On the Rolled Leaves and their Linked Characters in the Japanese Morning Glory (*Pharbitis Nil*)

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Introduction

The Japanese morning glory is cultivated in our country for ornamental purposes. Over a thousand years ago it was introduced into Japan, and since then hundreds of varieties have been preserved and multiplied by our cultivators. So far as our knowledge is concerned, the Japanese morning glory is one of the richest plants with respect to variations.

The author making use of such variations has been conducting breeding experiments for ten years, but he has not yet completed the studies owing to too many new problems presenting themselves before him. Since 1919 the results obtained have been, at times, reported in the Botanical Magazine in Japanese.

In this paper the genetic behavior of some forms of the rolled leaves will be presented and further discussions will be made on their linkages to some other characters. The rolled leaves are not uniform in appearance or in the genetic composition by which the trait is represented. In some cases they can not be distinguished phenotypically one from the other, while experimental analysis shows that apparently uniform rolled leaves consist of two genetic types. Curiously enough, two such rolled types exhibit linkage phenomena, each to another definite character. In these special states of genetic dependence we were afforded facilities for the differentiation of two rolled leaf factors. Besides these types, some different rolled leaves were found which will be discussed at the close of this paper.

The writer wishes to take this opportunity to express his hearty thanks to Prof. Kiichi Miyake, under whose direction his experiments have been conducted, to Mr. Kisaku Hashimoto for the substantial encouragement given to him, and to all his friends who have given much valuable assistance during his investigation.

Punched Leaf

The rolledness of the leaves in this plant is exhibited in varying degrees. The „punched" leaf, as it might be called, is the common form of the rolled leaf and the degree of rolledness is not strong; the margin of the lamina is weakly rolled up and the inner surface is uneven, giving just this „punched" appearance. On account of the weakness of this characteristic it sometimes disappears in the upper leaves of the vine. So far, the observations on this subject have, as a rule, been made during the early stages of the plant growth. With reference to the punchedness itself the degree may also be variable. Generally speaking, however, it is as described above.

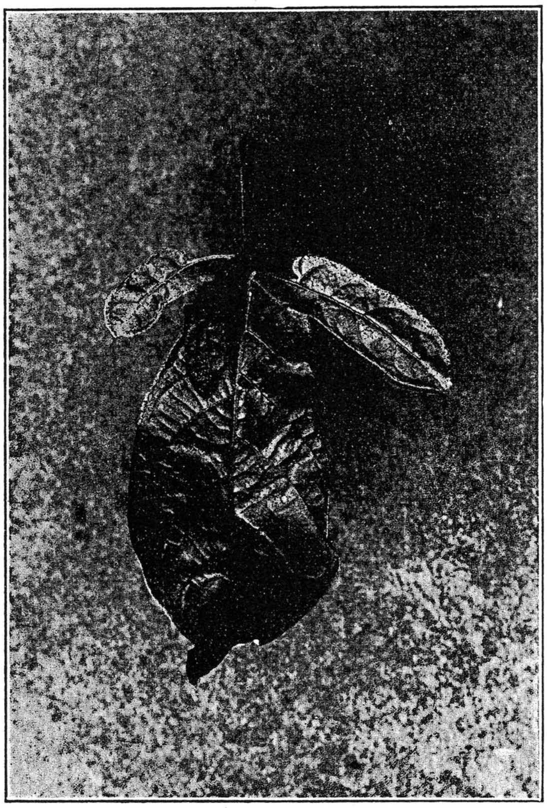

Fig. 1. Punched leaf (Leaf form, „Dragon-fly").

The punched character is a simple recessive to the normal. When the punched leaf is crossed to the normal even leaf, the F_1 plants bear almost normal leaves. On close observation, however, we see that the dominancy of the rolledness of the leaf condition is not perfect; the margin of the leaves put forth in the seedling stage may assume something of a roll, though it soon fades away in the upper leaves. As this condition, however, is not evident on casual observations made in the field, we may practically count them together with the normals. On self-fertilization of such F_1 plants we have obtained the following results:

Table 1

Cross	Even Leaf	Punched Leaf	Total
324 × 316	56	13	69
RA × 21 – 2	59	20	79
A × 71 – 2	93	46	139
β × 73	141	30	171
319 × 170	140	30	170
α × 65	88	20	108
170 × A2	229	88	317
M2 × 58 – 2	96	33	129
S3 × S5	46	17	63
65 × 505	293	93	386
RA × 58 – 2	44	27	71
RA × M1	79	21	100
RA × IH	81	25	106
RA × 71 – 2	210	79	289
SG × RA	56	19	75
β × 77 – 1	26	8	34
170 × 77 – 2	49	14	63
β × A2	36	14	50
314 × A2	238	47	285
β × 318	148	56	204
M2 × M4	104	38	142
M2 × M4b	46	26	72
Total	2358	764	3122
Expected	2341,5	780,5	3122

The segregation occurred quite normally, the alternative characters thus constituting an allelomorphic pair. The raising of the next gene-

Table 2

Cross	Number of Pedigree	Even Leaf	Punched Leaf	Total
324 × 316	34	782	253	1035
65 × 505	28	1744	514	2258
Total		2526	767	3293
Expected		2469,75	823,25	3293

ration does not show any novel results beyond those expected. Some of the even-leafed F_2 plants gave constant progenies, but the greater part of them made the segregation into the normal and the punched leaves. The summarizing data of the segregated F_3 families are shown in table 2. All of the punched F_2, however, bred true to type

Linkage of Punched Leaf and Variegation

Variegation is one of the most distinctive characters in this plant, and it acts as a recessive allelomorph to the wholly colored condition.

Table 3

Cross		Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
324 × 316		55	5	1	8	69
RA × 21−2	−1	37	5	7	1	50
	−2	13	7	2	7	29
RA × M1	−1	27	8	5	6	46
	−2	43	2	4	5	54
RA × IH	−1	25	3	1	3	32
	−2	51	11	4	8	74
β × 318	−1	56	8	4	23	91
	−2	22	3	4	4	33
	−3	55	4	7	14	80
A × 71−2	−1	21	6	2	8	37
	−2	15	4	1	5	25
	−3	16	4	2	9	31
	−4	21	2	3	2	28
	−5	10	3	2	3	18
β × 73	−1	64	5	5	8	82
	−2	38	3	3	5	49
	−3	28	2	3	7	40
RA × 71−2	−1	12	4	0	4	20
	−2	12	0	3	2	17
	−3	20	4	0	6	30
	−4	48	10	3	15	76
	−5	16	0	2	5	23
	−6	68	6	8	16	98
	−7	17	2	1	5	25
SG × RA		46	7	10	12	75
Total		836	118	87	191	1232
Expected (4,46 : 1)		821,5	102,5	102,5	205,5	1232

$\chi^2 = 5{,}97$ P = 0,12

When this marking, however, is segregated together with the punched leaf, it does not segregate very freely in the hybrid progeny. Experiment shows the occurrence of linkage. This special problem was discussed by Hagiwara (1919, 1921, 1922) and Imai (1919, 1921, 1924a).

If the linkage takes place between the punched leaf and the variegation, we should expect to obtain some coupling data in the cross of the double dominant and the double recessive. The families represented in the next table are those we should expect to produce the coupling segregation. The F_1 plants exhibited double dominant characteristics, the even and wholly colored leaves, and the F_2 generation composed of the following.

By glancing at the above-cited results, we can easily see that coupling segregations take place. The ratio of gametic distribution is calculated to be 4,46 : 1, consequently the frequency of crossover is 18,32 %.

Direct evidence as to the unequal arrangement of the gametic frequency may be obtained when a back-cross is made toward the double recessive. The writer performed this sort of mating with the F_1 plants derived from the coupling cross. The results obtained are shown in table 4. The experimental data were not sufficiently numerous, but they evidently show no uniform distribution in the gametic series. The frequency of crossover here calculated is 16,56 %.

Table 4

Back-Cross	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
F_1 (RA × IH) × vg	38	5	5	32	80
F_1 (β × 318) × β	26	8	6	25	65
Total	64	13	11	57	146
Expected (5,04 : 1)	60,5	12	12	60,5	146

$\chi^2 = 0{,}57$ P = 1 ±

We shall now return to a further discussion of the offspring of the F_2 plants. The F_3 crop (Table 5) was made through the progeny of a cross, 324 × 316. The F_3 families which segregated into the dihybrid scheme made again unusual assortments. A total of 29 families with such pedigrees were found. Out of them, twenty-six resulted just like those of the F_2 generation, or in other words they segregated again in a coupling manner. From this total number the gametic ratio is calculated to be 6,42 : 1, the crossover value being 13,48 %. The remaining three

Table 5. The F_3 Data of the Cross 324×316

Character of F_2	Pedigree Number	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
Self-colored and even	Total of 16 pedigrees	482	—	—	—	482
	Total of 4 pedigrees	125	39	—	—	164
	Expected	123	41	—	—	164
	Total of 6 pedigrees	145	—	48	—	193
	Expected	144,75	—	48,25	—	193
	3	48	3	4	11	66
	4	12	2	2	3	19
	6	45	3	4	9	61
	7	54	4	4	13	75
	8	15	2	2	6	25
	10	12	0	3	5	20
	12	8	0	0	2	10
	15	11	3	1	2	17
	17	9	0	0	2	11
	18	10	4	1	6	21
	20	6	1	3	3	13
	23	28	3	3	8	42
	25	32	3	2	7	44
	26	2	0	0	3	5
	27	8	0	0	1	9
	30	35	5	5	15	60
	31	2	2	0	2	6
	39	5	0	0	1	6
	41	35	3	2	10	50
	42	30	1	7	7	45
	53	14	1	1	2	18
	59	19	0	1	6	26
	63	22	2	1	2	27
	64	14	0	0	4	18
	67	6	1	0	2	9
	69	33	3	2	7	45
	Total	515	46	48	139	748
	Expected[1] (6,42 : 1)	514	47	47	140	748

[1] $\chi^2 = 0{,}05$ P = 1 ±

Character of F_2	Pedigree Number	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
Self-colored and even	13	18	8	9	0	35
	16	19	7	3	0	29
	35	21	9	10	0	40
	Total	58	24	22	0	104
Self-colored and Punched	Total of 5 pedigrees	—	112	—	40	152
	Expected	—	114	—	38	152
Variegated and even	Total of 1 pedigree	—	—	14	5	19
	Expected	—	—	14,25	4,75	19
Variegated and Punched	Total of 8 pedigrees	—	—	—	70	70

pedigrees gave no analogous segregation, but turned evidently into the repulsion scheme. Why should we obtain such repulsion families from the original coupling cross? It is easily understood when we recognise that the families have developed each from the F_2 plant which resulted from the union of two crossover gametes. In what proportion, then, should we expect their occurrence? Before making further statements on this problem let us attempt to discuss the results of the repulsion crosses. In the subsequent table are given the data of the repulsion segregation which we obtained from the crosses of the wholly colored leaf with punched surface and the variegated leaf with even lamina. The F_1 plants bore the even and self-colored leaves, and they gave:

The result of the calculation of the proportion of the gametic series on the basis of the above data is 1 : 2,10, that is, the frequency value of crossover is 32,26 %. Here, however, χ^2 is very high, namely 15,69, consequently the ,,goodness of fit" is extremely low. If we correct the numbers on the basis of the 3 : 1 ratio in the segregation of each character-pair and calculate it mathematically the result will be that the value of χ^2 is only 0,90 and P practically 1. Form the corrected numbers we estimate the gametic ratio as 1 : 3,05, the crossover being 24,69 %. On rearing the F_3 generation there reappeared, as might be expected, a number of families making the repulsion segregation. In table 7 will be tabulated the specimens obtained from the hybrid progeny derived from the cross 65 × 505. At this time the calculated gametic ratio is 1 : 2,82, so that the crossover value must be 26,18 %. Although the double heterozygotic F_2 each gave an abnormal segregation in the subsequent generation, they did not uniformly give the data for the repulsion segregation. Actually there were found a few exceptions which changed over to the coupling segregation. The occurrence of the families of the contrary segregation has already been seen in the F_3 data of the coupling cross. The phenomena of the coupling and repulsion are nothing but the alternative representations in the linkage inheritance. The union of two crossover gametes having different genetic composition should produce the double dominant, the wholly colored leaf with even lamina. Although it can not in the grown plants

Table 6

Cross		Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
319 × 170	−1	35	8	14	0	57
	−2	63	21	28	1	113
α × 65	−1	27	5	17	2	51
	−2	37	12	7	1	57
170 × A2	−1	73	36	25	2	136
	−2	65	38	34	3	140
	−3	24	8	8	1	41
170 × 77−2		36	14	13	0	63
M2 × 58−2	−1	35	11	20	0	66
	−2	31	22	10	0	63
M2 × M4	−1	26	14	17	3	60
	−2	41	24	16	1	82
314 × A2	−1	54	12	20	1	87
	−2	22	5	4	0	31
	−3	36	16	25	0	77
	−4	51	12	26	1	90
S3 × S5		33	17	13	0	63
65 × 505	−1	58	26	24	0	108
	−2	26	14	12	1	53
	−3	27	13	6	0	46
	−4	51	20	21	1	93
	−5	49	18	19	0	86
Total		900	366	379	18	1663
Expected		874,75	372,5	372,5	43,25	1663
(1 : 2,10)		$\chi^2 = 15,69$	P = 0,002			
Corrected total		861,58	390,385	390,385	20,65	1663
Expected		856,865	390,385	390,385	25,365	1663
(1 : 3,05)		$\chi^2 = 0,90$	P = 1 ±			

Table 7. The F_3 Data of the Cross 65×505

Character of F_2	Pedigree Number	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
Self-colored and even	Total of 1 pedigree	74	—	—	—	74
	Total of 2 pedigrees	88	21	—	—	109
	Expected	81,75	27,25	—	—	109
	Total of 8 pedigrees	518	—	169	—	687
	Expected	515,25	—	171,75	—	687
	1	59	22	21	3	105
	6	51	18	17	0	86
	7	16	10	6	1	33
	8	40	26	20	3	89
	11	26	7	8	0	41
	20	66	34	38	3	141
	21	36	17	15	0	68
	24	44	21	19	1	85
	26	83	31	31	2	147
	30	132	41	37	1	211
	31	117	37	41	0	195
	36	29	10	9	1	49
	39	28	5	9	1	43
	44	56	32	26	0	114
	45	18	5	10	0	33
	47	30	17	16	0	63
	50	27	12	16	3	58
	53	49	15	24	0	88
	57	29	7	12	0	48
	Total	936	367	375	19	1697
	Expected[1]) (1 : 1,82)	901,75	371	371	53,25	1697
	Corrected total	882,86	395,64	395,64	22,86	1697
	Expected[2]) (1 : 2,82)	877,11	395,64	395,64	28,61	1697
	15	70	10	10	15	105
	46	73	5	5	9	92
	49	53	3	7	14	77
	Total	196	18	22	38	274
	Expected[3]) (5,31 : 1)	185,5	20	20	48,5	274

[1]) $\chi^2=36,69$ $P=0\pm$ [2]) $\chi^2=1,19$ $P=0,72$ [3]) $\chi^2=3,27$ $P=0,36$

Character of F_2	Pedigree Number	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
Self-colored and punched	Total of 6 pedigrees	—	719	—	—	719
	Total of 5 pedigrees	—	115	—	33	148
	Expected	—	111	—	37	148
Variegated and even	Total of 10 pedigrees	—	—	602	—	602
	Total of 4 pedigrees	—	—	127	51	178
	Expected	—	—	133,5	44,5	178

be distinguished from that produced by the conjugation of two normal gametes, they give rise to quite different arrangements on the frequency of the expected four forms. Thus the change takes place as coupling → repulsion or repulsion → coupling. The intensity of the linkage in question is fortunately high enough to distinguish whether the segregation occurred in the coupling scheme or in the repulsion one.

To decide the average value of the linkage there are collected and tabulated in table 8 the available data which gave the coupling segre-

Table 8

Source	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
From Table 3	836	118	87	191	1232
From Table 5	515	46	48	139	748
From Table 7	196	18	22	38	274
Total	1547	182	157	368	2254
Expected (5,10:1)	1521	169,5	169,5	394	2254

$\chi^2 = 4,64$ $\quad$ $P = 0,20$

gation. From this grand total number we obtain 5,10:1 ratio in the gametic distributions, the value being changed into 16,38% of the frequency of crossover. Theoretically the intensity of the repulsion should be expected to be equal to that of the coupling. Then, we must examine to see how the expectation harmonizes with the observed data. If we collect the total data giving the repulsion segregation the numbers are:

Table 9

Source	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
From Table 5	58	24	22	0	104
From Table 6	900	366	379	18	1663
From Table 7	936	367	375	19	1697
Total	1894	757	776	37	3464
Expected (1:1,95)	1831,5	766,5	766,5	99,5	3464
	$\chi^2 = 41,63$	$P = 0 \pm$			
Corrected total	1797,51	811,40	811,40	43,68	3463,99
Expected (1:2,98)	1786,59	811,40	811,40	54,60	3463,99
	$\chi^2 = 2,25$	$P = 0,53$			

Now we have the gametic ratio of 1 : 2,98, the frequency of crossover 25,13 %. Comparing this value with that obtained from the total coupling data we note some discrepancy. The former value, however, may depend very closely upon the contents of the observed numbers, especially those of the double recessive class. For this reason we may, on the whole, attach considerable importance to the frequency calculated on the basis of the coupling data rather than that of the repulsion data. Consequently the frequency of crossover may be considered as about 16 %. This value is practically the same as that obtained in the backcross experiment.

It is natural to expect in the linkage inheritance that some disturbance should occur in the genotypic proportion of F_2. How well the expectation agrees with the actual results, we may see by inspecting table 10.

Table 10

Character of F_2	Genetic Composition	Coupling Cross		Repulsion Cross	
		Observed	Expected (4,5:1)	Observed	Expected (4,5:1)
Double dominant	Homo.	16	13,79	1	0,54
	Single hetero.	10	12,26	10	9,66
	Double hetero, normal	26	27,59	19	21,73
	„ „ reversed	3	1,36	3	1,07
	Total	55	55,00[1])	33	33,00[2])
Single dominants	Homo.	0	0,60	16	17,31
	Hetero.	6	5,40	9	7,69
	Total	6	6,00	25	25,00
Total		61		58	

[1]) $\chi^2 = 2,84$ P = 0,42 [2]) $\chi^2 = 4,23$ P = 0,24

The hypothesis offered here is thus verified by the trial examination from another viewpoint.

Two Types of Punched Leaves

A cross made by 326, a pure pedigree bearing the rolled leaves, exhibits some complications in the segregation of the punched leaves (Imai 1924c). In this case the proportion of two segregating forms, the normal and the punched leaves, quite deviated from that of the simple scheme. The leaves of the parental strain, 326, are not those of the so-called punched state in the strict sense of the word. The condition is very marked, the edge quite rolling up. The F_2 plants obtained by the cross, 326 × A5 (normal leaf), bore the rolled leaves, though this condition was only about half as marked, yet was a little stronger than the punched condition. The variation in the degree of rolledness is very apparent, going from the weak extremity of those in the punched condition to those as strongly rolled as the parental type. Since the variation was represented in an almost continuous series, it was difficult to classify them. Counting these rolled leaves together we obtained the data noted in table 11. The rolled leaves were quite numerous compared with the even ones, and the proportion of these two forms deviated far

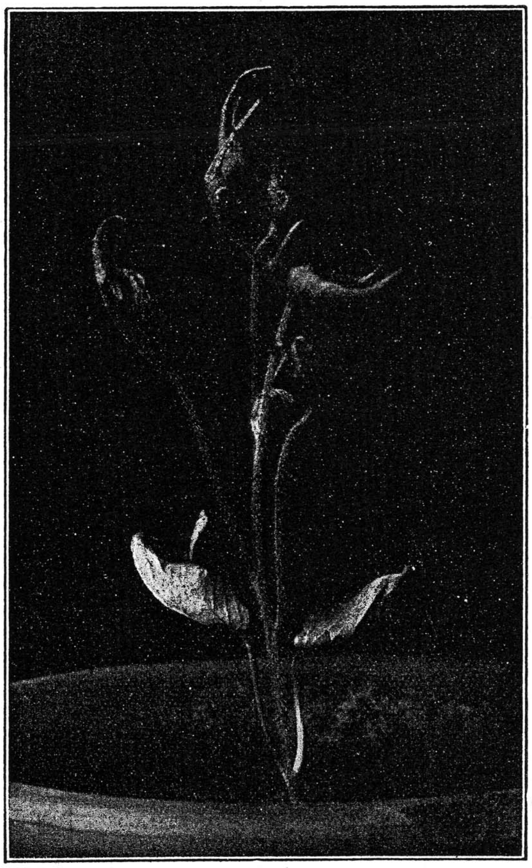

Fig. 2. A seedling of 326, the leaves strongly rolled up.

Table 11

Pedigree	Even Leaf	Rolled Leaf	Total
Total of 8 pedigrees	240	399	639
Expected on 5 : 11 ratio	199,7	439,3	639

D. = ±40,3 S.E. = ±10,95

from the simple expectation. The observad number of the normal class is proportionately 37,56 %, while that of the rolled class is 62,44 %. How shall we explain such an unusual result? For a while we shall depart from the consideration of the F_2 data, and proceed to represent the results of the next generation, to which we might look for a clue to solve the problem. From the F_3 data given in Appendix we note the following points: The normal F_2 members were partly (I) bred true to the normal, while the remainder (II) segregated into normals and rolleds in a simple ratio of 3 : 1. The rolled F_2 individuals, however, partly (III) bred constantly to the parental form, while the rest (IV) gave rise to the segregating families composed of two forms in an unusual ratio like that which occurred in F_2. The rolled leaves extracted from the families of the second class are just like those in the punched condition, and further evidence in the segregating ratio of one punched to three normals makes us identify the occurrence of the segregation of the punched factor. As will be discussed in the following section, some of the punched leaves exhibit linkage phenomena to the variegation, while the others generally accompany the „Sasa" leaves. In these special states of segregation two punched factors may be differentiated, each behaving as a recessive to the normal. From the fact that all of the descendants from the hybrids of the punched strains and the 326 had rolled leaves, we see that the latter parent also carries the punched factor. We observed, however, in general two grades of strong and weak conditions of rolledness in their segregating generations, and the observation roughly showed the simple recessive behavior of the latter state, though the differentiation between them was frequently obscure. So far we may recognize that the strong state of the rolled leaves, the 326 type, is due to the doubling of two punched factors. Now we shall represent the factors for this character by the symbol of *u*[1]), and the differentiation of two punched factors by u^v and u^s, respectively, adopt-

[1]) We commonly call the punched condition „Uchikomi". The „*u*" is the initial of this Japanese word.

ing the initial letter of each of their linked characters. Then the genetic composition of 326 should be $u^v u^v u^s u^s$, and consequently its mate is the quadruple large, $U^v U^v U^s U^s$. The F_1 plants between them should contain properly the double heterozygotic composition. Notwithstanding that both of the punched factors act each as a recessive to the even condition, why did the F_2 plants bear the rolled leaves instead of the normal ones? The conflicting fact apparent here may be solved by the recognition of the presence of interaction which takes place between the two punched factors. Neither factor can produce the punched leaf in its single heterozygotic condition, but in the double heterozygote the two factors acting together make up the rolled leaf. In the $U^v u^v U^s u^s$ condition the leaves rolled up into a state about intermediate between those of the $u^v u^v u^s u^s$ and the $U^v U^v U^s U^s$. Adding the properly punched state to these two, the strongly and the intermediately rolleds, we might have at least three grades in intensity of the rolledness of the F_2 leaves. Actually these series of gradation, however, exhibited almost continuous variation, which makes it impossible for us to work successfully on their classification.

We shall now turn back to sonsider the F_2 data. On self-fertilization of the rolled F_1 we would expect theoretically to obtain the following zygotes:

$$(1\,U^v U^s + 1\,U^v u^s + 1\,u^v U^s + 1\,u^v u^s) = \underbrace{1\,U^v U^v U^s U^s + 2\,U^v u^v U^s U^s + 2\,U^v U^v U^s u^s}_{\text{5 normal leaves}} + \underbrace{4\,U^v u^v U^s u^s + 1\,U^v U^v u^s u^s + 2\,U^v u^v u^s u^s + 1\,u^v u^v U^s U^s + 2\,u^v u^v U^s u^s + 1\,u^v u^v u^s u^s}_{\text{11 rolled leaves}}$$

In table 11 it was attempted to show how the F_2 data are satisfied by the theoretical numbers calculated on the above expectation. Unfortunately the deviation is very evident. But, as far as we can judge, some qualification should be made with respect to the actual numbers on account of the difficulty, which occurred sometimes in the distinction of the punched leaves and the single heterozygotic normals. Consequently ultimate judgment on this point should be reserved until the examination of the F_3 is made. The theoretical expectation of the F_3 generation is as follows.

Actually the expectation coincides perfectly with the result. Out of seventeen F_2 individuals bearing the normal leaves, eight gave only normal offspring composed of a total of 898, while the rest all segregated.

Table 12

Character of F_2	Ratio	Genetic Composition	Ratio	Expectation in F_3
Even leaf	5	$U^v U^v U^s U^s$	1	Breed true to even leaf
		$U^v U^v U^s u^s$	2	Segregate to three even : one rolled
		$U^v u^v U^s U^s$	2	
Rolled leaf	11	$U^v u^v U^s u^s$	4	Segregate to eleven rolled : five even
		$U^v U^v u^s u^s$	1	Breed true to rolled leaf
		$U^v u^v u^s u^s$	2	
		$u^v u^v U^s U^s$	1	
		$u^v u^v U^s u^s$	2	
		$u^v u^v u^s u^s$	1	

As will be seen from the following table, the generation thus segregated comprises two forms, the normal and rolled leaves, in the simplest proportion of almost exactly 3 : 1. A further revision may be needed as

Table 13

Pedigree Number	Even Leaf	Rolled Leaf	Total
1	196	63	259
2	63	13	76
3	124	62	186
4	40	7	47
8	110	34	144
14	13	3	16
19	12	3	15
33	50	19	69
58	4	1	5
Total	612	205	817
Expected on 3:1 ratio	612,75	204,25	817

to the results of the rolled F_2. The data showed thus: Out of forty-two rolled leaves, twenty-nine all produced the rolled leaves composed of 998, while the F_3 generation of the rest did not consist of uniform individuals. Such segregated families are tabulated in table 14. Here we should expect the ratio of the two sorts of leaf condition to be five normals to eleven rolled. Though the theoretical number calculated from such a proportion shows some deviation, yet it does not exceed 1,5-times the standard error. So far, it can be said that the proposed expectation practically coincides with the result.

Table 14

Pedigree Number	Even Leaf	Rolled Leaf	Total
7	58	111	169
9	7	14	21
10	56	98	154
11	3	5	8
15	47	102	149
16	7	11	18
26	45	140	185
27	10	24	34
34	76	142	218
36	28	30	58
37	25	58	83
54	32	62	94
59	5	6	11
Total	399	803	1202
Expected on 5:11 ratio	375,625	826,375	1202

D. = ± 23,375 S. E. = ± 16,07

From these discussions we may conclude that two punched factors occurred, which make up the rolled leaf in the double heterozygotic condition, notwithstanding each acts as a recessive to the normal. Such a sort of interaction of the analogous factors complicates somewhat the result of segregation.

Linked Characters to punched leaves

Owing to the fact that one of the parent of the cross, 326 × A5, assumes the common traits of the ,,Sasa", a further segregation on this point in the F_2 generation may be expected. The main features of the traits are the low shoulders and the sharp-pointed lobes of the lamina, and the split corolla. The characteristics are transmitted together as a unit and constitute the recessive allelomorph to the normal (Imai 1924b). In the present cross the segregation of this leaf form occurred quite according to expectation, but it showed a close linkage to the punchedness. As was stated in the preceeding section, the variegated leaf links to the punched leaf in its segregation. Thus the punchedness also makes linkage with the ,,Sasa". As regards the factor of punchedness, however, linkages to the variegation and to the ,,Sasa" are not the same. As was already stated the punched leaves of this cross were produced by either one of two factors. It is the facter u^v that links to the variegated leaf, and the other punched facter u^s to the „Sasa". By the duplication of linkage the F_2 generation of the cross, 326 × A5, assumes a complicated segregation, if we consider the assortments of four factors at a time. The actual number found is represented as follows:

Table 15

Pedigree Number	Non-„Sasa"				„Sasa"				Total
	Even		Rolled		Even		Rolled		
	Self-colored	Vari-egated	Self-colored	Vari-egated	Self-colored	Vari-egated	Self-colored	Vari-egated	
1	23	19	36	5	0	1	15	2	101
2	15	11	22	3	0	0	7	2	60
3	17	14	44	5	1	2	21	5	109
4	17	11	53	4	0	2	14	4	105
5	23	13	29	2	1	0	12	1	81
6	8	4	14	1	0	0	1	1	29
7	5	9	14	1	0	0	7	0	36
8	25	18	52	5	1	0	13	4	118
Total	133	99	264	26	3	5	90	19	639

At first sight the table seems to present a puzzle, but an analysis of the data shows the occurrence of duplicated linkage. On a close inspection of the above table, we see that the appearance of the variegated leaf in the rolled class was less than our expectation, while too many variegated leaves were obtained in the even class, so we may assume that linkage takes place between the variegated and punched forms. The

Table 16

Pedigree Number	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
2	47	13	16	0	76
3	88	59	36	3	186
4	30	6	10	1	47
8	83	34	27	0	144
14	10	3	3	0	16
19	7	3	5	0	15
Total	265	118	97	4	484
Expected (1:1,99)	255,5	107,5	107,5	13,5	484

$\chi^2 = 9{,}09 \qquad P = 0{,}03$

linkage, however, was disturbed and complicated by the overlapping of the segregation of one more punched factor which segregated quite independently of both of these linked factors. So the positive proof might be sought for in those F_3 families making the segregation in only two linking factors. By the F_3 data we found six families which made such a dihybrid segregation. The actual numbers of these families, with one exception, showed repulsion data. (Table 16.)

From the total number we obtain 33,44 % as the frequency of the crossover gametes. An exceptional family which gave the coupling segregation, however, is composed of:

Table 17

Pedigree Number	Self-colored and Even	Self-colored and Punched	Variegated and Even	Variegated and Punched	Total
1	188	15	8	48	259
Expected (9,74:1)	182,75	11,5	11,5	53,25	259

$\chi^2 = 2{,}80 \quad P = 0{,}43$

Here the frequency of crossover is calculated to be 9,31 %. The discrepancy in these two values of the frequency of the repulsion data and the coupling data is considerable, but it may be passed over on account of small number of specimens observed. Eventually as a result of the above data it may be accepted that the segregating factor for the punchedness in these families is u^s.

On the revisal of those data (see Appendix) of the F_3 generation segregated like F_2, we see again unusual distributions of the rolled leaves in the normal and the „Sasa" classes. The proportion of the rolled leaves in the normal population is 56,90 %, while in the „Sasa" class it is estimated to be 96,91 %. If the characters in question are assorted independently one from the other, we should expect to have equal distributions in such a relation. The difference may be considered as due to the influence of the linkage, which takes place between the two factors for the „Sasa" and the punched leaf. Owing to the duplicate segregations of the punched factors, the linked data in the F_3 generation were also complicated. One of the F_3 families, however, showed the dihybrid segregation of two linking factors, where the even and rolled leaves were produced in a simple 3:1 ratio, if we consider only the segregation of these alternative characters. The actual segregation is:

Table 18

Pedigree Number	Non-„Sasa" and Even	„Sasa" and Punched	Non-„Sasa" and Even	„Sasa" and Punched	Total
33	49	0	1	19	69
Expected (57,42:1)	51,25	0,5	0,5	16,75	69

$\chi^2 = 1{,}20 \quad P = 0{,}76$

Though the total number may not be sufficiently numerous to be relied upon, yet if we attempt to calculate the linkage value between the „Sasa" and the punched leaf with the above data, the frequency of crossover is 1,71 %. So far, at any rate, it may be said with certainty that a high linkage takes place between these two characters. The F_2 generation thus made the coupling segregation, and further, owing to the state of high linkage, all of the F_3 families which segregated into these characters in question gave also coupling results. Adding the numbers of these families, with the exception of the one which was above tabulated, to the F_2 result, we have the total data for such a segregation. The table thus obtained is:

Table 19

Pedigree Number	Non-„Sasa" and Even	Non-„Sasa" and Rolled	„Sasa" and Even	„Sasa" and Rolled	Total
F_2 (8 pedigrees)	232	290	8	109	639
F_3 7	56	71	2	40	169
F_3 9	7	8	0	6	21
F_3 10	55	54	1	44	154
F_3 11	3	1	0	4	8
F_3 15	47	71	0	31	149
F_3 16	6	8	1	3	18
F_3 26	45	90	0	50	185
F_3 34	73	103	3	39	218
F_3 36	28	20	0	10	58
F_3 37	25	37	0	21	83
F_3 54	31	41	1	21	94
F_3 59	3	3	0	3	11
F_3 Total	381	507	8	272	1168
Grand total	613	797	16	381	1807

The complication of the above data is due to the triple segregations of the factors for the „Sasa" and the two punched leaves. To estimate

Table 20

Genetic Composition	Normal Ratio		Actual Expectation				Phenotype
			$v \longleftrightarrow u^v = m:1$ (Rep.) $s_a \longleftrightarrow u^s = n:1$ (Coup.)		$m = 5$ $n = 16$		
$VV\ S_a S_a\ U^v U^v\ U^s U^s$	1	45	n^2	$2m^2n^2 + 4m^2n + 8mn^2 + 12mn + 5n^2 + 4m + 8n + 2$	256	27030	Non-„Sasa", even and self-colored
$Vv\ S_a S_a\ U^v U^v\ U^s U^s$	2		$2mn^2$		2560		
$VV\ S_a s_a\ U^v U^v\ U^s U^s$	2		$2n$		32		
$VV\ S_a S_a\ U^v u^v\ U^s U^s$	2		$2mn^2$		2560		
$VV\ S_a S_a\ U^v U^v\ U^s u^s$	2		$2n$		32		
$Vv\ S_a s_a\ U^v U^v\ U^s U^s$	4		$4mn$		320		
$Vv\ S_a S_a\ U^v u^v\ U^s U^s$	4		$2m^2n^2 + 2n^2$		13312		
$Vv\ S_a S_a\ U^v U^v\ U^s u^s$	4		$4mn$		320		
$VV\ S_a s_a\ U^v u^v\ U^s U^s$	4		$4mn$		320		
$VV\ S_a s_a\ U^v U^v\ U^s u^s$	4		$2n^2 + 2$		514		
$Vv\ S_a s_a\ U^v u^v\ U^s U^s$	8		$4m^2n + 4n$		1664		
$Vv\ S_a s_a\ U^v U^v\ U^s u^s$	8		$4mn^2 + 4m$		5140		
$vv\ S_a S_a\ U^v U^v\ U^s U^s$	1	15	m^2n^2	$3m^2n^2 + 4m^2n + 2mn^2 + 4mn + 2m^2$	6400	23730	Non-„Sasa", even and variegated
$vv\ S_a s_a\ U^v U^v\ U^s U^s$	2		$2m^2n$		800		
$vv\ S_a S_a\ U^v u^v\ U^s U^s$	2		$2mn^2$		2560		
$vv\ S_a S_a\ U^v U^v\ U^s u^s$	2		$2m^2n$		800		
$vv\ S_a s_a\ U^v u^v\ U^s U^s$	4		$4mn$		320		
$vv\ S_a s_a\ U^v U^v\ U^s u^s$	4		$2m^2n^2 + 2m^2$		12850		
$VV\ S_a S_a\ U^v u^v\ U^s u^s$	4	99	$4mn$	$7m^2n^2 + 14m^2n + 10mn^2 + 24mn + 9m^2 + 4n^2 + 14m + 10n + 7$	320	66606	Non-„Sasa", rolled and self-colored
$Vv\ S_a S_a\ U^v u^v\ U^s u^s$	8		$4m^2n + 4n$		1664		
$VV\ S_a s_a\ U^v u^v\ U^s u^s$	8		$4mn^2 + 4m$		5140		
$Vv\ S_a s_a\ U^v u^v\ U^s u^s$	16		$4m^2n^2 + 4m^2 +$ [$4n^2 + 4$		26728		
$VV\ S_a S_a\ u^v u^v\ U^s U^s$	1		m^2n^2		6400		
$Vv\ S_a S_a\ u^v u^v\ U^s U^s$	2		$2mn^2$		2560		
$VV\ S_a s_a\ u^v u^v\ U^s U^s$	2		$2m^2n$		800		
$Vv\ S_a s_a\ u^v u^v\ U^s U^s$	4		$4mn$		320		
$VV\ S_a S_a\ U^v U^v\ u^s u^s$	1		1		1		
$Vv\ S_a S_a\ U^v U^v\ u^s u^s$	2		$2m$		10		
$VV\ S_a s_a\ U^v U^v\ u^s u^s$	2		$2n$		32		
$Vv\ S_a s_a\ U^v U^v\ u^s u^s$	4		$4mn$		320		
$VV\ S_a S_a\ U^v u^v\ u^s u^s$	2		$2m$		10		
$Vv\ S_a S_a\ U^v u^v\ u^s u^s$	4		$2m^2 + 2$		52		
$VV\ S_a s_a\ U^v u^v\ u^s u^s$	4		$4mn$		320		
$Vv\ S_a s_a\ U^v u^v\ u^s u^s$	8		$4m^2n + 4n$		1664		
$VV\ S_a S_a\ u^v u^v\ U^s u^s$	2		$2m^2n$		800		
$Vv\ S_a S_a\ u^v u^v\ U^s u^s$	4		$4mn$		320		
$VV\ S_a s_a\ u^v u^v\ U^s u^s$	4		$2m^2n^2 + 2m^2$		12850		
$Vv\ S_a s_a\ u^v u^v\ U^s u^s$	8		$4mn^2 + 4m$		5140		
$VV\ S_a S_a\ u^v u^v\ u^s u^s$	1		m^2		25		
$Vv\ S_a S_a\ u^v u^v\ u^e u^s$	2		$2m$		10		
$VV\ S_a s_a\ u^v u^v\ u^s u^s$	2		$2m^2n$		800		
$Vv\ S_a s_a\ u^v u^v\ u^s u^s$	4		$4mn$		320		

Table 20

Genetic Composition	Normal Ratio		Actual Expectation: $v \longleftrightarrow u^v = m:1$ (Rep.), $s_a \longleftrightarrow u^s = n:1$ (Coup.)		Actual Expectation: $m = 5$, $n = 16$		Phenotype
$vv\ S_a S_a\ U^v u^v U^s u^s$	4	33	$4mn$	$2m^2n + 4mn^2 + 8mn + m^2 + 3n^2 + 6m + 6n + 3$	320	7482	Non-„Sasa", rolled and variegated
$vv\ S_a s_a\ U^v u^v U^s u^s$	8		$4mn^2 + 4m$		5140		
$vv\ S_a S_a\ u^v u^v U^s U^s$	1		n^2		256		
$vv\ S_a s_a\ u^v u^v U^s U^s$	2		$2n$		32		
$vv\ S_a S_a\ U^v U^v u^s u^s$	1		m^2		25		
$vv\ S_a s_a\ U^v U^v u^s u^s$	2		$2m^2n$		800		
$vv\ S_a S_a\ u^v u^v U^s u^s$	2		$2n$		32		
$vv\ S_a s_a\ u^v u^v U^s u^s$	4		$2n^2 + 2$		514		
$vv\ S_a S_a\ U^v u^v u^s u^s$	2		$2m$		10		
$vv\ S_a s_a\ U^v u^v u^s u^s$	4		$4mn$		320		
$vv\ S_a S_a\ u^v u^v u^s u^s$	1		1		1		
$vv\ S_a s_a\ u^v u^v u^s u^s$	2		$2n$		32		
$VV\ s_a s_a\ U^v U^v U^s U^s$	1	15	1	$4mn + 2m^2 + 4m + 2n + 3$	1	425	„Sasa", even and self-colored
$Vv\ s_a s_a\ U^v U^v U^s U^s$	2		$2m$		10		
$VV\ s_a s_a\ U^v u^v U^s U^s$	2		$2m$		10		
$VV\ s_a s_a\ U^v U^v U^s u^s$	2		$2n$		32		
$Vv\ s_a s_a\ U^v u^v U^s U^s$	4		$2m^2 + 2$		52		
$Vv\ s_a s_a\ U^v U^v U^s U^s$	4		$4mn$		320		
$vv\ s_a s_a\ U^v U^v U^s U^s$	1	5	m^2	$2m^2n + m^2 + 2m$	25	835	„Sasa", even and variegated
$vv\ s_a s_a\ U^v u^v U^s U^s$	2		$2m$		10		
$vv\ s_a s_a\ U^v U^v U^s u^s$	2		$2m^2n$		800		
$VV\ s_a s_a\ U^v u^v U^s u^s$	4	33	$4mn$	$3m^2n^2 + 6m^2n + 6mn^2 + 8mn + m^2 + 3n^2 + 2m + 4n$	320	30787	„Sasa", rolled and self-colored
$Vv\ s_a s_a\ U^v u^v U^s u^s$	8		$4m^2n + 4n$		1664		
$VV\ s_a s_a\ U^v U^v u^s u^s$	1		n^2		256		
$Vv\ s_a s_a\ U^v U^v u^s u^s$	2		$2mn^2$		2560		
$VV\ s_a s_a\ u^v u^v U^s U^s$	1		m^2		25		
$Vv\ s_a s_a\ u^v u^v U^s U^s$	2		$2m$		10		
$VV\ s_a s_a\ U^v u^v u^s u^s$	2		$2mn^2$		2560		
$Vv\ s_a s_a\ U^v u^v u^s u^s$	4		$2m^2n^2 + 2n^2$		13312		
$VV\ s_a s_a\ u^v u^v U^s u^s$	2		$2m^2n$		800		
$Vv\ s_a s_a\ u^v u^v U^s u^s$	4		$4mn$		320		
$VV\ s_a s_a\ u^v u^v u^s u^s$	1		m^2n^2		6400		
$Vv\ s_a s_a\ u^v u^v u^s u^s$	2		$2mn^2$		2560		
$vv\ s_a s_a\ U^v u^v U^s u^s$	4	11	$4mn$	$m^2n^2 + 2mn^2 + 4mn + n^2 + 2n + 1$	320	9569	„Sasa", rolled and variegated
$vv\ s_a s_a\ U^v U^v u^s u^s$	1		m^2n^2		6400		
$vv\ s_a s_a\ u^v u^v U^s U^s$	1		1		1		
$vv\ s_a s_a\ U^v u^v u^s u^s$	2		$2mn^2$		2560		
$vv\ s_a s_a\ u^v u^v U^s u^s$	2		$2n$		32		
$vv\ s_a s_a\ u^v u^v u^s u^s$	1		n^2		256		

the linkage value from these numbers we need some qualification upon which to base our calculation. On account of high linkage, it may be advisable to estimate the value from the segregating numbers in the „Sasa" column. Speaking of the contents of the even and rolled leaves we would except theoretically the following: In the F_1 plants carrying the triple heterozygotic compositions, $S_a s_a U^v u^v U^s u^s$, there should be a production of eight sorts of different gametes. Out of them, four gametes, $s_a U^v U^s$, $s_a U^v u^s$, $s_a u^v U^s$ and $s_a u^v u^s$, contribute to the development of the „Sasa" specimens. The ratio of these four sorts of germ-cells, then, may be designated as $1 s_a U^v U^s : n s_a U^v u^s : 1 s_a u^v U^s : n s_a u^v u^s$, when the linkage consideration is denoted by the application of n. The random combinations of these gametes will give:

$$\left.\begin{array}{r} 1 s_a s_a U^v U^v U^s U^s \\ 2n s_a s_a U^v U^v U^s u^s \\ 2 s_a s_a U^v u^v U^s U^s \end{array}\right\} 2n+3 \quad \text{Even leaves}$$

$$\left.\begin{array}{r} 4n s_a s_a U^v u^v U^s u^s \\ n^2 s_a s_a U^v U^v u^s u^s \\ 2n^2 s_a s_a U^v u^v u^s u^s \\ 1 s_a s_a u^v u^v U^s U^s \\ 2n s_a s_a u^v u^v U^s u^s \\ n^2 s_a s_a u^v u^v u^s u^s \end{array}\right\} 4n^2+6n+1 \quad \text{Rolled leaves}$$

Then the ratio of two phenotypes, the even and rolled leaves, is $2n+3 : 4n^2+6n+1$. If we calculate the value of n from this ratio in application of the observed numbers, the result is 11,89. Consequently the frequency of crossover is calculated as 7,76 %. This value differs considerably from 1,5 %, which is calculated by the observed number of family 33. As we have no further data on which to decide the delicate point of value, we must be contented with understanding only that a certain low percentage of crossover in the segregation of the „Sasa" and the punchedness takes place. Probably it may not be far from 5 %.

Thus the analysis shows the duplicate occurrences of two linkages, the one takes place between v and u^v, the other between s_a and u^s. In F_2 we should, then, expect theoretically the following gametic series:

$$\begin{aligned} & n V S_a U^v U^s + 1 V S_a U^v u^s + mn V S_a u^v U^s + m V S_a u^v u^s + 1 V s_a U^v U^s \\ & + n V s_a U^v u^s + m V s_a u^v U^s + mn V s_a u^v u^s + mn v S_a U^v U^s \\ & + m v S_a U^v u^s + n v S_a u^v U^s + 1 v S_a u^v u^s + m v s_a U^v U^s \\ & + mn v s_a U^v u^s + 1 v s_a u^v U^s + n v s_a u^v u^s \end{aligned}$$

In the above formula m was applied to the linkage consideration between v and u^{v}, and n to that of s_{a} and u^{s}. On the combination of these gametes we should expect to obtain an F_2 population as will be seen in Table 20.

Other rolled leaves

Besides these two punched leaves other forms of the rolled leaves are found. As already stated elsewhere (IMAI 1924a), the ,,Shishi" flower always accompanies something of the rolled leaf. The ,,Shishi" flower is one of the representations of doubling, the corolla being feathered and split sometimes into even several deformed pieces. Thê sexual organs, however, both stamens and pistil remain apparently unchanged, although they are functionless in most cases. On account of the monstrous form of the flower the ,,Shishi" race is regarded as one of the most valuable variations for the ornamental purpose. The Japanese pick up and transplant the ,,Shishi" seedlings by noting its accompanying rolled leaves[1]. Because of the fact that the ,,Shishi" flower usually produces no seeds, it is a common procedure to seek for this race among the progeny of the heterozygotic normals. In such a proceeding the multiple representations of the ,,Shishi" factor save much labor in practice. In inheritance, the ,,Shishi" flower behaves as a recessive to the single. When the punched factor is contained in the ,,Shishi" race, it produces what might be called a ,,grasped" leaf

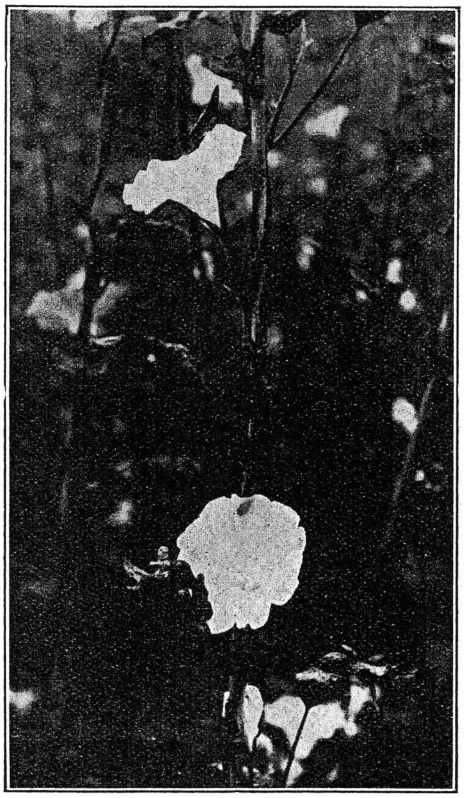

Fig. 3. ,,Dragon"-leafed stem with cup flowers.

[1]) The rolling feature is present even in the cotyledonous leaves.

(Miyake and Imai 1921). So the grasped leaf is the combined result of two factors.

There is another different form of the strongly rolled leaf, just like that of the grasped leaf. On account of its monstrous feature the form is called by the name of „Dragon“. The „Dragon“ leaf always accompanies the „cup“ flower. In the F_2 generation of the hybrids obtained by the cross of the punched and the „crapy“[1]) (Imai 1920) leaves we obtained some „Dragon“ leaves. The actual numbers obtained are:

Table 21

Cross	Normal	Crapy	Punched	„Dragon“	Total
M2 × M4	82	22	27	11	142
M2 × M4B	35	11	21	5	72
β × 318	112	36	42	14	204
Total	229	69	90	30	418
Expected	235,125	78,375	78,375	26,125	418

$\chi^2 = 3{,}58 \quad P = 0{,}33$

The result shows the segregation of two factors, the one being for the punched leaf and the other for the crapyness. The „Dragon“ leaf, then, is considered to be a double recessive. The „crapy“ leaf is invariably accompanied by the „cup“ flower, so the „Dragon“ leaf has the cupped flower also.

Summary

1. The punched condition of the leaf surface acts as a simple recessive to the normal.
2. About 16 % of linkage takes place between the punched leaf and the variegation.
3. The experiments on this problem were made both with respect to coupling and repulsion.
4. In a cross, two kinds of the punched leaves, each carrying an entirely different factor, were detected.
5. Each of these factors behaves as a recessive allelomorph to the normal. These factors, however, interacting on each other produce the rolled leaf in the double heterozygotic plants. Such hybrids give offspring composed of 11 rolled and 5 normals in every 16 individuals.

[1]) The crapyness behaves as a recessive to the normal.

6. Duplication of two punched factors in the homozygous condition results in a strongly rolled leaf.
7. One of the punched factors, denoted by u^v, links to the variegated (v), and another, named as u^s, makes linkage with the „Sasa“ type (s_a).
8. The linkage value of the factors, u^s and s_a, is about 5% or nearly so.
9. Besides these punched leaves other forms of the rolled leaves were found. The „Shishi“ flower is always accompanied by something of the rolled leaf. When the „Shishi“ factor is combined with the punched one a „grasped“ leaf is produced. Another highly rolled leaf called by the name of „Dragon“ is the combined representation of the two factors for punchedness and crapyness.

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Appendix

The F_3 Data of the Cross 326 × A 5.

Character of F_2	Pedigree Number	Non-"Sasa" Even Self-colored	Non-"Sasa" Even Vari-egated	Non-"Sasa" Rolled Self-colored	Non-"Sasa" Rolled Vari-egated	"Sasa" Even Self-colored	"Sasa" Even Vari-egated	"Sasa" Rolled Self-colored	"Sasa" Rolled Vari-egated	Total	Genetic Composition
Non-"Sasa", even and self-colored	55	7	—	—	—	—	—	—	—	7	?
	58	4	—	1	—	—	—	—	—	5	?
	2	47	16	13	0	—	—	—	—	76	$Vv\ S_a S_a\ U^v u^v\ U^s U^s$ (Repulsion)
	3	88	36	59	3	—	—	—	—	186	
	4	30	10	6	1	—	—	—	—	47	
	8	83	27	34	0	—	—	—	—	144	
	14	10	3	3	0	—	—	—	—	16	
	19	7	5	3	0	—	—	—	—	15	
	Total	265	97	118	4	—	—	—	—	484	
	1	188	8	15	48	—	—	—	—	259	" (Coupling)
Non-"Sasa", even and variegated	12	—	114	—	—	—	—	—	—	114	$vv\ S_a S_a\ U^v U^v\ U^s U^s$
	28	—	50	—	—	—	—	—	—	50	
	29	—	11	—	—	—	—	—	—	11	
	31	—	2	—	—	—	—	—	—	2	
	49	—	56	—	—	—	—	—	—	56	
	Total	—	233	—	—	—	—	—	—	233	
	6	—	5	—	—	—	3	—	—	8	$vv\ S_a s_a\ U^v U^v\ U^s U^s$
	33	—	49	—	0	—	1	—	19	69	$vv\ S_a s_a\ U^v U^v\ U^s u^s$
Non-"Sasa", rolled and self-colored	27	2	8	23	1	—	—	—	—	34	$Vv\ S_a S_a\ U^v u^v\ U^s u^s$
	7	28	28	64	7	0	2	29	11	169	$Vv\ S_a S_a\ U^v u^v\ U^s u^s$
	9	6	1	6	2	0	0	4	2	21	
	10	30	25	51	3	0	1	36	8	154	
	11	3	0	1	0	0	0	2	2	8	
	15	27	20	64	7	0	0	23	8	149	
	16	6	0	7	1	1	0	2	1	18	
	26	14	31	84	6	0	0	39	11	185	
	34	42	31	94	9	0	3	29	10	218	
	36	13	15	19	1	0	0	5	5	58	
	54	17	14	33	8	0	1	17	4	94	
	59	1	4	3	0	0	0	3	0	11	
	Total	187	169	426	44	1	7	189	62	1085	
	37	25	—	37	—	0	—	21	—	83	$VV\ S_a s_a\ U^v u^v\ U^s u^s$

The F_3 Data of the Cross 326 × A 5.

Character of F_2	Pedigree Number	Non-"Sasa" Even Self-colored	Non-"Sasa" Even Vari-egated	Non-"Sasa" Rolled Self-colored	Non-"Sasa" Rolled Vari-egated	"Sasa" Even Self-colored	"Sasa" Even Vari-egated	"Sasa" Rolled Self-colored	"Sasa" Rolled Vari-egated	Total	Genetic Composition
Non-"Sasa". rolled and self-colored	17	—	—	6	—	—	—	—	—	6	$VV S_a S_a - ? -$
	18	—	—	30	—	—	—	—	—	30	
	21	—	—	4	—	—	—	—	—	4	
	24	—	—	1	—	—	—	—	—	1	
	25	—	—	44	—	—	—	—	—	44	
	30	—	—	3	—	—	—	—	—	3	
	35	—	—	11	—	—	—	—	—	11	
	38	—	—	8	—	—	—	—	—	8	
	42	—	—	49	—	—	—	—	—	49	
	47	—	—	26	—	—	—	—	—	26	
	51	—	—	12	—	—	—	—	—	12	
	56	—	—	82	—	—	—	—	—	82	
	Total	—	—	270	—	—	—	—	—	270	
	20	—	—	38	—	—	—	11	—	49	$VV S_a s_a - ? -$
	32	—	—	9	—	—	—	4	—	13	
	39	—	—	122	—	—	—	30	—	152	
	44	—	—	35	—	—	—	10	—	45	
	52	—	—	130	—	—	—	36	—	166	
	53	—	—	13	—	—	—	9	—	22	
	Total	—	—	347	—	—	—	100	—	447	
	48	—	—	24	12	—	—	—	—	36	$Vv S_a S_a - ? -$
	22	—	—	82	26	—	—	12	5	125	$Vv S_a s_a - ? -$
	40	—	—	99	41	—	—	29	8	177	
	41	—	—	8	2	—	—	1	1	12	
	43	—	—	15	3	—	—	6	1	25	
	45	—	—	16	4	—	—	1	0	21	
	46	—	—	53	20	—	—	17	5	95	
	Total	—	—	273	96	—	—	66	20	455	
"Sasa"	23	—	—	—	—	—	2	—	—	2	$vv s_a s_a - ? -$
	13	—	—	—	—	—	—	4	—	4	$V? s_a s_a - ? -$
	50	—	—	—	—	—	—	4	—	4	
	Total	—	—	—	—	—	—	8	—	8	
	57	—	—	—	—	—	—	3	2	5	$Vv s_a s_a - ? -$
	5	—	—	—	—	—	—	—	6	6	$vv s_a s_a - ? -$