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EXPERIMENTS WITH A PEAR-LEAFED AND FASCIATED STRAIN OF THE JAPANESE MORNING GLORY.

BY YOSHITAKA IMAI.
(*Botanical Institute, Agricultural College, Tokyo Imperial University, Komaba, Tokyo.*)

(With Two Plates and Eleven Text-figures.)

CONTENTS.

INTRODUCTION.

THE phenomenon of fasciation has been observed in various groups of plants, and is generally of a temporary nature due to environmental stimulation, though sometimes hereditary. Several authors have made experiments on this character and have obtained fairly simple results. In the Japanese morning glory, fasciation was recognised in relatively early days. The results obtained by me in breeding experiments with the fasciated strain have shown that the case is somewhat complicated by the occurrence of three or more factors affecting its manifestation. In almost all cases fasciated stems are accompanied by pear leaves, owing to the occurrence of linkage, which further complicates the genetics of the pear-leafed and fasciated plants. Some pear-leafed fasciated examples bear funnel-shaped flowers, while others bear split ones. The experiments revealed the fact that a split corolla is the effect of the "maple" factor. Consequently we may commence our account with an outline of the hereditary behaviour of pear leaf.

HEREDITARY BEHAVIOUR OF PEAR LEAF.

The pear leaf (Figs. 1, 10 and 11, Pls. XVII and XVIII, figs. 1, 8 and 9) was so named because of its resemblance to a leaf of the pear, and it is sometimes called "Kujaku[1]" leaf or "Imo[2]" leaf by our fanciers. The hereditary behaviour of this leaf was studied by Miyake and Imai (1920), and Hagiwara (1925), who recognised its simple recessive nature to the normal. Pear leaves have either double or single flowers, and the present studies were carried on with strains of the latter.

Pear leaf versus *Normal leaf.*

In crosses between normal and pear leaves the F_1 plants bear quite normal leaves. Although the pear leaf resembled in shape the cordate (= heart) leaf, which produces some recessive effect upon the hybrid leaves of cordate and normal, the F_1 leaves of the present cross showed no influence of their heterozygous nature. The F_2 generation consisted of the alternative forms in a simple ratio as indicated in Table I.

TABLE I.

The F_2 *data obtained by the crossing of normal and pear leaves.*

Cross	Normal leaf	Pear leaf	Total
65 × BD-B	435	139	574
L × N 1	75	26	101
Total	510	165	675
Expected	506·25	168·75	675

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[1] "Kujaku" means peacock in Japanese. Pear leaves bear double flowers, in which the petaloid filaments stand out above the corollas rather like the crest of a peacock. The term was then applied to the leaves accompanying such double flowers, and eventually to pear leaves in general with no limitation in regard to their flowers.

[2] "Imo" means the Japanese yam (*Dioscorea*). The pear leaf resembles the leaf of some species of the Japanese yam in its form.

In Table II we have summarised the F_3 data, which we need not consider further as the results came out quite normally.

TABLE II.

The F_3 *data of the cross* 65 × BD–B.

Character of F_2	Pedigree number	Normal leaf	Pear leaf	Total
Normal leaf	8	242	—	242
	14	271	83	354
Pear leaf	7	—	125	125

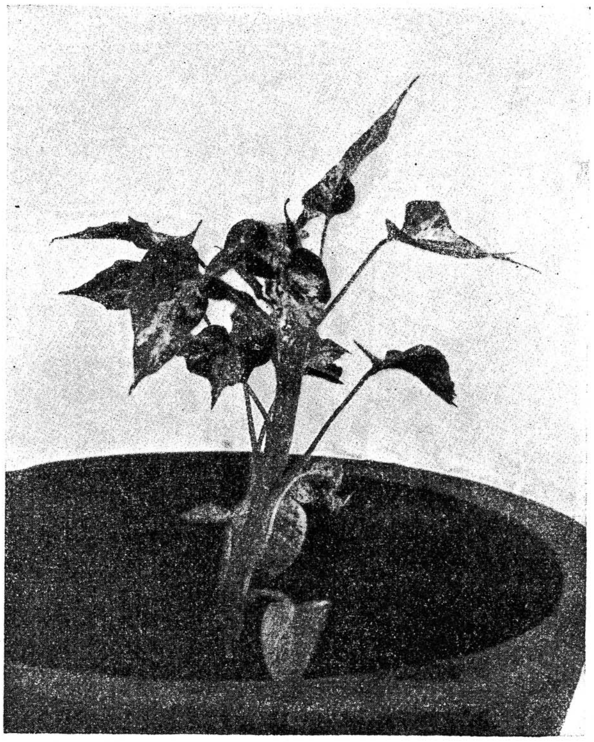


Fig. 1. A fasciated seedling bearing variegated pear leaves (A 5).

The Relation of Pear and Cordate Leaves.

To understand the factorial relations between the two roundish leaves, pear and cordate (Fig. 2), I made a cross between them. The F_1 plants bore normal three-lobed leaves, being entirely different from both parents, but the leaves had roundish lobes as an effect of the recessive cordate-leaf factor. Three families bred from such F_1 hybrids gave the results indicated in Table III.

TABLE III.

The F_2 *data obtained by the crossing of cordate and pear leaves.*

Cross	Normal leaf	Roundish normal leaf	Cordate leaf	Pear leaf	Total
A 1 × N 1	32	82	45	37	196
Expected	36·75	73·50	36·75	49·00	196

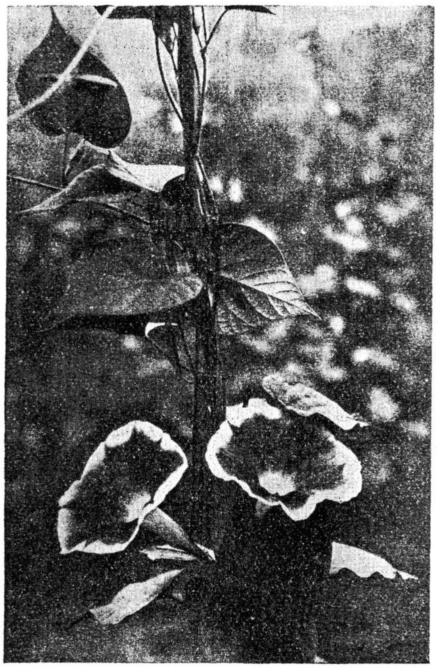


Fig. 2. Cordate leaf bearing normal, funnel-shaped flowers.

As the data obtained are closely in accordance with 3 : 6 : 3 : 4, a modified ratio of dihybrid segregation, it is clear that the factors for pear and cordate leaves belong to different series of allelomorphs. Both leaves are somewhat similarly roundish in shape, but the pear leaf is rather oval and has the peculiar habit of a slight broadening in form at the connecting part of its petiole and lamina, the latter having more or less sloping shoulders. These traits enable us easily to distinguish this leaf from a cordate one. The present cross, therefore, concerns the two factors **p**, pear leaf, and **h**, cordate leaf. The normal F_1 leaf is the combined result of two dominant factors, as far as the present cross is concerned, and the double recessive leaf retains its pear-leafed form. Under these circumstances, the expected ratio in F_2 should be:

1**PPHH** + 2**PpHH**	3 normal leaves
2**PPHh** + 4**PpHh**	6 roundish normal leaves
1**PPhh** + 2**Pphh**	3 cordate leaves
1**ppHH** + 2**ppHh** + 1**pphh**	4 pear leaves

This ratio conforms fairly closely to the actual result as indicated in Table III.

The Relation of Pear and "Rangiku" leaves.

The "Rangiku" leaf (Pl. XVII, fig. 2) is represented by **i**, a recessive leaf-form factor to the normal (Imai, 1925). This factor affects the shape of cotyledons and leaves, the type of flowering, etc., in a complex manner. The cotyledons have shortened lobes, just like those of radishes, and are sometimes branched. The leaves are split irregularly into sharp-pointed lobes, and the flowers are composed of polypetalous corollas rugose in form (Pl. XVII, fig. 4). In the crosses made between "Rangiku" and pear leaves, I obtained normal-leafed F_1 hybrids reverting to their prototype, and the next generation consisted of segregating families as represented in Table IV.

TABLE IV.

The F_2 *data obtained by the crossing of "Rangiku" and pear leaves.*

Cross	Normal leaf	"Rangiku" leaf	Pear leaf	"Rangiku"-pear leaf	Total
M 3 × N 1	82	12	14	1	109
M 3 × N 2	142	34	21	5	202
Total	224	46	35	6	311
Expected	174·94	58·31	58·31	19·44	311

The deviation is conspicuous, though it seems to be caused by the early death of the recessive segregates. The discrepancy in the segregating ratio, which is due to the meagre production of the recessive segregates, is not rarely to be met with in the hybrid progeny of the Japanese morning glory, and the present case, therefore, is not unusual. The cross concerns the segregation of the factors, pear (**p**) and "Rangiku" (**i**) leaves. From the doubly heterozygous F_1 we should expect an F_2 segregation as follows:

1**IIPP** + 2**IiPP** + 2**IIPp** + 4**IiPp**	9 normal leaves
1**iiPP** + 2**iiPp**	3 "Rangiku" leaves
1**IIpp** + 2**Iipp**	3 pear leaves
1**iipp**	1 "Rangiku"-pear leaf

Now we have a new type through the combination of two recessive factors. The specimens had narrow pear leaves, which were split, with shortened and broad petioles (Fig. 3), peculiar in shape, and somewhat small flowers with creased corollas, which are the trait of "Rangiku." The smallness of the corolla, however, is a general characteristic of the flowers of pear leaves.

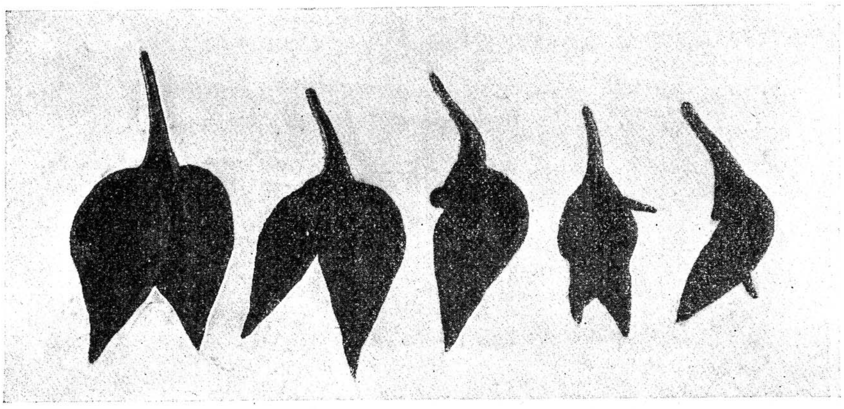


Fig. 3. Samples of "Rangiku"-pear leaves.

On the Pear-leafed strain with Split Corollas.

The pear-leafed strains used in the above cross had perfect funnel-shaped corollas, while A 5, a pure pedigree strain, had five split corollas (Pl. XVII, fig. 1). The split flowers could be identified with the maple type (Pl. XVII, fig. 6) by their relatively broad petals, and breeding tests made this clear (Imai, 1925).

The result of cross 81–1 × A 5. 81–1, one of the parents of the present cross, had normal leaves and funnel-shaped flowers. The F_1 plants bore normal leaves and flowered with perfect corollas, and gave rise to the F_2 generation shown in Table V.

TABLE V.

The F_2 *data of the crossing of normal leaf and pear leaf with split corolla.*

Cross	Normal leaf	Maple leaf	Pear leaf with perfect corolla	Pear leaf with split corolla	Total
81–1 × A 5	71	21	24	6	122
Expected	68·625	22·875	22·875	7·625	122

The genetic origin of the maple is attributed to A 5, which bears maple-type flowers as stated above. Hence the present segregation concerns the factors, **p** and **m**, the latter being responsible for the maple. Theoretically, the F_2 segregation should be:

1MMPP + 2MmPP + 2MMPp + 4MmPp	9 normal leaves
1mmPP + 2mmPp	3 maple leaves
1MMpp + 2Mmpp	3 pear leaves with perfect corollas
1mmpp	1 pear leaf with split corolla

The pear-leafed F_2 segregates will have either perfect corollas (Pl. XVIII, fig. 8) or split ones (Pl. XVIII, fig. 9), according to their genetic composition with respect to the maple factor. Consequently the pear-leafed parent must have been a double recessive for the factors in question.

The result of crosses 22–1 × A 5 *and* 350 × A 5. The present crosses concern the relation of pear and dragon-fly leaves, the latter being transmitted as a recessive to the normal. The genetic nature of the dragon-fly leaf, however, does not seem to be simple in some cases. The F_1 plants of dragon-fly × pear had normal leaves and gave rise to the F_2 shown in Table VI.

TABLE VI.

The F_2 *data of the crossing of dragon-fly leaf and pear leaf with split corolla.*

Cross	Normal leaf	Dragon-fly leaf	Maple leaf	Pear leaf with perfect corolla	Elongated pear leaf with perfect corolla	Pear leaf with split corolla (contains elongated one)	Total
22–1 × A 5	43	4	14	12	1	2	76
350 × A 5	76	6	29	22	5	8	146
Total	119	10	43	34	6	10	222
Expected	93·66	31·22	41·63	31·22	10·41	13·88	222·02

The segregating number of dragon-fly leaves is distinctly below that required in theory, which may perhaps point to this character being of a more complex nature. For our present purpose however we may regard it as simple, and consider that we are dealing with the three factors of **p**, **m** and **t**, the last being responsible for the dragon-fly leaf. Among the pear-leafed F_2, we found some long-shaped ones, which are doubtless pear leaves carrying the dragon-fly factor. The F_2 result of the present cross (**ttMMPP** × **TTmmpp**), therefore, may be expected to be as follows:

1TTMMPP + 2TtMMPP + 2TTMmPP + 2TTMMPp + 4TtMmPP + 4TtMMPp + 4TTMmPp + 8TtMmPp 27 normal leaves
1ttMMPP + 2ttMmPP + 2ttMMPp + 4ttMmPp 9 dragon-fly leaves
1TTmmPP + 2TtmmPP + 2TTmmPp + 4TtmmPp + 1ttmmPP + 2ttmmPp 12 maple leaves
1TTMMpp + 2TtMMpp + 2TTMmpp + 4TtMmpp + 1ttMMpp + 2ttMmpp 12 pear leaves with perfect corollas (contain long-shaped pear leaves)
1TTmmpp + 2Ttmmpp + 1ttmmpp 4 pear leaves with split corollas (contain long-shaped pear leaves)

The theoretical expectation fits the observed data fairly well provided that we do not lay stress upon the low proportion of dragon-fly leaves.

The result of crosses 320 × A 5 *and* M 3 × A 5. In these two cases a pear leaf with split corollas was crossed with a "Rangiku" leaf. Consequently the segregation may be expected to be somewhat complicated. From the normal-leafed F_1 we raised F_2, which was composed of eight phenotypes, as represented in Table VII.

TABLE VII.

The F_2 *data of the crossing of "Rangiku" leaf and pear leaf with split corolla.*

Cross	Normal leaf	"Rangiku" leaf	Maple leaf	Pear leaf with perfect corolla	"Mitsuo" leaf	"Rangiku"-pear leaf with perfect corolla	Pear leaf with split corolla	"Rangiku"-pear leaf with split corolla	Total
320 × A 5	37	6	9	4	1	0	0	0	57
M 3 × A 5	102	31	44	31	9	5	4	1	227
Total	139	37	53	35	10	5	4	1	284
Expected	119·81	39·94	39·94	39·94	13·31	13·31	13·31	4·44	284

It is clear from the observed data that the factors now concerned are **p**, **i** and **m**, and, according to our expectation, the triple heterozygous F_1, obtained by the crossing **PPiiMM** × **ppIImm**, should give the F_2 members as follows:

1IIMMPP + 2IiMMPP + 2IIMmPP + 2IIMMPp + 4IiMmPP + 4IiMMPp + 4IIMmPp + 8IiMmPp 27 normal leaves
1iiMMPP + 2iiMmPP + 2iiMMPp + 4iiMmPp 9 "Rangiku" leaves
1IImmPP + 2IimmPP + 2IImmPp + 4IimmPp 9 maple leaves
1IIMMpp + 2IiMMpp + 2IIMmpp + 4IiMmpp 9 pear leaves with perfect corollas
1iimmPP + 2iimmPp 3 "Mitsuo" leaves
1iiMMpp + 2iiMmpp 3 "Rangiku"-pear leaves with perfect corollas
1IImmpp + 2Iimmpp 3 pear leaves with split corollas
1iimmpp 1 "Rangiku"-pear leaf with split corolla

TABLE VIII.

The F_3 *data of the cross* M 3 × A 5, *showing the segregation of leaf form.*

Number of pedigree	Normal leaf	"Rangiku" leaf	Maple leaf	Pear leaf with perfect corolla	"Mitsuo" leaf	"Rangiku"-pear leaf with perfect corolla	Pear leaf with split corolla	"Rangiku"-pear leaf with split corolla	Total	Genetic composition
Offspring of the normal-leafed F_2.										
2	31	—	—	—	—	—	—	—	31	**IIMMPP**
Expected	31	—	—	—	—	—	—	—	31	
2	23	7	—	—	—	—	—	—	30	**IiMMPP**
Expected	22·5	7·5	—	—	—	—	—	—	30	
1	5	—	1	—	—	—	—	—	6	**IIMmPP**
Expected	4·5	—	1·5	—	—	—	—	—	6	
2	10	—	—	9	—	—	—	—	19	**IIMMPp**
Expected	14·25	—	—	4·75	—	—	—	—	19	
5	73	21	19	—	7	—	—	—	120	**IiMmPP**
Expected	67·5	22·5	22·5	—	7·5	—	—	—	120	
3	49	12	—	13	—	2	—	—	76	**IiMMPp**
Expected	42·75	14·25	—	14·25	—	4·75	—	—	76	
8	146	—	49	64	—	—	10	—	269	**IIMmPp**
Expected	151·31	—	50·44	50·44	—	—	16·81	—	269	
9	127	40	39	37	8	13	4	1	269	**IiMmPp**
Expected	113·48	37·83	37·83	37·83	12·61	12·61	12·61	4·20	269	
Offspring of the "Rangiku"-leafed F_2.										
1	—	7	—	—	1	—	—	—	8	**iiMmPP**
Expected	—	6	—	—	2	—	—	—	8	
1	—	21	—	—	—	5	—	—	26	**iiMMPp**
Expected	—	19·5	—	—	—	6·5	—	—	26	
4	—	52	—	—	19	16	—	4	91	**iiMmPp**
Expected	—	51·19	—	—	17·06	17·06	—	5·69	91	

TABLE VIII (*continued*).

Number of pedigree	Normal leaf	"Rangiku" leaf	Maple leaf	Pear leaf with perfect corolla	"Mitsuo" leaf	"Rangiku"-pear leaf with perfect corolla	Pear leaf with split corolla	"Rangiku" pear leaf with split corolla	Total	Genetic composition
Offspring of the maple-leafed F_2.										
2	—	—	36	—	—	—	—	—	36	IImmPP
Expected	—	—	36	—	—	—	—	—	36	
1	—	—	13	—	2	—	—	—	15	IimmPP
Expected	—	—	11·25	—	3·75	—	—	—	15	
2	—	—	24	—	—	—	8	—	32	IImmPp
Expected	—	—	24	—	—	—	8	—	32	
6	—	—	114	—	27	—	26	10	177	IimmPp
Expected	—	—	99·56	—	33·19	—	33·19	11·06	177	
Offspring of the pear-leafed F_2 with perfect corolla.										
3	—	—	—	61	—	—	—	—	61	IIMMpp
Expected	—	—	—	61	—	—	—	—	61	
3	—	—	—	83	20	—	—	—	103	IiMMpp
Expected	—	—	—	77·25	25·75	—	—	—	103	
3	—	—	—	34	—	—	9	—	43	IIMmpp
Expected	—	—	—	32·25	—	—	10·75	—	43	
2	—	—	—	40	17	—	4	2	63	IiMmpp
Expected	—	—	—	35·44	11·81	—	11·81	3·94	63	
Offspring of the "Rangiku"-pear-leafed F_2 with perfect corolla.										
1	—	—	—	—	—	1	—	—	1	iiMMpp?
Expected	—	—	—	—	—	1	—	—	1	
1	—	—	—	—	—	83	—	14	97	iiMmpp
Expected	—	—	—	—	—	72·75	—	24·25	97	

Expectation agrees in essential points with the actual data in Table VII, except for the low proportion of the combined recessive segregates. The "Mitsuo" leaves are to be regarded as a double recessive form of maple and "Rangiku." They are irregularly lobed in a peculiar way differing somewhat from "Rangiku" leaves. The term "Mitsuo," meaning "three-tailed," was derived from a variety of goldfish which has a tail so named. The flowers of this specimen are of the split "Rangiku" type (Pl. XVII, fig. 5).

An F_3 generation was raised from the F_2 of the cross M 3 × A 5, the result being summarised in Table VIII. It shows that the hypothesis put forward above covers the F_3 results.

The result of cross 326 × A 5. By hybridising A 5 with 326, which is a pure pedigree strain bearing cordate "Sasa" leaves (Fig. 4) and split flowers, we obtained normal leaves with roundish lobes in F_1. Table IX contains the F_2 data obtained from such hybrids.

TABLE IX.

The F_2 *data of the crossing of cordate "Sasa" leaf and pear leaf with split corolla.*

Cross	Normal leaf	Roundish normal leaf	Cordate leaf	Maple leaf	Cordate maple leaf	Pear leaf with perfect corolla	Pear leaf with split corolla	Normal "Sasa" leaf	Roundish-normal "Sasa" leaf	Cordate "Sasa" leaf	Maple-"Sasa" leaf	Cordate maple-"Sasa" leaf	Pear-"Sasa" leaf with split corolla	Pear-"Sasa" leaf with narrowly split corolla	Total
326 × A 5	74	154	76	69	13	108	28	11	33	15	14	10	28	6	639
Expected	67·39	134·79	67·39	67·39	22·46	89·86	29·95	22·46	44·93	22·46	22·46	7·49	29·95	9·98	638·96

The production of fourteen F_2 phenotypes is due to the segregation of the $\mathbf{s_a}$-factor, which is responsible for the "Sasa" leaf (Imai, 1925), besides the factors of **p**, **h** and **m**, the cross producing the quadruply heterozygous F_1. The "Sasa" leaves always accompany split corollas, but the petals are a little narrower than those of the maple. The factor does not markedly change the various leaf forms, but it modifies them in a particular way into the respective "Sasa" leaves (Figs. 4, 5, 6, 7 and 8). Thus the combination of the factors for maple and "Sasa," gives narrowly split corollas divided down to the bottom of the flower

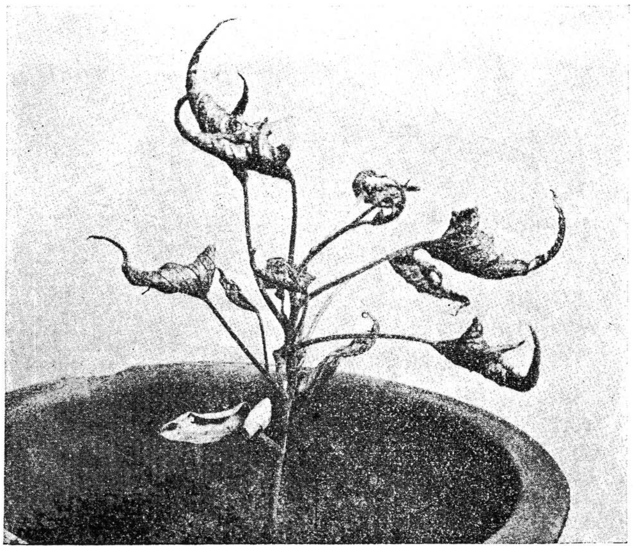


Fig. 4. A seedling of 326, bearing cordate "Sasa" leaves.

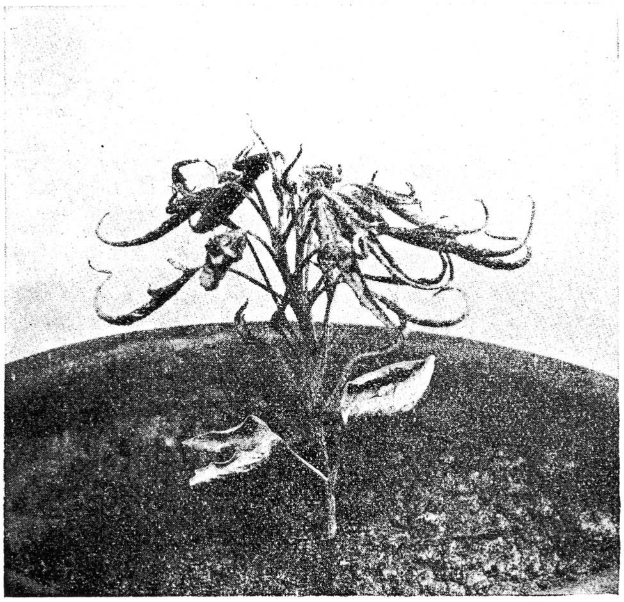


Fig. 5. A seedling bearing maple-"Sasa" leaves.

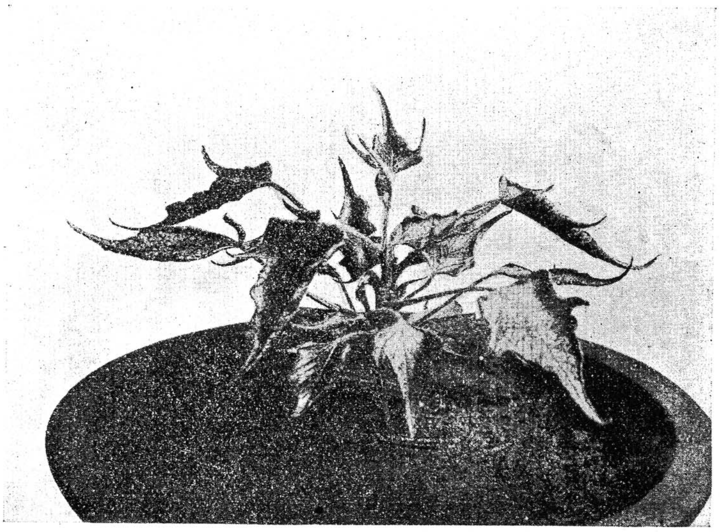


Fig. 6. A seedling bearing cordate maple-"Sasa" leaves.

Fig. 7. A seedling bearing pear-"Sasa" leaves. Fasciated!

tube (Pl. XVII, fig. 3), each factor by itself, however, resulting in split corollas with undivided tubes (Pls. XVII and XVIII, figs. 6 and 10).

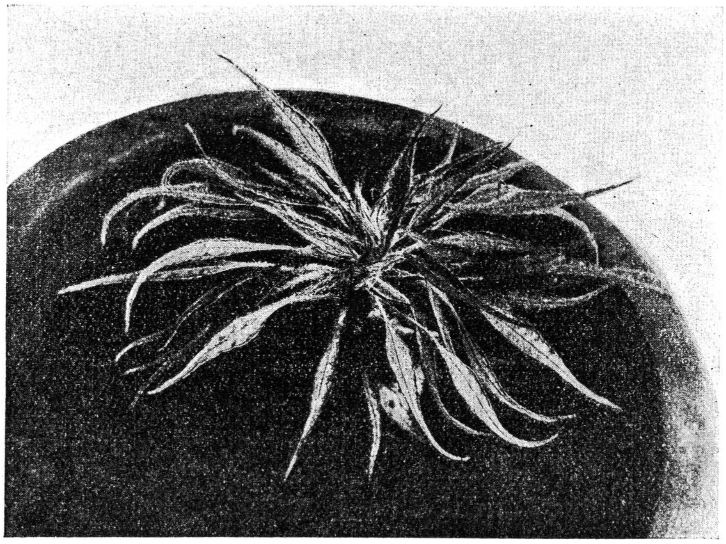


Fig. 8. A pear-"Sasa"-leafed seedling carrying maple factors. Note the slender leaves! The specimen is fasciated and the abnormality can be seen by its flattening bud. (Photographed from above.)

The genetic composition of the parents can be presumed as $\mathbf{s_as_ahhMMPP}$ and $\mathbf{S_aS_aHHmmpp}$ respectively. From the quadruply heterozygous F_1 we may expect the following F_2:

$1\mathbf{S_aS_aHHMMPP} + 2\mathbf{S_as_aHHMMPP} + 2\mathbf{S_aS_aHHMmPP} + 2\mathbf{S_aS_aHHMMPp} + 4\mathbf{S_as_aHHMmPP}$
$+ 4\mathbf{S_as_aHHMMPp} + 4\mathbf{S_aS_aHHMmPp} + 8\mathbf{S_as_aHHMmPp}$ 27 normal leaves

$2\mathbf{S_aS_aHhMMPP} + 4\mathbf{S_as_aHhMMPP} + 4\mathbf{S_aS_aHhMmPP} + 4\mathbf{S_aS_aHhMMPp} + 8\mathbf{S_as_aHhMmPP}$
$+ 8\mathbf{S_as_aHhMMPp} + 8\mathbf{S_aS_aHhMmPp} + 16\mathbf{S_as_aHhMmPp}$ 54 roundish normal leaves

$1\mathbf{S_aS_ahhMMPP} + 2\mathbf{S_as_ahhMMPP} + 2\mathbf{S_aS_ahhMmPP} + 2\mathbf{S_aS_ahhMMPp} + 4\mathbf{S_as_ahhMmPP}$
$+ 4\mathbf{S_as_ahhMMPp} + 4\mathbf{S_aS_ahhMmPp} + 8\mathbf{S_as_ahhMmPp}$ 27 cordate leaves

$1\mathbf{S_aS_aHHmmPP} + 2\mathbf{S_as_aHHmmPP} + 2\mathbf{S_aS_aHhmmPP} + 2\mathbf{S_aS_aHHmmPp} + 4\mathbf{S_as_aHhmmPP}$
$+ 4\mathbf{S_as_aHHmmPp} + 4\mathbf{S_aS_aHhmmPp} + 8\mathbf{S_as_aHhmmPp}$ 27 maple leaves

$1\mathbf{S_aS_ahhmmPP} + 2\mathbf{S_as_ahhmmPP} + 2\mathbf{S_aS_ahhmmPp} + 4\mathbf{S_as_ahhmmPp}$ 9 cordate maple leaves

$1\mathbf{S_aS_aHHMMpp} + 2\mathbf{S_as_aHHMMpp} + 2\mathbf{S_aS_aHhMMpp} + 2\mathbf{S_aS_aHHMmpp} + 4\mathbf{S_as_aHhMMpp}$
$+ 4\mathbf{S_as_aHHMmpp} + 4\mathbf{S_aS_aHhMmpp} + 8\mathbf{S_as_aHhMmpp} + 1\mathbf{S_aS_ahhMMpp} + 2\mathbf{S_as_ahhMMpp}$
$+ 2\mathbf{S_aS_ahhMmpp} + 4\mathbf{S_as_ahhMmpp}$ 36 pear leaves with perfect corollas

$1\mathbf{S_aS_aHHmmpp} + 2\mathbf{S_as_aHHmmpp} + 2\mathbf{S_aS_aHhmmpp} + 4\mathbf{S_as_aHhmmpp} + 1\mathbf{S_aS_ahhmmpp}$
$+ 2\mathbf{S_as_ahhmmpp}$ 12 pear leaves with split corollas

$1\mathbf{s_as_aHHMMPP} + 2\mathbf{s_as_aHHMmPP} + 2\mathbf{s_as_aHHMMPp} + 4\mathbf{s_as_aHHMmPp}$
9 normal "Sasa" leaves

$2\,\mathrm{s_as_aHhMMPP} + 4\,\mathrm{s_as_aHhMmPP} + 4\,\mathrm{s_as_aHhMMPp} + 8\,\mathrm{s_as_aHhMmPp}$
18 roundish normal "Sasa" leaves
$1\,\mathrm{s_as_ahhMMPP} + 2\,\mathrm{s_as_ahhMmPP} + 2\,\mathrm{s_as_ahhMMPp} + 4\,\mathrm{s_as_ahhMmPp}$ 9 cordate "Sasa" leaves
$1\,\mathrm{s_as_aHHmmPP} + 2\,\mathrm{s_as_aHhmmPP} + 2\,\mathrm{s_as_aHHmmPp} + 4\,\mathrm{s_as_aHhmmPp}$
9 maple-"Sasa" leaves (Fig. 5)
$1\,\mathrm{s_as_ahhmmPP} + 2\,\mathrm{s_as_ahhmmPp}$ 3 cordate maple-"Sasa" leaves (Fig. 6)
$1\,\mathrm{s_as_aHHMMpp} + 2\,\mathrm{s_as_aHhMMpp} + 2\,\mathrm{s_as_aHHMmpp} + 4\,\mathrm{s_as_aHhMmpp} + 1\,\mathrm{s_as_ahhMMpp}$
$+ 2\,\mathrm{s_as_ahhMmpp}$ 12 pear-"Sasa" leaves with split corollas (Fig. 7, Pl. XVIII, fig. 7)
$1\,\mathrm{s_as_aHHmmpp} + 2\,\mathrm{s_as_aHhmmpp} + 1\,\mathrm{s_as_ahhmmpp}$
4 pear-"Sasa" leaves with narrowly split corollas (Fig. 8)

This expectation not only covers the F_2 data fairly well, but agrees also with the F_3 results which are collected and summarised in Table X.

BEHAVIOUR OF FASCIATION IN INHERITANCE.

An Introductory Remark.

Fasciation is a teratological character widely spread in various plant groups (see especially Masters (1869), Penzig (1890–94), Worsdell (1915), White (1916), Shirai (1925), etc.). Much literature has been published on fasciation treating of its occurrence, origin, morphology, physiology, heredity and so on. Fasciation has been universally recognised among herbs, shrubs and even trees, leading sometimes to the production of giant monstrosities. It is, however, in most cases, a transient phenomenon, due to the stimulation of some environmental conditions or to accidental effects. As distinct from these accidental fasciations, there are records of plants exhibiting heritable fasciation, in each of which a genetical basis for the manifestation of the abnormality is involved. Some of them breed true to the abnormality in successive generations without exception, though there may be exhibited much variation in the degree of the flattening of the affected part, while others throw varying percentages of normals according to their environment or to selection. De Vries (1903) made a series of experiments with some fasciated plants.

We may cite below some of the papers dealing with the systematic analysis of fasciation by experimental crossing. The classical work of Mendel (1865) on peas includes the inheritance of fasciation or *umbellatum* character. According to him and his followers, the abnormality is transmitted as a recessive to the normal condition. East and Hayes (1911) detected a case of the simple dominance of the fasciated ear in *Zea mays*. According to the experiments made by Emerson (1912), the fasciated ear of maize was transmitted as a recessive to the normal, quite

TABLE X.

The F_3 *data of the cross* 326 × A 5, *showing the segregation of leaf form.*

Number of pedigree	Normal leaf	Roundish normal leaf	Cordate leaf	Maple leaf	Cordate maple leaf	Pear leaf	Normal "Sasa" leaf	Roundish normal "Sasa" leaf	Cordate "Sasa" leaf	Maple-"Sasa" leaf	Cordate maple-"Sasa" leaf	Pear-"Sasa" leaf	Total	Genetic composition
Offspring of the normal-leafed F_2.														
2	44	—	—	20	—	—	—	—	—	—	—	—	64	$S_aS_aHHMmPP$
Expected	48	—	—	16	—	—	—	—	—	—	—	—	64	
1	204	—	—	—	—	55	—	—	—	—	—	—	259	$S_aS_aHHMMPp$
Expected	194·25	—	—	—	—	64·75	—	—	—	—	—	—	259	
2	125	—	—	36	—	52	33	—	—	10	—	16	272	$S_aS_aHHMmPp$
Expected	114·75	—	—	38·25	—	51·00	38·25	—	—	12·75	—	17·00	272	
Offspring of the roundish-normal-leafed F_2.														
2	42	93	53	—	—	—	—	—	—	—	—	—	188	$S_aS_aHhMMPP$
Expected	47	94	47	—	—	—	—	—	—	—	—	—	188	
2	4	17	6	8	3	—	—	—	—	—	—	—	38	$S_aS_aHhMmPP$
Expected	7·125	14·25	7·125	7·125	2·375	—	—	—	—	—	—	—	38	
5	69	174	82	63	17	62	—	—	—	—	—	—	467	$S_aS_aHhMmPp$
Expected	65·67	131·34	65·67	65·67	21·89	116·75	—	—	—	—	—	—	466·99	
1	32	70	28	—	—	—	5(1)	21	10	—	—	—	166	$S_as_aHhMMPP$
Expected	31·125	62·25	31·125	—	—	—	10·375	20·75	10·375	—	—	—	166	
3	51	92	53	47	18	—	16	20	13	8(1)	1	—	319	$S_as_aHhMmPP$
Expected	44·86	89·72	44·86	44·86	14·95	—	14·95	29·91	14·95	14·95	4·98	—	318·99	
5	45	104	50	56	12	80	19(1)	21	22	13	3	25	450	$S_as_aHhMmPp$
Expected	47·46	94·92	47·46	47·46	15·82	84·38	15·82	31·64	15·82	15·82	5·27	28·13	450	

Offspring of the cordate-leafed F_2.

1	—	—	1	—	—	—	—	—	—	—	—	—	1	**$S_aS_a$hhMMPP?**
Expected	—	—	1	—	—	—	—	—	—	—	—	—	1	
1	—	—	11	—	5	—	—	—	—	—	—	—	16	**$S_aS_a$hhMmPP**
Expected	—	—	12	—	4	—	—	—	—	—	—	—	16	
2	—	—	72	—	—	34	—	—	—	—	—	—	106	**$S_aS_a$hhMMPp**
Expected	—	—	79·5	—	—	26·5	—	—	—	—	—	—	106	
1	—	—	1	—	1	1	—	—	—	—	—	—	3	**$S_aS_a$hhMmPp?**
Expected	—	—	1·69	—	0·56	0·75	—	—	—	—	—	—	3	
2	—	—	122	—	26	—	—	—	51(1)	—	8	—	207	**$S_as_a$hhMmPP**
Expected	—	—	116·44	—	38·81	—	—	—	38·81	—	12·94	—	207	
3	—	—	144	—	21	54	—	—	32	—	11	17	279	**$S_as_a$hhMmPp**
Expected	—	—	117·70	—	39·23	52·29	—	—	39·23	—	13·08	17·43	278·96	

Offspring of the maple-leafed F_2.

1	—	—	—	49	12	15	—	—	—	—	—	—	76	**S_aS_aHhmmPp**
Expected	—	—	—	42·75	14·25	19·00	—	—	—	—	—	—	76	
1	—	—	—	18	—	—	—	—	—	7	—	—	25	**S_as_aHHmmPP**
Expected	—	—	—	18·75	—	—	—	—	—	6·25	—	—	25	
1	—	—	—	42	20	—	—	—	—	15	6	—	83	**S_as_aHhmmPP**
Expected	—	—	—	46·69	15·56	—	—	—	—	15·56	5·19	—	83	
1	—	—	—	97	—	30	—	—	—	30	—	12(1)	169	**S_as_aHHmmPp**
Expected	—	—	—	95·06	—	31·69	—	—	—	31·69	—	10·56	169	
2	—	—	—	44	11	25	—	—	—	15	1	9	105	**S_as_aHhmmPp**
Expected	—	—	—	44·30	14·77	19·69	—	—	—	14·77	4·92	6·56	105	

Offspring of the cordate-maple-leafed F_2.

1	—	—	—	—	9	—	—	—	—	—	4	—	13	**$S_as_a$hhmmPP**
Expected	—	—	—	—	9·75	—	—	—	—	—	3·25	—	13	

TABLE X (*continued*).

Offspring of the pear-leafed F_2 with perfect corolla.

Number of pedigree	Pear leaf with perfect corolla	Pear leaf with split corolla	Pear-"Sasa" leaf with entire corolla	Pear-"Sasa" leaf with narrowly split corolla	Total	Genetic composition
6	85	—	—	—	85	**S_aS_a(?)MMpp**
Expected	85	—	—	—	85	
2	7	3	—	—	10	**S_aS_a(?)Mmpp**
Expected	7·5	2·5	—	—	10	
3	25	4	8	1	38	**S_as_a(?)Mmpp**
Expected	21·375	7·125	7·125	2·375	38	
Offspring of the pear-leafed F_2 with split corolla.						
2	—	10	—	—	10	**S_aS_a(?)mmpp**
Expected	—	10	—	—	10	
1	—	15	—	6	21	**S_as_a(?)mmpp**
Expected	—	15·75	—	5·25	21	

Offspring of the normal-"Sasa"-leafed F_2.

Number of pedigree	Normal "Sasa" leaf	Maple-"Sasa" leaf	Pear-"Sasa" leaf with split corolla	Pear-"Sasa" leaf with narrowly split corolla	Total	Genetic composition
2	10	—	—	—	10	**s_as_aHHMMPP**
Expected	10	—	—	—	10	
1	3	1	—	—	4	**s_as_aHHMmPP**
Expected	3	1	—	—	4	

Offspring of the cordate-"Sasa"-leafed F_2.

Number of pedigree	Cordate "Sasa" leaf	Cordate maple-"Sasa" leaf	Pear-"Sasa" leaf with split corolla	Pear-"Sasa" leaf with narrowly split corolla	Total	Genetic composition
1	2	—	—	—	2	**$s_as_a$hhMMPP ?**
Expected	2	—	—	—	2	
1	2	1	2	0	5	**$s_as_a$hhMmPp**
Expected	2·81	0·94	0·94	0·31	5	

N.B. Some records of the flower type of the pear-leafed segregates may be incomplete and doubtful cases are not considered in classification.

The numeral in brackets represents the number of the plants which made somatic variation to a non-"Sasa" condition.

contrary to the one observed by the former investigators. In some strains, however, the hereditary behaviour of fasciation was not simple, and he thought that two factors were probably involved. White (1916) studied the inheritance of a fasciated *Nicotiana* by crossing it with its normal prototype and found it to be of a simple Mendelian type, the heterozygotes being intermediate in form. The result was not so simple, however, when the fasciated strain was crossed with the normals of different varieties. According to White, such complexity is due to a difference in the "genotypical environments." Nagai (1926) in his recently published data on the inheritance of soy-beans worked with fasciation, and concluded that it was of a simple recessive nature.

In the Japanese morning glory fasciated specimens have long been recognised. Now we find the strains either breeding true or throwing some normals. The oldest figure of a fasciated specimen of this plant is

Fig. 9. A fasciated specimen illustrated in an old book, *Asagao-Sô*, 1817.

the one given in *Kadan-Asagao-Tsû* (1815), which was published over one hundred and ten years ago. The attractive illustrations of this monstrosity (Fig. 9) are found in various other old books. According to these old authors, the heritability of fasciation was not strong in their days, but it was sometimes considered to be a temporary expression of the normals due to a "disease" or "supernutrition." We may conclude, therefore, that strains breeding true to the character are of relatively recent origin.

Yamaguchi (1916) studied the fasciation of the Japanese morning glory from a morphological and physiological point of view, but his paper contains no genetic analysis. Hagiwara (1924, 1926) published his genetic results on the fasciated morning glory and assumed two recessive factors for an abnormal manifestation. His data, however, did not contain sufficient individuals to solve such a complex problem.

My experiments on fasciation were started in 1921 and the hybrid generations ran to F_4 in one cross, including a very extensive cultivation of F_3. My conclusion is so complex that it contains some points incompatible with that which was drawn by Hagiwara.

The Results of Experiments.

The fasciated pedigree strain used as one of the parents in my breeding experiments was A 5, a pear leaf with a split corolla (Fig. 1, Pl. XVII, fig. 1). The strain has bred true to the type for generations on self-fertilisation, and the progeny always consisted of specimens having distinctly flattened stems. By crossing this strain with normals we raised the F_1 plants, which are quite normal, representing the dominancy of normality. In the F_2 generation, the fasciated segregates were relatively very few as is indicated in Table XI.

TABLE XI.

The F_2 *data showing the segregation of fasciation and the related character.*

Class	Cross	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total	% of fasciated stems
A	326 × A 5	467	153	2	17	639	2·97
	81-1 × A 5	92	27	—	3	122	2·46
Total		559	180	2	20	761	2·89
B	320 × A 5	53	3	—	1	57	1·75
	350 × A 5	111	34	—	1	146	0·68
	M 3 × A 5	186	40	—	1	227	0·44
	22-1 × A 5	61	15	—	—	76	0·00
Total		411	92	—	3	506	0·59
Grand total		970	272	2	23	1267	1·97

In the grand total, the fasciated stems form only 1·97 per cent. The proportion in which fasciated plants appear varies considerably in different crosses, though, roughly speaking, it may be classified into two categories, viz. a relatively high proportion (class A) and a relatively low one (class B). In class A, two crosses, 326 × A 5 and 81–1 × A 5, gave fasciated plants in the proportion of 2·97 per cent. and 2·46 per cent. respectively, the average being 2·89 per cent. In the other crosses, class B, three matings, 320 × A 5, 350 × A 5 and M 3 × A 5, gave only one fasciated individual in each F_2 progeny, which numbered respectively 57, 146 and 227. The remaining cross 22–1 × A 5 segregated no fasciated specimen among 76 F_2 offspring. The average ratio of the fasciated stems in class B was only 0·59 per cent.

An analysis of class A. With the cross 326 × A 5 I made a genetic analysis of fasciation on a comparatively extensive scale. The proportion

TABLE XII.

The F_3 *data of the cross* 326 × A 5, *showing the segregation of fasciation and the related character.*

Offspring of the normal stemmed and non-pear-leafed F_2.

Pedigree number	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total	% of fasciated stems
Total of 19 pedigrees	1282	—	—	—	1282	—
Total of 8 pedigrees	324	106	—	—	430	—
43	24	—	1	—	25	4·00
1	205	41	—	13	259	5·02
7	128	32	—	9	169	5·33
10	115	31	—	8	154	5·19
11	7	—	—	1	8	12·50
12	95	6	1	12	114	11·40
28	29	12	—	9	50	18·00
32	12	—	—	1	13	7·69
33	51	10	—	8	69	11·59
34	167	42	—	9	218	4·13
36	40	14	—	4	58	6·90
40	128	38	1	10	177	6·21
42	41	6	—	2	49	4·08
46	74	17	1	3	95	4·21
49	43	1	—	12	56	21·43
54	63	23	—	8	94	8·51
57	3	1	—	1	5	20·00
Total	1201	174	3	110	1588	7·12
Offspring of the normal stemmed and pear-leafed F_2.						
Total of 5 pedigrees	—	34	—	—	34	—
4	—	41	—	6	47	12·77
6	—	6	—	2	8	25·00
16	—	15	—	3	18	16·67
17	—	5	—	1	6	16·67
19	—	13	—	2	15	13·37
29	—	9	—	2	11	18·18
35	—	8	—	3	11	27·27
38	—	6	—	2	8	25·00
41	—	11	—	1	12	8·33
55	—	5	—	2	7	28·57
Total	—	119	—	24	143	16·78

TABLE XIII.

The other F_3 data of the cross 326 × A 5, showing the segregation of fasciation and the related character.

Offspring of the normal-stemmed and non-pear-leafed F_2.

Pedigree number	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total	% of fasciated stems
Total of 30 pedigrees	2167	—	—	—	2167	—
Total of 17 pedigrees	791	226	—	—	1017	—
90	29	—	1	—	30	3·33
111	2	—	1	—	3	33·33
128	244	—	1	—	245	0·41
Total	275	—	3	—	278	1·08
60	21	—	—	5	26	19·23
63	115	24	—	1	140	0·71
68	16	2	—	1	19	5·26
72	115	24	—	6	145	4·14
77	47	7	1	10	65	16·92
78	40	11	—	1	52	1·92
79	78	4	—	24	106	22·64
82	56	8	—	12	76	15·79
83	77	2	1	17	97	18·56
86	36	1	1	14	52	28·85
97	43	13	—	2	58	3·45
98	44	15	—	6	65	9·23
99	144	13	—	33	190	17·37
101	17	—	—	4	21	19·05
103	65	6	1	25	97	26·80
104	5	1	—	1	7	14·29
105	97	22	—	5	124	4·03
106	31	8	—	4	43	9·30
112	108	28	—	7	143	4·90
113	96	28	—	11	135	8·15
116	67	17	—	4	88	4·55
117	84	20	—	4	108	3·70
118	116	15	—	19	150	12·67
120	12	2	—	1	15	6·67
121	25	5	—	3	33	9·09
122	113	28	—	4	145	2·76
126	59	18	—	3	80	3·75
127	72	16	—	4	92	4·35
129	70	2	—	26	98	26·53
132	15	5	—	2	22	9·09
133	98	3	1	21	123	17·89
136	47	14	—	8	69	11·59
137	43	10	—	3	56	5·36
138	79	16	—	10	105	9·52
139	79	29	—	10	118	8·47
142	73	19	—	3	95	3·16
146	17	—	1	3	21	19·05
148	22	10	—	1	33	3·03
152	72	20	—	7	99	7·07
158	57	17	—	18	92	19·57
159	175	28	—	13	216	6·02
160	145	34	—	8	187	4·28
173	52	2	—	7	61	11·48
176	86	—	2	26	114	24·56
177	77	23	—	6	106	5·66
178	27	—	—	8	35	22·86
179	59	14	—	3	76	3·95
180	119	27	—	8	154	5·19
181	31	8	—	5	44	11·36
Total	3242	619	8	427	4296	10·13

TABLE XIII (*continued*).

Pedigree number	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total	% of fasciated stems
Offspring of the normal-stemmed and pear-leafed F_2.						
Total of 7 pedigrees	—	56	—	—	56	—
64	—	7	—	1	8	12·50
73	—	14	—	4	18	22·22
93	—	3	—	1	4	25·00
95	—	14	—	3	17	17·65
96	—	10	—	3	13	23·08
123	—	31	—	7	38	18·42
131	—	6	—	2	8	25·00
145	—	13	—	1	14	7·14
151	—	10	—	3	13	23·08
161	—	10	—	1	11	9·09
165	—	8	—	2	10	20·00
Total	—	126	—	28	154	18·18
Offspring of the fasciated and pear-leafed F_2, including false normals.						
110	—	—	—	17	17	100·00
144	—	1	—	25	26	96·15
155	—	—	—	2	2	100·00
162	—	1	—	2	3	66·67
169*	—	1	—	9	10	90·00
182*	—	—	—	2	2	100·00
183	—	3	—	2	5	40·00
Total	—	6	—	59	65	90·77

The asterisked pedigrees are the progenies of false normals.

of the fasciated stems in F_2 from this cross was 2·97 per cent., which stands between the recessive ratios of 6·25 per cent. of a dihybrid polymery and 1·56 per cent. of a trihybrid one. In F_3 the segregating proportion varies considerably as indicated in Table XII. Table XIII contains the data of the other F_3, the record of which was taken from the bed when the seedlings were about one foot high. If we make a variation table in regard to the segregating proportion of the fasciateds in each F_3 pedigree, the result will be as represented in Table XIV, and

TABLE XIV.

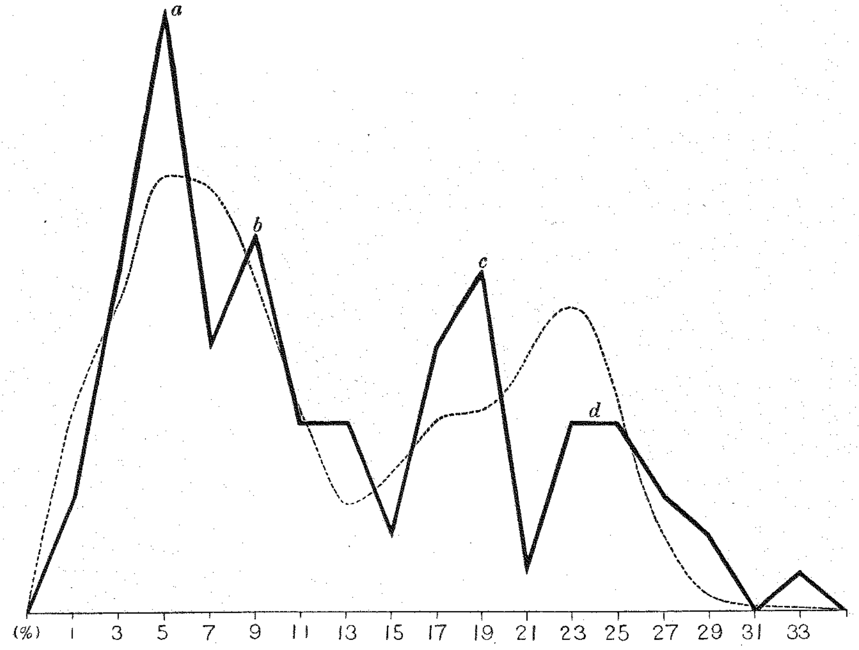
Variation table of the frequency in the segregating proportion of fasciation.

Segregating percentage	1	3	5	7	9	11	13	15	17	19	21
From Table XII	—	1	6	3	2	2	3	—	3	2	1
From Table XIII	3	8	10	4	8	3	2	2	4	7	—
Total	3	9	16	7	10	5	5	2	7	9	1

Segregating percentage	23	25	27	29	31	33	Total	Average proportion
From Table XII	—	2	1	1	—	—	27	12·93 %
From Table XIII	5	3	2	1	—	1	63	12·27 %
Total	5	5	3	2	—	1	90	12·47 %

TABLE XV.

The variation curves of the observed and theoretical frequency distributions in the proportion of the fasciated segregates in the F_3 *pedigrees.*



(Expectation was made without consideration of the occurrence of the false normals.)

Thick line.........Observed frequency Dotted line.........Theoretical frequency

the curve represented in Table XV by a thick line is drawn on the basis of these figures. The frequency curve in the diagram agrees with no simply segregating result, as it contains several high and low modes. Of these, the mode *d* is sure to have been made up by a body of the monohybrid segregating families, and the result must be accounted for by presuming more than two factors constituting the non-cumulative polymery in inheritance. An analysis of the data shows that the case concerns three factors, and that the triple recessives are the fasciated stems. If we represent these factors by $\mathbf{f}^1$, $\mathbf{f}^2$ and $\mathbf{f}^3$, the fasciated parent of the cross is to be regarded as $\mathbf{f}^1\mathbf{f}^1\mathbf{f}^2\mathbf{f}^2\mathbf{f}^3\mathbf{f}^3$, and its partner as a trebly dominant homozygote. From the trebly heterozygous F_1 we should have the following F_2 segregates:

$1\,F^1F^1F^2F^2F^3F^3 + 2\,F^1f^1F^2F^2F^3F^3 + 2\,F^1F^1F^2f^2F^3F^3 + 2\,F^1F^1F^2F^2F^3f^3 + 4\,F^1f^1F^2f^2F^3F^3$
$+ 4\,F^1f^1F^2F^2F^3f^3 + 4\,F^1F^1F^2f^2F^3f^3 + 8\,F^1f^1F^2f^2F^3f^3 + 1\,f^1f^1F^2F^2F^3F^3 + 2\,f^1f^1F^2f^2F^3F^3$
$+ 2\,f^1f^1F^2F^2F^3f^3 + 4\,f^1f^1F^2f^2F^3f^3 + 1\,F^1F^1f^2f^2F^3F^3 + 2\,F^1f^1f^2f^2F^3F^3 + 2\,F^1F^1f^2f^2F^3f^3 + 4\,F^1f^1f^2f^2F^3f^3$
$+ 1\,F^1F^1F^2F^2f^3f^3 + 2\,F^1f^1F^2F^2f^3f^3 + 2\,F^1F^1F^2f^2f^3f^3 + 4\,F^1f^1F^2f^2f^3f^3 + 1\,f^1f^1f^2f^2F^3F^3 + 2\,f^1f^1f^2f^2F^3f^3$
$+ 1\,f^1f^1F^2F^2f^3f^3 + 2\,f^1f^1F^2f^2f^3f^3 + 1\,F^1F^1f^2f^2f^3f^3 + 2\,F^1f^1f^2f^2f^3f^3$ 63 normal stems
$1\,f^1f^1f^2f^2f^3f^3$ 1 fasciated stem

In such a trihybrid, the theoretical proportion of the fasciateds is only 1·56 per cent., about half as much as that of the actual case (2·98 per cent.!). How can this difference be accounted for? According to my opinion, this can be explained as a result of linkage between two fasciation factors. In attempting to estimate the precise behaviour of the factorial relation, we meet with a serious difficulty in the occurrence of *false normals* as fluctuations from among the fasciateds. Among the fasciated F_2, those which produced some seeds and gave an opportunity to test their offspring are Nos. 110, 144, 155, 162 and 183, five in number. Some of them gave only fasciated progeny, while the others threw some normals. Hagiwara (1926) regarded such normals as mutants without observing their offspring. In my view, however, they are to be attributed to fluctuations in the manifestation of fasciation. If such is the case we should have a result similar to that from the false normals which appeared in these pedigrees. Two normals obtained in F_3 of Nos. 144 and 162 were prepared for such a test. On selfing, they gave 2 normals and 10 fasciateds in one case and in the other 3 fasciateds only in F_4. This result agrees with the data observed in the progeny of certain fasciated segregates. No one could have told that these F_4 plants were the progeny of a false F_3 normal without a record of the preceding generation. Nos. 169 and 182 were both F_2 plants having quite normal stems, but for the most part their progeny consisted of fasciated segregates as shown in Table XIII. The result they gave is precisely similar to that from the five fasciated F_2 plants cited above. With such evidence, we can safely conclude that the normals which appeared among the progeny of the fasciated families were due to a false manifestation induced by fluctuation, or, in other words, plants which are genotypically fasciated sometimes remain normal throughout their growth. The degree of flattening of the stem in the parental fasciated pedigree strain, A 5, is very evident (Fig. 1) and it always breeds true to the type, throwing no false normals. The fasciated specimens found in F_2, F_3 and F_4, however, differed from one another in their degree of flattening, varying through all gradations (Figs. 10 and 11, Pl. XVIII, figs. 8 and 9). In the least fasciated individuals, the flattening occurs only in a portion of the stem, most of the parts remaining quite normal. Such plants may be recorded as normals in

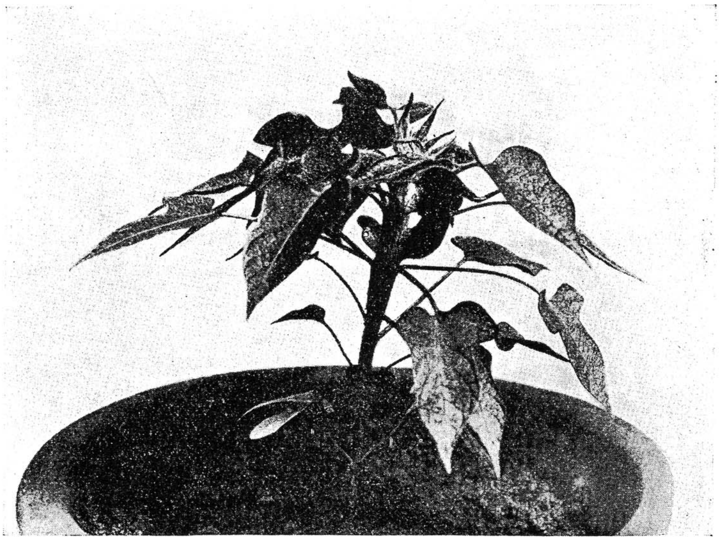


Fig. 10. A fasciated segregate bearing pear leaves. Pear leaves sometimes are lobed nearly like roundish normal leaves.

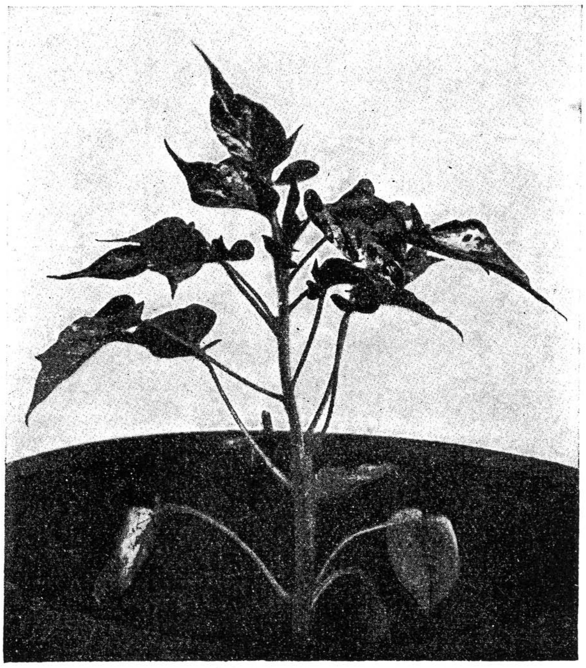


Fig. 11. Weakly fasciated pear leaf. Note the disordered phyllotaxy!

an early census, but they reveal themselves as fasciateds on later observation. Hagiwara (1926) observed a specimen, on which only a branch was fasciated, and he regarded this as due to a bud-variation. Plants of such a nature, however, were of not infrequent occurrence in my experiments, and no difference between the progenies of the fasciated and normal parts could be detected by examining their inheritance. So it appears to be a little premature to attribute such a case to bud-variation.

On the evidence cited above, we must recognise the occurrence of false normals in the hybrid progeny of the present cross. This would affect the ratio of the fasciated segregates, and the deficit in their expected numbers may be roughly estimated from the data recorded on the progeny of the fasciateds and false normals. From these data we must reckon 8 false normals to 66 fasciateds in 74 plants, a deficit among the fasciateds of 10·81 per cent. The proportion may be calculated in another way, *i.e.* from the ratio of the false normals to the fasciateds in F_2. The false normals detected in F_2, however, were only 2 in number, from which meagre figure we cannot expect to obtain a more precise value than the former case. The deficit of 10·81 per cent., however, was calculated not only on the basis of an insufficient number, but it contains also some unfavourable points. The occurrence of false normals shows that the environment had some effect upon the manifestation of fasciation. But, as already pointed out, the parental pedigree strain, A 5, always breeds true to its type. Hence the determination of the fasciated character in this pedigree strain is so perfect that the environment cannot affect its manifestation, though the fasciation may vary somewhat in degree. Why then does the manifestation fluctuate in the hybrid progeny, and not in the parental pedigree strain? The inconstancy of fasciation in its inheritance was in early days a general phenomenon in the cultivation of the Japanese morning glory. In my opinion, the difference is due to the occurrence of a modifier or modifiers, which affect the degree and production of fasciation in its manifestation. The old fasciation accompanied such a factor or factors in their fluctuating representation, while in some strains, which we now have, these factors have slipped out. In the present cross, they came from the normal parent, and segregation in respect of them takes place in the hybrid progeny. It would be a troublesome business to determine the precise behaviour of such a modifier or modifiers, and the solution of this problem will be attempted in my future experiments. The data, on which the value of the deficit was estimated, therefore, must contain something impure ~~in them~~, so that its value must be regarded as representing only an approximate figure.

If we neglect the deficit of fasciated plants the value of crossing over between two fasciation factors may be estimated by the formula,

$$\frac{x^2}{16x^2 + 32x + 16} = \frac{19}{639}.$$

From this formula the gametic ratio is determined to be 2·22 : 1. If we assume the fasciation factors that are linked together to be **f**^{1} and **f**^{2}, about 31 per cent. of crossing over takes place between them. A tentative application of the 10·81 per cent. deficit in this calculation will change the figure of 19 fasciateds into 19 ÷ (100% − 10·81%) = *ca.* 21 fasciateds, including the false normals. On this view, a more precise gametic ratio is estimated to be 2·64 : 1 or *ca.* 3 : 1, or about 20–25 per cent. of crossing over. If we calculate the F_2 expectation on the basis of a 3 : 1 gametic ratio, the result is as shown in Table XVI.

TABLE XVI.

The theoretical F$_2$ *in the segregation of fasciation.*

	Its ratio			Its ratio	
Genotype	Formula	Value ($x=3$)	Phenotype	Formula	Value ($x=3$)
$\mathbf{F^1F^1F^2F^2F^3F^3}$	x^2	9	Normal	$15x^2+32x+16$	247
$\mathbf{F^1F^1F^2F^2F^3f^3}$	$2x^2$	18			
$\mathbf{F^1F^1F^2f^2F^3F^3}$	$2x$	6			
$\mathbf{F^1f^1F^2F^2F^3F^3}$	$2x$	6			
$\mathbf{F^1F^1F^2F^2f^3f^3}$	x^2	9			
$\mathbf{F^1F^1f^2f^2F^3F^3}$	1	1			
$\mathbf{f^1f^1F^2F^2F^3F^3}$	1	1			
$\mathbf{F^1F^1F^2f^2F^3f^3}$	$4x$	12			
$\mathbf{F^1f^1F^2F^2F^3f^3}$	$4x$	12			
$\mathbf{F^1f^1F^2f^2F^3F^3}$	$2x^2+2$	20			
$\mathbf{F^1f^1F^2f^2F^3f^3}$	$4x^2+4$	40			
$\mathbf{F^1F^1F^2f^2f^3f^3}$	$2x$	6			
$\mathbf{F^1f^1F^2F^2f^3f^3}$	$2x$	6			
$\mathbf{F^1F^1f^2f^2F^3f^3}$	2	2			
$\mathbf{F^1f^1f^2f^2F^3F^3}$	$2x$	6			
$\mathbf{f^1f^1F^2F^2F^3f^3}$	2	2			
$\mathbf{f^1f^1F^2f^2F^3F^3}$	$2x$	6			
$\mathbf{F^1f^1F^2f^2f^3f^3}$	$2x^2+2$	20			
$\mathbf{F^1f^1f^2f^2F^3f^3}$	$4x$	12			
$\mathbf{f^1f^1F^2f^2F^3f^3}$	$4x$	12			
$\mathbf{F^1F^1f^2f^2f^3f^3}$	1	1			
$\mathbf{F^1f^1f^2f^2f^3f^3}$	$2x$	6			
$\mathbf{f^1f^1F^2F^2f^3f^3}$	1	1			
$\mathbf{f^1f^1F^2f^2f^3f^3}$	$2x$	6			
$\mathbf{f^1f^1f^2f^2F^3F^3}$	x^2	9			
$\mathbf{f^1f^1f^2f^2F^3f^3}$	$2x^2$	18			
$\mathbf{f^1f^1f^2f^2f^3f^3}$	x^2	9	Fasciated	x^2	9
Total	$16x^2+32x+16$	256		$16x^2+32x+16$	256

As discussed above, the F_2 data may be fairly accounted for by the hypothesis suggested by me, though its confirmation must depend upon the data of succeeding generations. We may now test it with the F_3 results.

Part of the F_3 plants were sown in the beginning of May and the seedlings were later transplanted into a field where the plants were allowed full growth. The data from these plants are collected in Table XII. But as my means were limited I was unable to raise a sufficient number of plants in this way. For further data I made seed-bed observations on the remaining F_3 seeds sown in early June. Fcrtunately the weather was reasonably fair, and relatively few seedlings were damaged in the crowded culture. A record of them was taken when they were about one foot in height, as summarised in Table XIII. Owing to doubts whether cases of weak fasciation would be evident in early development, I feared that some fasciated specimens might have been missed in this record, because the census was taken before the attainment of full growth. However, this fear proved to be almost groundless, at least in the present case, for the average segregating proportion of the fasciateds was 12·93 per cent. in the normally full-grown culture and 12·27 per cent. in the mass culture, representing practically the same result. This fact may admit of a discussion of both sets of data together. The variation curve of the segregating frequency of such combined F_3 pedigrees is polymodal, as indicated by a thick line in Table XV, in which we may point out roughly four definite modes, *a*, *b*, *c* and *d*. The expected segregating types of the F_3 pedigrees are calculated in Table XVII, on the basis of 3 : 1 gametic ratio in the linkage between $\mathbf{F^1}$ and $\mathbf{F^2}$.

TABLE XVII.

The theoretical segregating types of F_3 *in the segregation of fasciation.*

Genetic composition	Linkage	Ratio	Normal *versus* fasciation	Formula	% of fasciation	Segregating type
$\mathbf{F^1f^1F^2f^2F^3f^3}$	Coupling	36	247 : 9	$15x^2+32x+16:x^2$	3·52	III
	Repulsion	4	255 : 1	$16x^2+32x+15:1$	0·39	I
$\mathbf{F^1f^1F^2f^2f^3f^3}$	Coupling	18	55 : 9	$3x^2+8x+4:x^2$	14·06	V
	Repulsion	2	63 : 1	$4x^2+8x+3:1$	1·56	II
$\mathbf{F^1f^1f^2f^2F^3f^3}$		12	15 : 1	15 : 1	6·25	IV
$\mathbf{f^1f^1F^2f^2F^3f^3}$		12				
$\mathbf{F^1f^1f^2f^2f^3f^3}$		6	3 : 1	3 : 1	25·00	VI
$\mathbf{f^1f^1F^2f^2f^3f^3}$		6				
$\mathbf{f^1f^1f^2f^2F^3f^3}$		18				

Thus we expect six segregating types. The theoretical number and its average value of each segregating type applied to the total observed are represented at the bottom lines of Table XVIII. In an attempt to make a curve analysis on the basis of these figures, we obtained a variation distribution of the segregating types as indicated in the body of the table.

TABLE XVIII.

Variation table of the frequency distribution in the segregating types of fasciation in F_3.

	Segregating type							
%	I	II	III	IV	V	VI	Total (theoretical)	Ob-served
1	2·105	0·539	2·856	0·027	—	—	5·518	3
3	0·742	0·523	6·677	0·286	—	—	8·228	9
5	0·265	0·371	9·414	1·590	—	—	11·640	16
7	0·048	0·133	6·677	4·451	0·001	—	11·310	7
9	0·004	0·024	2·386	6·276	0·018	—	8·708	10
11	—	0·002	0·429	4·451	0·215	—	5·097	5
13	—	—	0·039	1·590	1·193	0·001	2·823	5
15	—	—	0·002	0·286	3·338	0·032	3·658	2
17	—	—	—	0·026	4·707	0·358	5·091	7
19	—	—	—	0·001	3·338	1·988	5·327	9
21	—	—	—	—	1·193	5·564	6·757	1
23	—	—	—	—	0·215	7·845	8·060	5
25	—	—	—	—	0·018	5·564	5·582	5
27	—	—	—	—	0·001	1·988	1·989	3
29	—	—	—	—	—	0·358	0·358	2
31	—	—	—	—	—	0·032	0·032	—
33	—	—	—	—	—	0·001	0·001	1*
Total (theoretical)	3·158	1·579	28·421	18·947	14·211	23·684	90·000	90
Average	0·526	2·210	4·868	9·526	16·632	23·264	12·466	12·466

$\sigma = 4{\cdot}079$, in the total variation.
$\sigma = 1{\cdot}207$, in the variation for each segregating type.
$\chi^2 = 24{\cdot}575$. $P = 0{\cdot}078$.

* This was neglected in the calculation of χ^2, because its progeny consisted of only three individuals.

The sum of these six variation numbers, as given under the column of "Total," is not very different from that of the number observed as represented in the next column, the value of P being 0·078. The figures thus theoretically estimated were drawn in a curve with a dotted line in Table XV, in which a comparison is made with the observed frequency. Neither of two curves entirely overlaps the other, but we can see a rough resemblance between them. On comparing the two curves, the mode *c* of the thick line stands out beyond the dotted line. The larger part of this peak may be expected to be composed of the families of segregating type V, and suggests a somewhat more intense linkage between $\mathbf{f}^1$ and $\mathbf{f}^2$. The hypothesis offered above seems to be verified by the F_3 results, though the calculation here attempted was made in ignorance of the occasional failure of fasciated plants to manifest their fasciation, which may frequently occur in the hybrid progeny. The deficit in fasciateds should vary with the segregation of the modifiers if more than two of them entered into this cross. Under this circumstance, the prediction of the exact number expected is a difficult matter.

On my view the expected ratio of homogenous and segregating families is 114 to 133, and we shall see how this expectation is realised in the observed data. Of 183 non-fasciated F_3 families, 120 contained over twenty individuals each. The composition of these families is indicated in Table XIX, those containing but few progeny being omitted.

TABLE XIX.

A genotypic comparison of F_2 *for the segregation of fasciation.*

	True-breeding	Segregating	Total
Observed	56	64	120
Expected	55·38	64·62	120

The number theoretically calculated on the basis of 114 : 133 thus accords fairly well with the actual data.

The genetic behaviour of fasciation reveals the complexity of the problem even more when the study is extended to other crosses, and I have found a more complicated case in another cross, the data of which are represented in the next section.

An analysis of class B. The results given in Table XI indicate roughly two types of segregation, viz. a relatively higher and a relatively lower proportion in the production of the fasciated segregates, the average proportion in the latter class, *B*, being only 0·59 per cent., or only about one-fifth of that of the former class, *A*. This lower proportion is not a matter of accidental occurrence, but depends upon a genetic difference. That this is not a speculative suggestion is evident from an inspection of the data collected in Table XX containing the F_3 results of the cross M 3 × A 5, a cross of class *B*. The data, however, do not contain enough individuals for attempting a curve analysis. In the calculation of fasciation in the total normal F_3 progenies, 5·75 per cent. is the result of the cross 326 × A 5, while that of cross M 3 × A 5 is only 3·54 per cent. We raised the offspring of two F_2 fasciateds, of which one (No. 23) produced three specimens with flattened stems, while the other (No. 34) gave sixteen offspring of which seven were false normals. From such evidence, the difference may be regarded genetically either as due to the occurrence of an additional fasciation factor, or of a modifier or modifiers. Hence segregation in the hybrid progeny of the present cross

TABLE XX.

The F_2 *data of the cross* M 3 × A 5, *showing the segregation of fasciation and the related character.*

Offspring of the normal-stemmed and non-pear-leafed F_2.

Pedigree number	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total	% of fasciated stems
Total of 13 pedigrees	218	—	—	—	218	—
Total of 29 pedigrees	643	169	—	—	812	—
15	15	5	—	2	22	9·09
16	17	4	—	3	24	12·50
27	19	11	—	1	31	3·23
45	15	2	—	3	20	15·00
46	32	8	—	1	41	2·44
58	10	5	—	1	16	6·25
62	12	7	—	2	21	9·52
Total	120	42	—	13	175	7·43
Offspring of the normal-stemmed and pear-leafed F_2.						
Total of 3 pedigrees	—	26	—	—	26	—
8	—	41	—	9	50	18·00
12	—	7	—	1	8	12·50
18	—	26	—	4	30	13·33
31	—	41	—	8	49	16·33
37	—	32	—	5	37	13·51
44	—	26	—	6	32	18·75
48	—	43	—	1	44	2·27
53	—	44	—	3	47	6·38
63	—	21	—	5	26	19·23
Total	—	281	—	42	323	13·00
Offspring of the fasciated and pear-leafed F_2.						
23	—	—	—	3	3	100·00
34	—	7	—	9	16	56·25
Total	—	7	—	12	19	63·16

should be more complicated than that of the cross 326 × A 5. The proportions of non-fasciated families which breed true to normal, and those which segregate fasciateds, should be somewhat different from the proportions observed in the previous cross; for some increase may be expected in the proportion of the former sort of families. Actually we have 26 families of the former and 14 of the latter, omitting those containing less than twenty individuals. The proportion of segregating families in the total is 35 per cent., and 53·33 per cent. in the previous cross, representing a somewhat conspicuous difference as was expected.

On the Two-factor Hypothesis.

Hagiwara (1924, 1926) interpreted fasciation in terms of two factors, one of which was that for pear leaf. In my view, however, his data were not sufficient for establishing his hypothesis. The fact that his fasciated plants invariably bore pear leaves led him to conclude incorrectly that pear leaf was a manifestation of one of the fasciated factors, but this was owing to the fact that his data were not numerous enough to allow for breakage of the linkage. He postulated an ever-sporting nature of the factors concerned with the production of fasciation, but his conclusion, as far as I can judge, was surely taken from confused data.

The Lack of Physiological Fasciation.

The occurrence of non-heritable fasciation is a widespread phenomenon in various plant groups. In the Japanese morning glory, however, all fasciation would appear to have a factorial basis, and I have observed no single fasciated individual, which might have been physiologically produced during my thirteen years' culture of this plant. I have observed over three hundred thousand full-grown individuals, but I found no such fasciated plant! Hence we may conclude that the Japanese morning glory is a species in which physiological fasciation hardly, if ever, occurs.

THE BREAKAGE OF ACCOMPANIMENT OF FASCIATION AND PEAR LEAF.

Fasciation is almost always accompanied by pear leaf and this was also the case in old times. Fasciation seems to have made its appearance in pear leaves because specimens illustrated in the early literature invariably bore pear leaves (Fig. 9). Hagiwara (1924, 1926) regarded this accompaniment as a manifold effect of the pear leaf factor, which, combined with another factor, produces a fasciated stem. In my experiments, however, I obtained a few non-pear-leafed fasciateds in the hybrid progeny, so that we cannot retain this hypothesis any longer.

As was experimentally proved, my original fasciated pedigree strain, A 5, was pear leaf carrying the maple factor (Fig. 1, Pl. XVII, fig. 1). On crossing this strain with normals we produced some fasciateds in F_2, as indicated in Table XI; most of them bore pear leaves, but there were a few exceptions which bore non-pear leaves[1]. Such specimens were repeatedly observed in F_3 from the same cross (see Tables XII and XIII).

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[1] They produced no seeds.

How can we account for these exceptional individuals? We may, probably rightly, attribute them to the existence of crossing over between the factors for pear leaf and fasciation, in which case the next problem is to determine the fasciation factor in question and the linkage value.

Leaving the F_2 data for the moment, we may review the F_3 results of the cross 326 × A 5. Among the F_3 pedigrees we can recognise cases in which segregation on a dihybrid scheme occurred for pear leaf and its linked fasciation factor (the latter being one of the three fasciation factors). The families collected in Table XXI are regarded as recessively homozygous for the other fasciation factors, and so the appearance of fasciation is attributable to the segregation of one factor only.

TABLE XXI.

The F_3 *data showing the dihybrid segregation of fasciation and pear leaf.*

(From Tables XII and XIII.)

Pedigree number	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total
49	43	1	—	12	56
60	21	—	—	5	26
79	78	4	—	24	106
83	77	2	1	17	97
86	36	1	1	14	52
101	17	—	—	4	21
129	70	2	—	26	98
133	98	3	1	21	123
146	17	—	1	3	21
176	86	—	2	26	114
178	27	—	—	8	35
Total	570	13	6	160	749
Expected	552·25	9·50	9·50	177·75	749

$\chi^2 = 4{\cdot}927$. $P = 0{\cdot}179$.

In the total number, 749, I counted 166 fasciated specimens, or 22·16 per cent., which figure, as was stated above, must be somewhat augmented by taking into account the false normals. The deficit among the fasciateds on this account is, as pointed out earlier, about 11 per cent. If this value is taken in the present case, the 166 segregated fasciateds must be increased to *ca.* 184, *i.e.* 24·57 per cent. of the total, a simple recessive ratio. The occurrence of false normals may be justly expected in the present case, and the segregating number corrected accordingly. But the application does not seem to be so simple when we consider that the deficit may vary in different families according to the segregation of modifiers. The fasciateds with non-pear leaves were not generally so evident in the flattening of their stems as those with pear leaves. One may therefore expect among them a somewhat higher deficit than among the pear-leafed fasciateds. The segregating numbers, if necessary, must be corrected under these conditions. So we have no alternative but to calculate the linkage value with the original data as they stand. From the total number in Table XXI, the gametic ratio is about 40 : 1, or 2·44 per cent. of crossing over. This strong linkage will lead to fasciated specimens being almost always accompanied by pear leaves in an experiment carried on a small scale. As indicated in the former section, we assumed three factors, $\mathbf{f}^1$, $\mathbf{f}^2$ and $\mathbf{f}^3$, for fasciation, of which $\mathbf{f}^1$ and $\mathbf{f}^2$ are linked together with a medium frequency of crossing over. Now that we have discussed the occurrence of a close linkage between the two factors for pear leaf and for fasciation, a question arises as to which one of the three fasciation factors is linked with **p**. If either $\mathbf{f}^1$ or $\mathbf{f}^2$ is linked with **p**, these three factors must form a linkage group, while if $\mathbf{f}^3$ is the one that is linked, then $\mathbf{f}^3$ and **p** should segregate independently of $\mathbf{f}^1$ and $\mathbf{f}^2$. From an inspection of the F_3 data (see Tables XII and XIII) I have picked out families showing similar segregation and collected them in Table XXII.

The type of segregation is unusual in that the average frequency of the fasciated segregates is 13·91 per cent., and it can be identified with

TABLE XXII.

The F_3 *data showing linkage in a complicated segregating type.*

(From Tables XII and XIII.)

Pedigree number	Normal stem with non-pear leaf	Normal stem with pear leaf	Fasciated stem with non-pear leaf	Fasciated stem with pear leaf	Total
12	95	6	1	12	114
28	29	12	—	9	50
33	51	10	—	8	69
77	47	7	1	10	65
82	56	8	—	12	76
99	144	13	—	33	190
106	31	8	—	4	43
118	116	15	—	19	150
121	25	5	—	3	33
136	47	14	—	8	69
138	79	16	—	10	105
158	57	17	—	18	92
181	31	8	—	5	44
Total	808	139	2	151	1100
Expected	817·58	127·77	7·45	148·69	1101·49

$\chi^2 = 5{\cdot}121$. $P = 0{\cdot}165$.

type V in Table XVII. In this type, the ratio of the normal and fasciated is 55 : 5, *i.e.* the proportion of the latter is about 14 per cent. The abnormal percentage of the fasciated is due to coupling between $\mathbf{f}^1$ and $\mathbf{f}^2$. If **p** segregated independently of these factors, it could not give such an unfamiliar ratio in these pedigrees. Consequently, we must conclude that $\mathbf{f}^1$ (or $\mathbf{f}^2$) is closely linked with **p**. Between $\mathbf{f}^1$ and $\mathbf{f}^2$ there is about 20–25 per cent. of crossing over, and, at the same time, between **p** and $\mathbf{f}^1$ about 2·5 per cent. So these three factors may be considered to occupy loci on the same chromosome in a definite arrangement.

THE MODE OF SEGREGATION OF MAPLE AND VARIEGATION IN CROSSES INVOLVING FASCIATION.

Hagiwara (1924) recognized two characters, maple and variegation, as linked with fasciation. The F_2 data, on which his consideration was based, did not seem to be enough to draw a conclusion, making it necessary to confirm his result with more data.

On the Maple Factor.

In Table XXIII, I have collected my data showing the segregation of maple and fasciation in fasciation crosses.

TABLE XXIII.

The F_2 *data showing the segregation of fasciation and maple corolla.*

Cross	Normal stem with perfect corolla	Normal stem with split corolla	Fasciated stem with perfect corolla	Fasciated stem with split corolla	Total
326 × A 5	485	135	14	5	639
81–1 × A 5	91	28	2	1	122
320 × A 5	46	10	1	0	57
350 × A 5	108	37	1	0	146
M 3 × A 5	168	58	1	0	227

The result seems not to point to any special relation between the characters in question. Hagiwara's F_2 data, however, showed a relatively high coupling. The flowers of pear leaves are sometimes irregularly deformed and broken, especially in the fasciateds (Pl. XVIII, fig. 8).

On the Variegation Factor.

The data showing segregation in variegation and fasciation are collected in Table XXIV from my fasciation crossings.

TABLE XXIV.

The F_2 *data showing the segregation of fasciation and variegation.*

Cross	Normal stem with self-coloured leaf	Normal stem with variegated leaf	Fasciated stem with self-coloured leaf	Fasciated stem with variegated leaf	Total
326 × A 5	481	139	8	11	639
320 × A 5	47	9	—	1	57
350 × A 5	113	32	—	1	146
M 3 × A 5	174	52	—	1	227

These crosses were made with a fasciated strain bearing variegated leaves as one of the parents, and therefore, a relatively high production of the parental type, if any linkage occurs, was expected. Actually a majority of the fasciated segregates bore variegated leaves, which indicated the occurrence of a special segregation. As formerly stated, fasciation was induced by the meeting of three recessive factors, $\mathbf{f}^1$, $\mathbf{f}^2$ and $\mathbf{f}^3$, and it must be decided which of these three showed linkage, if any, with the variegation factor. If either $\mathbf{f}^1$ or $\mathbf{f}^2$ is linked with **v**, the variegation factor, this last factor should show linkage with **p**, the pear leaf factor, since $\mathbf{f}^1$, $\mathbf{f}^2$ and **p** are linked together. To determine this it would be best to test a dihybrid segregation with pear and variegated leaves. The data obtained by **PV** × **pv** are collected in Table XXV, while Table XXVI gives the result of the cross **Pv** × **pV**. If linkage took place between the factors in question, we should expect coupling in the former table and repulsion in the latter, whereas independent segregation is actually the case in both tables. This test suggests that the fasciation factor which is linked with **v** is neither $\mathbf{f}^1$ nor $\mathbf{f}^2$, but possibly $\mathbf{f}^3$. To verify this and the linkage value, I carefully inspected the F_3 data, but

TABLE XXV.

The F_2 *data showing the segregation of pear leaf and variegation in the crossing of* **PV** × **pv**.

Cross	Self-coloured non-pear leaf	Variegated non-pear leaf	Self-coloured pear leaf	Variegated pear leaf	Total
M 3 × A 5	143	43	31	10	227
22–1 × A 5	44	17	12	3	76
350 × A 5	87	24	26	9	146
320 × A 5	44	9	3	1	57
326 × A 5	366	103	123	47	639
Total	684	196	195	70	1145
Expected	644·06	214·69	214·69	71·56	1145

$\chi^2 = 5{\cdot}943$. $P = 0{\cdot}115$.

TABLE XXVI.

The F_2 *data showing the segregation of pear leaf and variegation in the crossing of* **Pv** × **pV**.

Cross	Self-coloured non-pear leaf	Variegated non-pear leaf	Self-coloured pear leaf	Variegated pear leaf	Total
65 × BD–B	327	108	113	26	574
26–2 × BD–B	256	78	42	7	383
Total	583	186	155	33	957
Expected	538·31	179·44	179·44	59·81	957

$\chi^2 = 19{\cdot}333$. $P = 0{\cdot}0002$[*].

[*] This value is very low, mainly due to the excess and meagre productions in double dominant and double recessive classes.

I failed to secure any decided clue owing to the complicated segregation of the characters. Be that as it may, the F_3 data seem to show a linkage of the same order as the F_2 data, *i.e.* of about 20–25 per cent. of crossing over between $\mathbf{f}^3$ and **v**. Hagiwara supposes the occurrence of a very high linkage (70 : 1 gametic ratio).

This investigation was carried on under the direction of Prof. K. Miyake, to whom I wish to express my hearty thanks, as well as to Mr K. Hashimoto, who gave me great encouragement to complete this study. I also thank Messrs B. Kanna and K. Tabuchi for their friendly help in my experiments. Thanks are also due to Mr S. Takahashi, who kindly lent me his old books on the Japanese morning glory.

Summary.

1. Pear leaf behaves as a simple recessive to the normal.
2. Pear leaf resembles cordate leaf in shape, but the genetic factors upon which these characters depend are entirely different.
3. The pear leaf factor combined with the "Rangiku" factor represents a particular leaf with a contracted and broadened petiole.
4. Pear leaf carrying the maple factor can be hardly distinguished from a normal pear leaf in appearance. The flower of the former, however, is split into lobes, while that of the latter is perfect, though sometimes it is deformed and slightly divided.
5. When homozygous for the "Rangiku" factor, the maple assumes the so-called "Mitsuo" leaf, the flower of which blooms in a split "Rangiku" way.
6. The pear leaf combined with the "Sasa" factor gives a slender, narrow leaf of the pear type, and a split corolla.

7. Though the original fasciated strain bred true to this abnormality, the fasciated specimens obtained in the hybrid progeny frequently give some normals.

8. A continuous variation in the degree of fasciation is exhibited among the segregates. In the most weakly fasciated specimens only a portion of the stem is flattened, and some genotypically fasciated plants, which remain normal throughout their growth, betray their nature by giving abundant fasciateds in their offspring.

9. Fasciation, which is a recessive character, occurs on a few individuals in F_2 from crosses with normals, the ratio of the fasciateds being only about 2 per cent. on an average.

10. In an examination of the experimental data we can detect two forms of segregating ratios with relatively higher and lower proportions of fasciated plants.

11. In the former case, the factors concerned with the production of fasciation are considered to be three, viz. $\mathbf{f}^1$, $\mathbf{f}^2$ and $\mathbf{f}^3$.

12. The factors $\mathbf{f}^1$ and $\mathbf{f}^2$ show linkage with about 20–25 per cent. of crossing over.

13. A marked variation in the degree of fasciation and in the appearance of false normals may be accounted for by the occurrence and segregation of a modifier or modifiers, which qualify the manifestation of the trait.

14. The lower proportion of fasciated plants in certain crosses is considered to be due to the occurrence of an additional fasciation factor, or of a modifier or modifiers.

15. The marked accompaniment of fasciated stem with pear leaf is due to linkage, with about 2·5 per cent. crossing over, between **p** (pear leaf factor) and $\mathbf{f}^1$. The three factors, **p**, $\mathbf{f}^1$ and $\mathbf{f}^2$, therefore, may be considered to be located on the same chromosome in a definite arrangement.

16. The fasciation factor $\mathbf{f}^3$ is linked with **v**, a variegation factor, with about 20–25 per cent. of crossing over, thus constituting another linkage group.

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EXPLANATION OF PLATES XVII—XVIII.

Fig. 1. A variegated, pear-leafed specimen (A 5) bearing split flowers. Note the relatively broad split petals!

Fig. 2. A "Rangiku"-leafed specimen. Note the irregularly lobed leaves and disordered flower-buds!

Fig. 3. Variegated maple-"Sasa" leaf bearing a narrowly split flower divided down to the bottom of flower tube.

Fig. 4. "Rangiku" leaf bearing a creased flower. The gamopetalous corolla is unusually composed of numerous petals.

Fig. 5. "Mitsuo" leaf bearing a split flower, which, on account of the polypetalous constitution, is much divided.

Fig. 6. Maple leaf bearing split corollas. This type of flower is the same as that of Fig. 1.

Fig. 7. Pear-"Sasa" leaf with split flowers. Note the more or less closed funnel-shaped type of flower, and compare it with that of Fig. 9 on this plate. The somewhat closed corolla or "gentian" flower is an effect of the pear leaf factor.

Fig. 8. A pear-leafed specimen with a broadly fasciated stem. Note the disordered corollas!

Fig. 9. A pear-leafed and fasciated specimen carrying maple factors. Note the irregular and split corollas!

Fig. 10. Normal "Sasa" leaf bearing split flowers.


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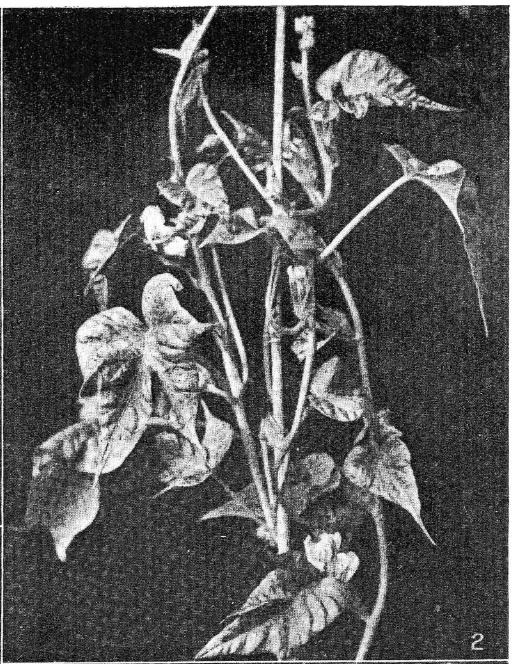
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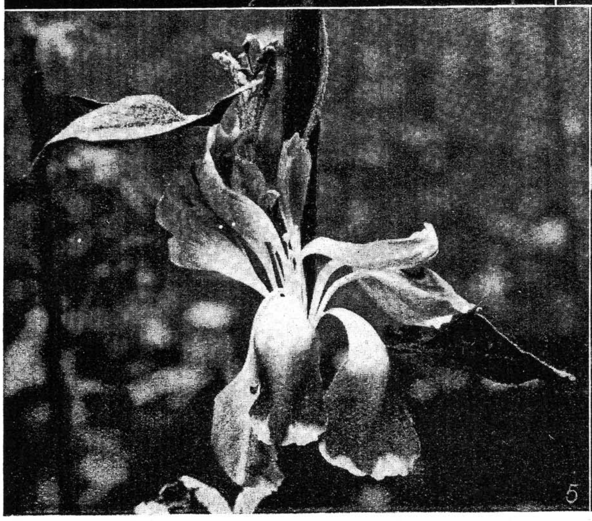
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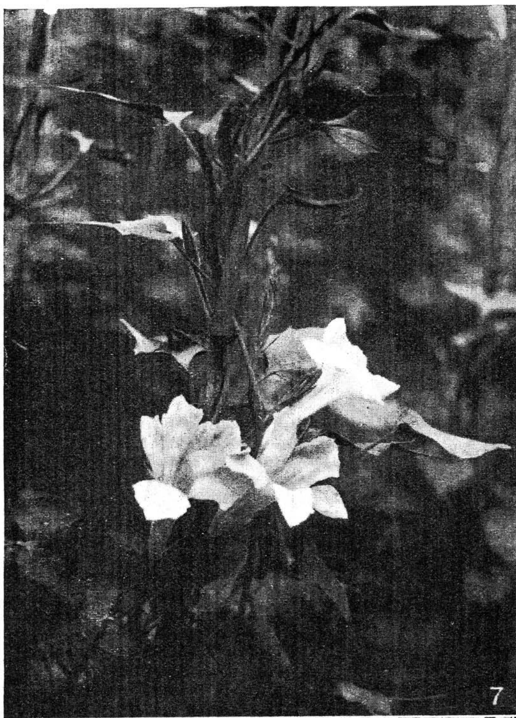

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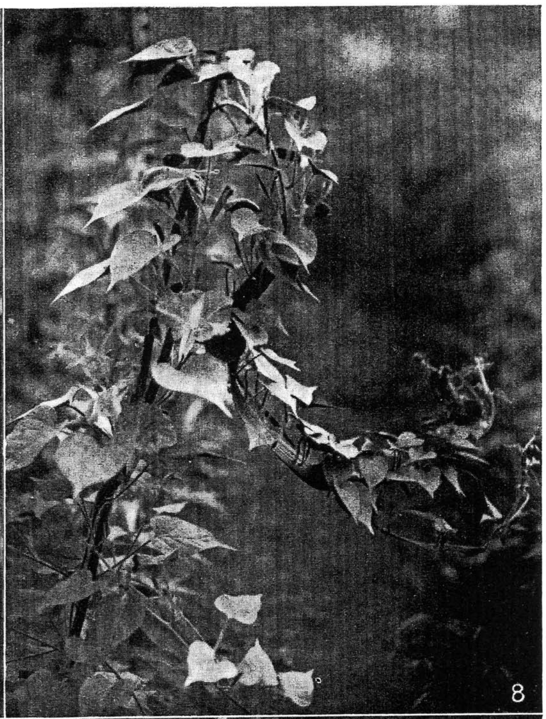

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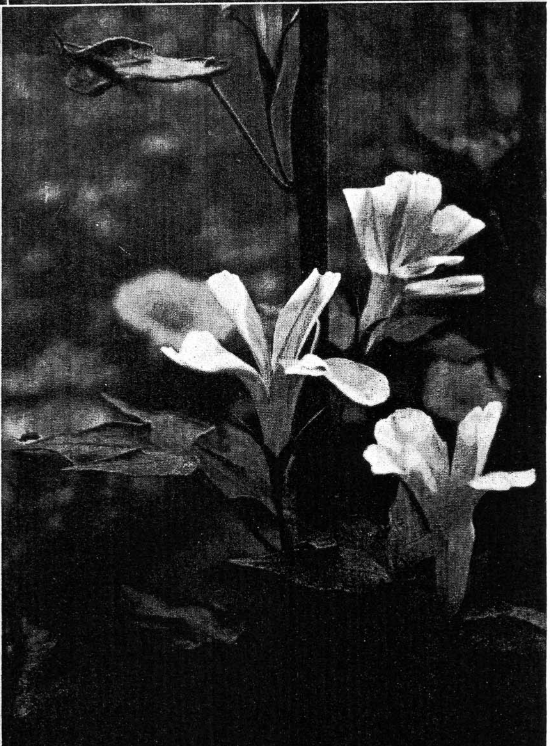

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