individuals. Practically, however, even if this were so, the frequency of such an occurrence would be low, only about one case in every six hundred trials, so we cannot be far wrong in taking for granted that the consideration of such occurrence may be placed outside the problem.

Let us now attempt to make a quantitative estimate of the frequency of the occurrence of the mutation, $\mathbf{m}' \rightarrow \mathbf{m}$. As was stated, we can recognise that the maple mutants are possibly due to the result of gametic mutation. If we regard all the maple mutants to be originated by factorial change in gametogenesis the following calculation may be made: In the normal leaves which are heterozygous for the willow factor two sorts of gamete, $\mathbf{M}$ and $\mathbf{m}'$, would be expected in an equal ratio. Actually, however, the contents of gametes are complicated by the ever-sporting occurrence of the willow factor in the maples. Let us represent the frequency value of the mutation, $\mathbf{m}' \rightarrow \mathbf{m}$, by x, and denote the total of the gametes as 2, then, the contents of the gametes actually produced must be supposed to be $1\mathbf{M} + (1 - x)\,\mathbf{m}' + x\mathbf{m}$, namely in the ratio of 1 normal gamete : $1 - x$ willow gamete : x maple gamete. On sexual combination of these three sorts of gametes we should expect to obtain the following zygotes:

$$\{1\mathbf{M} + (1 - x)\,\mathbf{m}' + x\mathbf{m}\}^2 = 1\mathbf{MM} + 2\,(1 - x)\,\mathbf{Mm}' + 2x\mathbf{Mm} + (1 - x)^2\,\mathbf{m}'\mathbf{m}' + 2\,(1 - x)\,x\mathbf{m}'\mathbf{m} + x^2\mathbf{mm}.$$

The frequency value of the occurrence of the maple mutation, then, may be calculated on the basis of the above formula. By the formula we understand that the respective frequency of the homozygous normal, the heterozygous normal for the willow, and the heterozygous normal for the maple is in the proportion of $1 : 2\,(1 - x) : 2x$. If the examined total numbers, the sum of the data of Tables IV, VI, VIII and IX, are applied to the above ratios the following formulae may be deduced:

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[1] My opinion on this view will be stated in a future paper.

$$\frac{\mathbf{MM}}{\mathbf{Mm'}} = \frac{1}{2\,(1-x)} = \frac{82}{179} \quad \text{...........Formula 1,}$$

$$\frac{\mathbf{MM}}{\mathbf{Mm}} = \frac{1}{2x} = \frac{82}{1} \quad \text{...........Formula 2,}$$

$$\frac{\mathbf{Mm'}}{\mathbf{Mm}} = \frac{2\,(1-x)}{2x} = \frac{179}{1} \quad \text{...........Formula 3.}$$

As Formula 1 gives a minus answer, this case may be placed outside this calculation. From Formula 2 we get the result of 0·0061, and from Formula 3 that of 0·0056, a very similar value. On the basis of these values a frequency of mutation of the $\mathbf{m'} \rightarrow \mathbf{m}$ of about one in every one hundred and seventy gametes may be expected. Another calculation may be made on the basis of the numbers of the maple and willow leaves. The formula is:

$$\frac{\mathbf{mm} + \mathbf{mm'}}{\mathbf{m'm'}} = \frac{x^2 + 2\,(1-x)\,x}{(1-x)^2} = \frac{61}{3417} \quad \text{...Formula 4.}$$

On account of the fact that we cannot distinguish[1] the **mm**-carrying and the **mm'**-carrying maples, because they produce no seeds, two genotypes are considered together in the calculation of this formula. The answer obtained from this formula is 0·0091, showing a value approximating those calculated from Formulas 2 and 3. Critically speaking, the former results are more reliable than the latter; for since the latter were calculated on the basis of a single plant of the **Mm**-class they have only a rough value. For this reason the frequency of the mutation of the $\mathbf{m'} \rightarrow \mathbf{m}$ may be considered to be 0·0091, or 0·91 per cent. When we consider, however, the respective percentage of the mutability in the different crosses it varies to a considerable extent as will be seen from the subsequent table:

TABLE XI.

Cross	Willow leaf	Maple leaf	Total	Mutability
Y 3 pedigrees	127	2	129	0·78 %
65 × 505	2421	53	2474	1·08 %
326 × 505	671	1	672	0·07 %
M 3 × 505	198	5	203	1·24 %
Total	3417	61	3478	0·91 %

In short, the frequency varies in extent from 0·07 per cent. to 1·24 per cent. Such a considerable variation of the values in the different

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[1] Practically, only one case in every one hundred and eleven maple mutants may be expected in the homozygotic condition, if we calculate the proportion on the basis of 0·9 per cent. as the frequency for the maple mutation.

crosses, it would seem could hardly be attributed to the chances of sampling. I am inclined to think it is the result of the modifier or modifiers which influence the frequency of the mutability. This hypothesis, however, must be tested by future study.

I wish to take this opportunity to express my hearty thanks to Prof. K. Miyake, under whose direction the experiments were conducted, and to Mr K. Hashimoto for the substantial encouragement he so kindly gave. Last but not least I would also express my cordial thanks to Messrs B. Kanna and K. Tabuchi for their friendly help in my investigation. Without these gentlemen the completion of the present study might have been doubtful.

SUMMARY.

1. The willow leaf acts as a recessive to the normal.

2. The willow factor (**m′**) represents the narrow-lobed cotyledon and the willow leaf as well as the narrow split corolla.

3. The factor for the normal, maple and willow leaves may constitute a triple system of allelomorphs.

4. The order of dominancy of these factors is the normal (**M**) → the maple (**m**) → the willow (**m′**).

5. The willow factor produces the roundish willow leaf in combination with the factor for the heart leaf.

6. The filamentous willow leaf is produced as a combined result of the factors for the willow and the "Sasa" leaves. The flower of this strain blooms into a five-lobed filamentous corolla.

7. On combining the factors for the willow and the "Rangiku" leaves we get the split willow leaf, which blooms into a flower with characteristics of both factors; namely the flower is creased and split.

8. Maple bud-sports were rarely, but habitually, observed on the willow plants.

9. The frequency of the occurrence of such sporting plants among the willows is estimated to be 0·17 per cent.

10. More frequently maple rogues appeared in the segregating families for the willow leaf.

11. The origin of these variations, both bud-sport and individual rogue, lies in the result of mutation of the **m′** → **m**.

12. The maple rogues seem to originate, at least in the majority of cases, through the occurrence of mutation in gametogenesis.

13. The frequency of the gametic mutation of the **m′** → **m** is 0·91

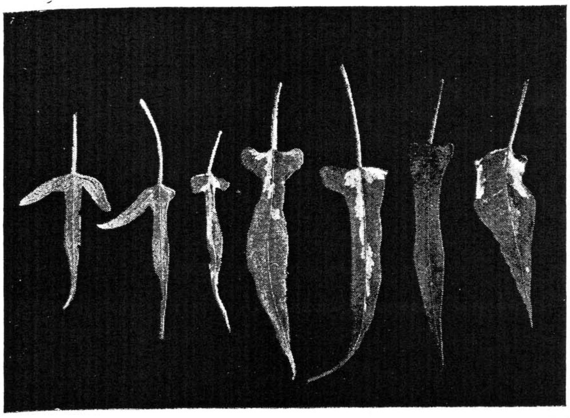


Fig. 1.

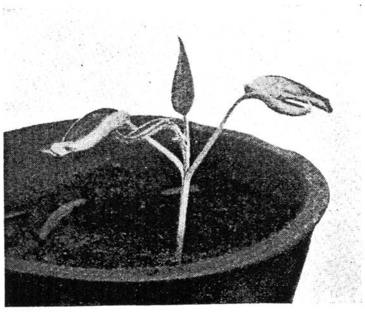


Fig. 2.

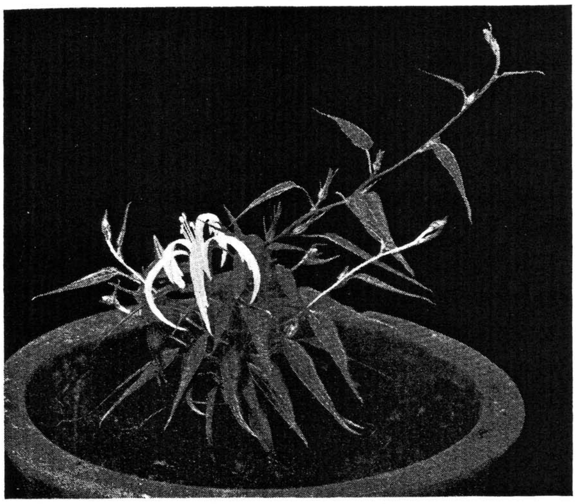


Fig. 3.

Fig. 4.

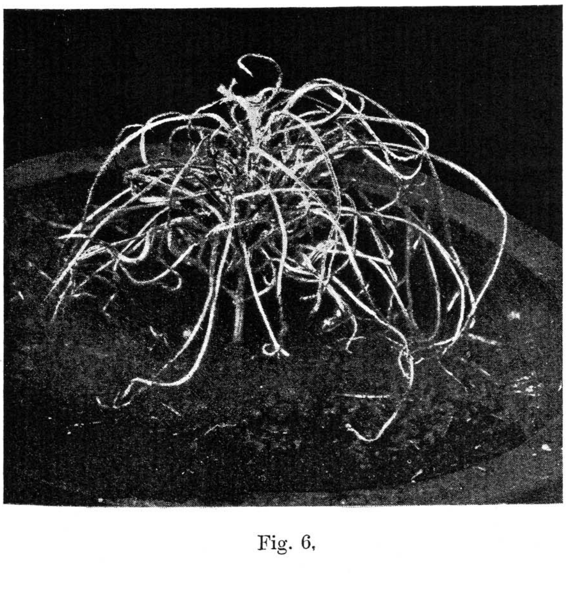
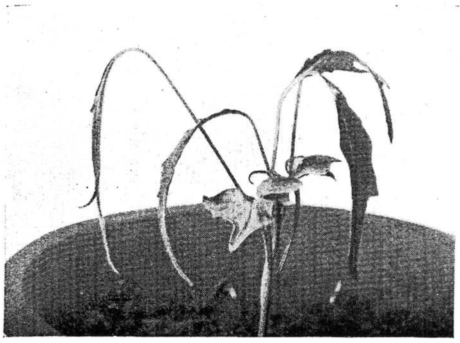


Fig. 6,

Fig. 5.



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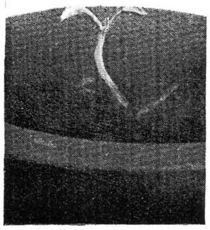

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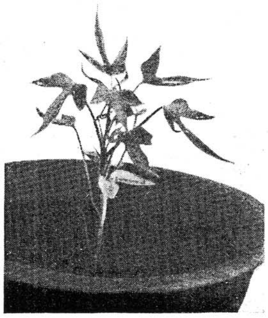

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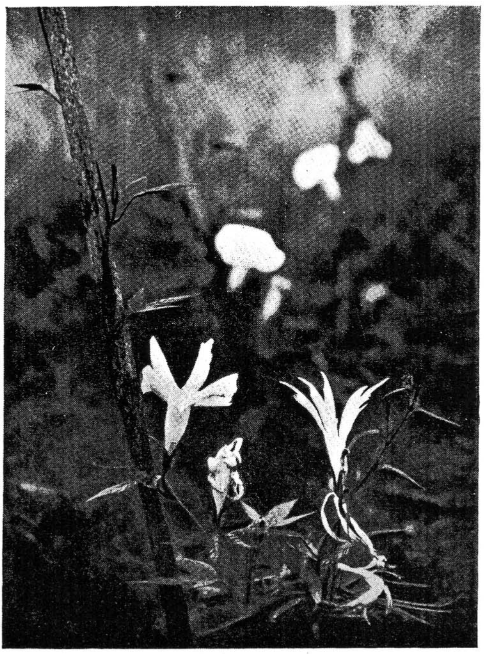

Fig. 10.

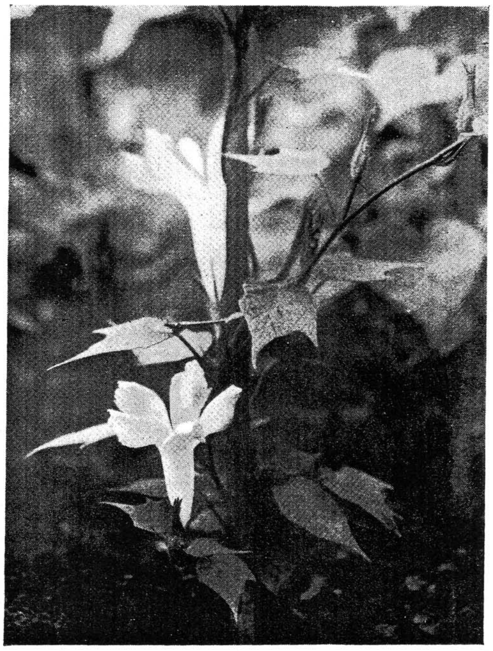

Fig. 12.

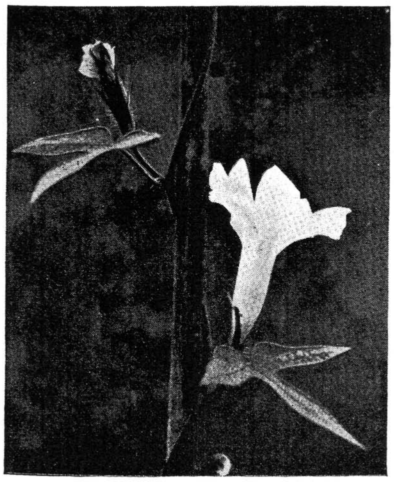

Fig. 11.

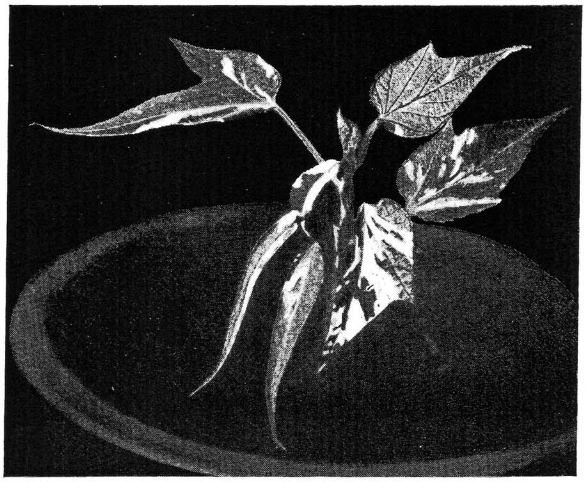

Fig. 13.

per cent., showing that there is about one chance of such an occurrence among one hundred and ten willow gametes.

14. The frequency, however, varies considerably in the different crosses.

15. The willow leaf invariably produces no seeds. This is also true in the maple mutants, which are considered to be heterozygotic for the willow factor.

EXPLANATION OF PLATES IX, X.

Fig. 1. Variation of the common willow leaf.

Fig. 2. Seedling of the roundish willow bearing punched leaves.

Fig. 3. Blooming roundish willow plant.

Fig. 4. Slender three-lobed willow specimen, an extreme form of the normal willow.

Fig. 5. Blooming roundish willow cultivated in the field.

Fig. 6. Filamentous willow specimen.

Fig. 7. Seedling of the split willow specimen with irregular-shaped cotyledons.

Fig. 8. Seedling of the split willow with cotyledons in the shape of tiny spatula.

Fig. 9. Seedling of a maple mutant with slender three-lobed leaves.

Fig. 10. A willow bearing a maple bud-sport. Note the marked contrast in foliage and flower.

Fig. 11. A portion of the stem of a maple mutant with five-split flower.

Fig. 12. Heart-shaped maple mutant with the "maple blooming" flowers.

Fig. 13. A roundish willow leafed seedling making a vegetative variation toward the heart-shaped maple. Note the two largest leaves which are a mosaic of half willow and half maple.