STUDIES OF INHERITANCE IN THE JAPANESE *CONVOLVULUS*.

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(With Plate II and One Text-figure.)

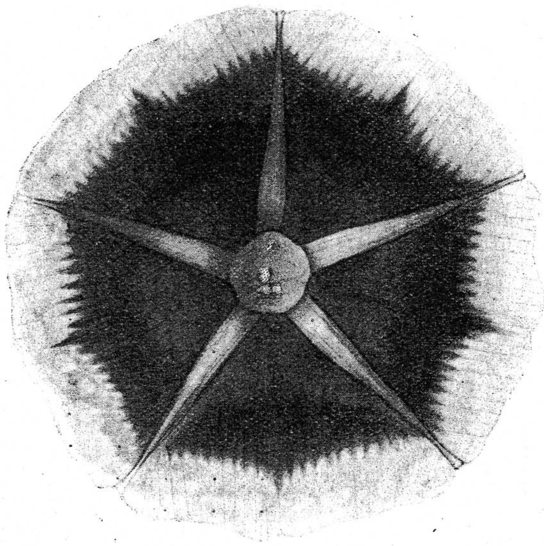
[*Note.* In the present state of the postal service it has not been possible to submit this paper to the author for revision. EDD.]

CONTENTS.

INTRODUCTION.

THE Japanese *Convolvulus*, closely related to the Morning Glory of the Americans and known under the popular name "Asagao[1]," is very extensively cultivated here since immemorial time as an ornamental plant, and contains an abundant number of races which are characterised by remarkable variation in the form and colour of leaves as well as flowers. As I have been studying the hereditary behaviour of several characters in this species for some years, and have reached definite conclusions in some respects, I am going to publish here the results of these investigations. All experiments contained in this paper were conducted in my garden in Yokohama.

The inheritance of the Japanese *Convolvulus* has already been studied by three authors, Tanaka[2], Toyama[3] and Takezaki[4]. Of these I will speak below only about the investigations of Takezaki, some of whose



Corolla with "hukurin," seen from above.

[1] This plant has been variously called by our systematists *Ipomoea hederacea*, *Pharbitis hederacea*, *P. Nil*, etc., and I am not able to decide myself which name is really the right one.

[2] *Idengaku Kyôkwasyo* (A text-book of Genetics in Japanese), Tôkyô, 1915, pp. 32 ff. and 96 ff.

[3] *Nippon Ikusyugakukwai Kwaihô* (Journal of the Japanese Breeders' Association), I. 1, 1916, pp. 8, 9.

[4] Ditto, pp. 12, 13 with many tables.

results are in agreement with mine. According to him the green colour of leaves behaves as dominant towards the yellow (*chlorina*), and in F_2 the ratio of green and yellow plants is 3 : 1. The genetic behaviour of flower colour is very complex, but if we classify plants simply into those with coloured and those with white flowers, white is recessive, and in F_2 the ratio of the two kinds of plants is 3 : 1. In some of these coloured flowers the corolla is white at its margin, so as to form a ring-shaped white patch (see the text-fig.),—what Japanese gardeners call the "hukurin[1]." Takezaki studied the inheritance of white-margined flowers, and found that the "hukurin" is produced by a special factor acting as a white dominant at the margin of the corolla so that the hybrid between a race with white-margined flowers and another with fully-coloured ones was found to produce the former kind of flowers in F_1 and to segregate in F_2 into the ratio 3 white-margined : 1 fully-coloured. Moreover, he reported that in certain cases there is even a factor which inhibits the action of that producing the "hukurin" part.

EXPERIMENTS.

The plants originally used in my experiments are characterised as follows:

A. Leaf is yellow[2] (*chlorina*) (Pl. II, fig. 6), and flower white, though its throat is tinged with extremely light magenta (Pl. II, fig. 2).

B. Leaf is green (Pl. II, fig. 5), and flower dark-red[3] (Pl. II, fig. 1).

These two parents were cultivated for two years before my experiments had begun, and since then this cultivation has been continued during five years. Both of them were found during cultivation to breed true entirely to their respective types.

In 1913 I performed the hybridisation between these two plants in both reciprocal ways, and in 1914 three individuals from each were grown for the purpose of further experiments.

(*a*) F_1 *Generation.*

Leaf was green: that is, green is dominant to yellow. Flower-colour was entirely different from that of either parent, and was light

[1] I shall sometimes use this word to indicate such a white patch.

[2] The word "yellow" is used always in this paper for brevity's sake, but naturally it means yellowish green.

[3] This colour corresponds nearly to No. 42 (Rouge) of the "Code des Couleurs" by Klincksieck and Valette, Paris, 1908.

magenta[1]. The corolla is not however fully coloured, and it is white at its margin not wholly, but only near each of the five notches of its limb. Such white patch is also called "hukurin," and the words "hukurin" and "white-margined" used below refer always to flowers which are edged with white partially in such way. Both reciprocal hybrids were entirely similar to each other (Pl. II, fig. 3).

(*b*) F_2 *Generation.*

The mode of segregation of flower-colour in F_2 is rather complex. Not only are there found flowers of white, dark-red, and magenta colour exactly similar to that of the two original parents and the F_1 plant, respectively, but we have also those of scarlet colour (Pl. II, fig. 4), and in each of these colours—dark-red, magenta, and scarlet—there are three gradations of their intensity, sharply distinguishable from each other. The detailed study of the segregation of flower-colour is now under way, and will be dealt with in a future paper. For the present time, for simplicity's sake, I will call magenta and scarlet simply by the collective name *red,* and make no distinction of the intensities of colour just noticed.

The details of the segregation of leaf- and flower-colour in F_2 are shewn in Table I.

TABLE I.

F_2 *generation.*

Leaf-colour	Flower-colour	White-margined or fully-coloured	$A \times B$				$B \times A$				Grand totals
			a[2]	*b*	*c*	Totals	*d*	*e*	*f*	Totals	
green	red ...	white-margined	20	7	46	73	9	4	48	61	134
		fully-coloured	6	4	16	26	5	1	20	26	52
	dark-red	white-margined	9	2	29	40	5	5	22	32	72
		fully-coloured	4	0	15	19	2	5	10	17	36
	white	... ...	15	4	23	42	11	5	36	52	94
yellow	red ...	white-margined	5	5	27	37	3	8	30	41	78
		fully-coloured	1	2	14	17	2	2	14	18	35
	dark-red	white-margined	0	0	0	0	0	0	0	0	0
		fully-coloured	0	0	0	0	0	0	0	0	0
	white	... ...	4	2	13	19	1	1	11	13	32
		Totals ...	64	26	183	273	38	31	191	260	533

We will consider now leaf-colour, "hukurin" and flower-colour separately.

[1] This lies between No. 566 and 571 (Violet rouge) of the "Code des Couleurs."

[2] The letters *a*—*f* in the Tables indicate the different individuals of the 6 F_1 plants which were bred from.

1. *Leaf-colour.*

The results of my investigation are in perfect accord with those of Takezaki (p. 61), and it will be readily seen from Table II that here the segregation occurs in the simplest Mendelian fashion.

TABLE II.

F_1 plants	Results			Expected			
	Green	Yellow	Totals	Green	Yellow	α[1]	δ[2]
$A \times B\,(a+b+c)$	200	73	273	204·75	68·25	± 4·75	±7·150
$B \times A\,(d+e+f)$	188	72	260	195·00	65·00	± 7·00	±6·982
Totals ...	388	145	533	399·75	133·25	±11·75	±9·997

2. *"Hukurin."*

As before stated, in spite of the fact that neither the one nor the other of the parents shews externally any sign of the "hukurin," this character appears in the F_1 plants, and moreover, it will be seen from Table III that in F_2 the ratio of plants with white-margined and those with fully-coloured flowers is 3 : 1. As of course we cannot distinguish between the white-margined and the non-white-margined condition in perfectly white flowers, plants with the latter kind of flowers are not included in this Table.

TABLE III.

F_1 plants		Results			Expected			
		White-margined	Fully-coloured	Totals	White-margined	Fully-coloured	α	δ
$A \times B$	(a)	34	11	45	33·75	11·25	± 0·75	±9·186
,,	(b)	14	6	20	15·00	5·00	± 1·00	±1·937
,,	(c)	102	45	147	110·25	36·75	± 8·25	±5·250
$B \times A$	(d)	17	9	26	19·50	6·50	± 2·50	±2·208
,,	(e)	17	8	25	18·75	6·25	± 1·75	±4·165
,,	(f)	100	44	144	108·00	36·00	± 8·00	±5·196
Totals		284	123	407	305·25	101·75	±21·25	±8·736

From the above table we see that the number of plants with white-margined flowers really obtained is always smaller than might be theoretically expected, except in $A \times B\,(a)$. We have however to make here the two following remarks. In the first place, the area of the "hukurin" part was very variable according to individuals, notwithstanding the fact that all plants were grown under exactly similar conditions. Thus not rarely the "hukurin" was represented by very

[1] Deviation from the theoretical number.

[2] Standard error.

insignificant white spots in the five notches of the corolla; moreover, even in one and the same individual, which has very slightly white-margined flowers, I was able to discern the "hukurin" sometimes clearly but sometimes not at all, according to different stages of their development, so that it would not be improbable that some plants with such very slightly white-margined flowers were erroneously entered as being without them. Secondly, I have learned by experience that the mode of cultivation has great influence over the production of the "hukurin." Plants were generally grown in a field, but some of them were cultivated in pots, for example a certain number of (*c*) and (*f*) in Table III. The difference of the results due to the method of cultivation will be explained by reference to Table IV.

TABLE IV.

	Cultivated in field			Cultivated in pot		
F_1 plants	White-margined	Fully-coloured	Totals	White-margined	Fully-coloured	Totals
$A \times B$ (*c*)	38	13	51	64	32	96
$B \times A$ (*f*)	53	19	72	48	24	72
Totals ...	91	32	123	112	56	168
Percentage	73·98	26·20		66·66	33·33	

As will be seen from the above Table, while in the field culture plants with white-margined flowers and those with fully-coloured ones are 74 and 26, respectively, i.e. are almost exactly in the ratio 3 : 1, in the pot culture there are 67 and 33, respectively, i.e. the number of plants with white-margined flowers is relatively much smaller in the latter case than in the former. Plants in (*a*), (*b*), (*d*), and (*e*) were all cultivated in the field, and we see that here the ratio of the two kinds of plants is nearly equal to 3 : 1 in each case, and the very small deficiency of plants with white-margined flowers from the theoretical expectation in these cases may be probably due to the first of the two causes above mentioned. That in the case of pot culture we see always a definite deficiency, may be perhaps due to the fact that pots are generally too dry in summer without special precautions. As is well known through the investigations of several botanists, the formation of anthocyanin in leaves is very much accelerated when leaves live under very dry conditions. Thus, according to Wheldale[1], we see the development of anthocyanin in *Pelargonium* which was insufficiently watered; also Miyoshi[2] observed

[1] *The Anthocyanin Pigments of Plants.* Cambridge, 1916, p. 24.

[2] *Journ. Coll. Science*, Tôkyô Imp. University, Vol. XXVII. 1909, pp. 1—5.

that leaves of trees in the East Indies, Ceylon and Java redden during the dry period in the same way as autumnal leaves do in the temperate regions. Again Pellew[1] reports that the amount of pigment in petals of both white and blue plants of *Campanula carpatica* varies according to the moisture condition of the soil, flowers becoming much darker after rain.

In our case it would not therefore be unlikely that owing to the summer drought some anthocyanin would develop in the "hukurin" part and make white-margined flowers look like fully-coloured ones, especially in plants grown in pots.

3. *Flower-colour.*

As will be seen from Table I there occur no dark-red flowers in yellow-leaved plants. As flowers of this colour are found exclusively on green plants, it might perhaps be concluded that some coupling or repulsion took place between flower- and leaf-colour. But such is not really the case, as will be easily seen from Table V.

TABLE V.

		Results			Expected			
F_1 plants	Leaf-colour	No. of coloured flowering plants	No. of white flowering plants	Totals	No. of coloured flowering plants	No. of white flowering plants	α	δ
$A \times B\ (a+b+c)$	Green	158	42	200	150·00	50·00	±8·00	±6·124
$B \times A\ (d+e+f)$	,,	136	52	188	141·00	47·00	±5·00	±5·937
Totals		294	94	388	291·00	97·00	±3·00	±8·592
$A \times B\ (a+b+c)$	Yellow	54	19	73	54·75	18·25	±0·75	±3·700
$B \times A\ (d+e+f)$	,,	59	13	72	54·00	18·00	±5·00	±3·674
Totals		113	32	145	108·75	36·25	±4·25	±5·241
Gross totals		407	126	533	399·75	133·25	±7·25	±9·997

In this Table plants are classified into two groups according to their flower-colour, i.e. those with white and those with coloured flowers. From this we see that the ratio of individuals of these two classes, both in green as well as yellow plants, is 3 : 1, despite the fact above noticed that in the latter there were found no plants with dark-red flowers. It will be readily understood from these considerations that we have here to deal with neither coupling nor repulsion.

In green plants the number of those with red, dark-red and white flowers respectively is in the ratio 2 : 1 : 1, as shewn in Table VI.

[1] *Journal of Genetics*, Vol. VI. pp. 317—339.

TABLE VI.

F_1 plants	Results: Red	Results: Dark-red	Results: White	Results: Totals	Expected: Red	Expected: Dark-red	Expected: White	α: $R+D:W$	α: $R+W:D$	δ
$A \times B\ (a+b+c)$	99	59	42	200	100	50	50	±8·00	± 9·00	±6·124
$B \times A\ (d+e+f)$	87	49	52	188	94	47	47	±5·00	± 2·00	±5·937
Totals	186	108	94	388	194	97	97	±3·00	±11·00	±8·529

(c) F_3 *Generation.*

Seeds were obtained from 31 F_2 plants, with which to study the F_3 generation. The following are the results of these studies.

1. *Leaf-colour.*

It will be seen from Table VII that in respect to leaf-colour we have obtained exactly the same results as in F_2 (compare Table II).

TABLE VII.

Pedigree No. of F_2 plants	Results: Green	Results: Yellow	Results: Totals	Expected: Green	Expected: Yellow	α	δ
7	8	6	14	10·50	3·50	±2·50	±1·620
9	36	7	43	32·25	10·75	±3·75	±2·889
22	76	26	102	76·50	25·50	±0·50	±4·373
31	80	19	99	74·25	24·75	±5·75	±4·265
44	39	11	50	37·50	12·50	±1·50	±2·810
45	10	3	13	9·75	3·25	±0·25	±1·561
11 (*a*)	12	6	18	13·50	4·50	±1·50	±1·836
14 (*a*)	6	2	8	6·00	2·00	±0·00	±1·225
15 (*a*)	11	5	16	12·00	4·00	±1·00	±1·732
15 (*b*)	12	1	13	9·75	3·25	±2·25	±1·561
39 (*b*)	7	1	8	6·00	2·00	±1·00	±1·225
Totals	297	87	384	288·00	96·00	±9·00	±8·485

From their behaviour in F_3 it was apparent that 20 of the 31 F_2 plants were homozygous for leaf-colour. Of these 10 were green and 10 were yellow. Table VIII gives the total number of F_3 plants obtained from these 20 homozygous F_2 individuals.

TABLE VIII.

Leaf-colour of F_2 plants	Total number of families of F_2 plants	Leaf-colour of F_3 plants: Green	Leaf-colour of F_3 plants: Yellow
Green ...	10	241	0
Yellow ...	10	0	564

2. "*Hukurin.*"

We have got exactly the same results as in F_2, as shewn in Table IX (compare Table III).

TABLE IX.

Pedigree No. of F_2 plants	Results			Expected			
	White-margined	Fully-coloured	Totals	White-margined	Fully-coloured	a	δ
14	43	21	64	48·00	16·00	±5·00	±2·289
16	37	11	48	36·00	12·00	±1·000	±3·000
19	35	14	49	36·75	12·25	±1·75	±3·030
31	76	23	99	74·25	24·75	±1·75	±4·308
32	20	7	27	20·25	6·75	±0·25	±2·250
38	18	5	23	17·25	5·75	±0·75	±2·077
39	32	11	43	32·25	10·75	±0·25	±2·839
55	24	13	37	27·75	9·25	±3·75	±2·634
11 (*a*)	11	3	14	10·50	3·50	±0·50	±1·620
15 (*b*)	10	2	12	9·00	3·00	±1·00	±1·500
Totals	306	110	416	312·00	104·00	±6·00	±8·832

From the above Table we see that the ratio of plants with white-margined and with fully-coloured flowers is 3 : 1, and in this case, when we compare the ratios of the number of these two kinds of plants in the field- as well as in the pot-cultures to each other we see also in the latter case a certain deficiency of plants of white-margined flowers.

We have got 4 families of plants which contain the "hukurin" factor in homozygous condition, and 9 families where it is entirely absent, as shewn in Table X.

TABLE X.

	Total number of families in F_2	White-margined	Fully-coloured
White-margined ...	4	109	0
Fully-coloured ...	9	0	301

3. *Flower-colour.*

It would be *a priori* easily seen from the results in F_2 that all F_2 plants with white flowers will produce in F_3 again those with white ones. Though I could not obtain many seeds from plants of these families the results shewn in Table XI will fully confirm this expectation.

We could find no families of plants which breed true constantly to dark-red flowers.

TABLE XI.

	Pedigree No. of F_2 plants	Leaf-colour of F_3 plants	Flower-colour of F_3 plants: Dark-red	Red	White
α	3	green	0	0	23
	10	,,	0	0	10
	26	,,	0	0	12
β	56	yellow	0	0	56
γ	7	green	0	0	8
		yellow	0	0	6
	45	green	0	0	10
		yellow	0	0	3
		Totals ...	0	0	128

We have obtained the two families of plants which breed true to yellow leaves and red flowers, as indicated in Table XII.

TABLE XII.

Pedigree No. of F_2 plants	Leaf-colour of F_3 plants	Flower-colour of F_3 plants: Dark-red	Red	White
16	yellow	0	48	0
49 (*b*)	,,	0	18	0
	Totals ...	0	66	0

The families which segregate into plants with red and those with white flowers are found only among yellow F_2 plants; in F_3 the ratio of red and white is 3 : 1, as shewn in Table XIII.

TABLE XIII.

Pedigree No. of F_2 plants	Leaf-colour of F_3 plants	Results: Dark-red	Red	White	Totals	Expected: Dark-red	Red	White	α	δ
17	yellow	0	64	20	84	0	63·00	21·00	±1·00	±3·969
18	,,	0	77	25	102	0	76·50	25·50	±0·50	±4·373
19	,,	0	49	13	62	0	46·50	15·50	±2·50	±3·410
38	,,	0	23	6	29	0	21·75	7·25	±1·25	±2·332
39	,,	0	43	7	50	0	37·50	12·50	±5·50	±3·062
59	,,	0	35	20	55	0	41·25	13·75	±6·25	±3·211
60	,,	0	46	22	68	0	51·00	17·00	±5·00	±3·571
	Totals	0	337	113	450	0	337·50	112·50	±0·50	±9·186

The families of plants which segregate into those with dark-red and those with white flowers are found only among those which remain constantly green in F_3, and the ratio of dark-red and white is 3 : 1, as shewn in Table XIV.

TABLE XIV.

Pedigree No. of F_2 plants	Leaf-colour of F_3 plants	Results: Red	Dark-red	White	Totals	Expected: Red	Dark-red	White	α	δ
14	green	0	65	14	79	0	59·25	19·75	±5·75	±3·849
32	,,	0	27	8	35	0	26·25	8·75	±0·75	±2·562
55	,,	0	37	11	48	0	36·00	12·00	±1·00	±3·000
11 (*b*)	,,	0	7	3	10	0	7·50	2·50	±0·50	±1·370
23 (*a*)	,,	0	3	2	5	0	3·75	1·25	±0·75	±0·967
23 (*b*)	,,	0	8	1	9	0	6·75	2·25	±1·25	±1·299
24 (*b*)	,,	0	9	2	11	0	8·25	2·75	±0·75	±1·436
	Totals	0	156	41	197	0	147·75	49·25	±8·25	±6·078

The families of plants which segregate into those with red and those with dark-red flowers are found only among those which segregate into green and yellow plants in F_3. The results are indicated in Table XV.

TABLE XV.

Pedigree No. of F_2 plants	Leaf-colour of F_3 plants	Results: Red	Dark-red	White	Totals	Grand totals
9	green	23	13	0	36	43
	yellow	7	0	0	7	
31	green	48	32	0	80	99
	yellow	19	0	0	19	
44	green	22	17	0	39	50
	yellow	11	0	0	11	
14 (*a*)	green	4	2	0	6	8
	yellow	2	0	0	2	
15 (*a*)	green	6	5	0	11	16
	yellow	5	0	0	5	
15 (*b*)	green	2	9	0	11	12
	yellow	1	0	0	1	
39 (*b*)	green	3	3	0	6	7
	yellow	1	0	0	1	

In the above Table the total number of individuals with red and of those with dark-red flowers in green plants is 108 and 81, respectively, and although this ratio seems to be somewhat different from the expected 2 : 1, yet the deviation lies within the range of thrice the standard error, because the former is $\pm$ 11 and the latter is $\pm$ 6·481.

We had the two families of plants which segregated in the same way as in F_2, as shewn in Table XVI.

We have no yellow plants with white flowers in No. 11 (*a*), but this is no doubt due to the small number of experiments. In other families

TABLE XVI.

Pedigree No. of F_2 plants	Leaf-colour	Results: No. of coloured flowering plants	Results: No. of white flowering plants	Totals	Expected: No. of coloured flowering plants	Expected: No. of white flowering plants	α	δ
22	green	54	21	75	56·25	18·75	±2·25	±3·750
11 (*a*)	,,	8	4	12	9·00	3·00	±1·00	±1·500
	Totals	62	25	87	65·25	21·75	±3·25	±4·039
22	yellow	18	8	26	19·50	6·50	±1·50	±2·208
11 (*a*)	,,	6	0	6	4·50	4·50	±1·50	±1·060
	Totals	24	8	32	24·00	24·00	± 0	±2·450
	Gross totals	86	33	119	89·25	89·25	±3·25	±4·724

we see that the ratio of individuals with coloured and white flowers is 3 : 1.

In the above Table, if we classify flower-colour of green plants into *red* and *dark-red*, we see that their ratio is 2 : 1, as was the case in F_2 (see Table VI). This is shewn in Table XVII.

TABLE XVII.

Pedigree No. of F_2 plants	Results: Red	Results: Dark-red	Results: Totals	Expected: Red	Expected: Dark-red	α	δ
22	35	19	54	36·00	18·00	±1·00	±3·697
11 (*a*)	6	2	8	5·33	2·67	±0·67	±1·334
Totals	41	21	62	41·33	20·67	±0·33	±3·712

(*d*) F_4 *Generation.*

Seeds were obtained from 43 F_3 plants. The results in F_4 are shewn below.

1. *Leaf-colour.*

Only the families of plants which segregated into green and yellow plants are shewn in the following Table.

TABLE XVIII.

Pedigree No. of F_3 plants	Results: Green	Results: Yellow	Results: Totals	Expected: Green	Expected: Yellow	α	δ
9—23	74	21	95	71·25	23·75	± 2·75	±4·221
22— 1	78	30	108	81·00	27·00	± 3·00	±4·500
22— 4	51	16	67	50·25	16·75	± 0·75	±3·544
31— 1	43	15	58	43·50	14·50	± 0·50	±3·298
31—10	39	9	48	36·00	12·00	± 3·00	±3·000
44— 2	79	15	94	70·50	23·50	± 8·50	±4·198
44— 6	34	10	44	33·00	11·00	± 1·00	±2·693
Totals	398	116	514	385·50	128·50	±12·50	±9·817

In the above Table the deviation of the total number (= ± 12·50) is somewhat larger than the standard error (= ± 9·817), but the difference between them is not very large. Furthermore, if we examine each family separately we see that only in No. 44—2 is the deviation larger than the standard error but even here not larger than twice the latter, so that the results in this case are similar to those gained in F_2 and F_3 (see Tables II and VII).

2. "*Hukurin.*"

Seeds were obtained from 17 F_3 plants with white-margined flowers and we had in F_4 8 families of plants which breed true to the "hukurin" condition. The results from 9 families of plants which exhibited the segregation are shewn in Table XIX.

TABLE XIX.

Pedigree No. of F_3 plants	Results			Expected			
	White-margined	Fully-coloured	Totals	White-margined	Fully-coloured	α	δ
14— 2	55	26	81	60·75	20·25	± 5·75	± 3·897
14— 9	74	22	96	72·00	24·00	± 2·00	± 4·243
31—10	35	13	48	36·00	12·00	± 1·00	± 3·000
32— 7	29	6	35	26·25	8·75	± 2·75	± 2·562
38— 2	21	9	30	22·50	7·50	± 1·50	± 2·535
39— 1	69	29	98	73·50	24·50	± 4·50	± 3·824
39— 3	26	11	37	27·75	9·25	± 1·75	± 2·633
39— 7	85	33	118	88·50	29·50	± 3·50	± 4·704
55— 4	34	14	48	36·00	12·00	± 2·00	± 3·000
Totals	428	163	591	443·25	147·75	±15·25	±10·527

From these results we see that they are in perfect agreement with those obtained in F_3 (see Table IX). As the number of plants with white-margined flowers was relatively smaller in pot- than in field-culture, we find always some deficiency of plants with white-margined flowers under the expected number.

3. *Flower-colour.*

The results are shewn in Table XX, (*a*)—(*h*).

The segregation shewn in (*a*) is similar to that occurring in F_2; that shewn in (*b*) and in (*c*) is, respectively, similar to that shewn in Tables XV and XIV. The segregation shewn in (*d*) was not observed in F_3. The segregation shewn in (*e*), (*f*), (*g*) and (*h*) is similar to that in Table XI (α), Table XIII, Table XII, and Table XI (β), respectively.

TABLE XX.

	Pedigree No. of F_3 plants	Leaf-colour	Red	Dark-red	White	Totals	Grand totals
(a)	22— 4	green	23	11	17	51	67
		yellow	13	0	3	16	
(b)	9—23	green	51	23	0	74	95
		yellow	21	0	0	21	
	22— 1	green	51	27	0	78	108
		yellow	30	0	0	30	
	31— 1	green	29	14	0	43	58
		yellow	15	0	0	15	
	31—10	green	22	17	0	39	48
		yellow	9	0	0	9	
	44— 2	green	54	25	0	79	94
		yellow	15	0	0	15	
	Totals	green	207	106	0	313	403
		yellow	90	0	0	90	
	44— 6	green	0	34	0	34	44
		yellow	0	10	0	10	
(c)	14— 2	green	0	81	25	106	
	22—11	,,	0	18	6	24	
	32— 7	,,	0	35	17	52	
	55— 4	,,	0	48	9	57	
	Totals	...	0	182	57	239	
(d)	9— 4	green	0	35	0	35	
	14—19	,,	0	96	0	96	
	31— 9	,,	0	18	0	18	
	32— 6	,,	0	26	0	26	
	44— 3	,,	0	35	0	35	
	Totals	...	0	210	0	210	
(e)	10— 1	green	0	0	5	5	
	10— 5	,,	0	0	5	5	
	23— 1	,,	0	0	11	11	
	32— 5	,,	0	0	51	51	
	45— 1	,,	0	0	10	10	
	Totals	...	0	0	82	82	
(f)	22— 3	yellow	57	0	20	77	
	38— 1	,,	24	0	8	32	
	39— 1	,,	98	0	40	138	
	39— 2	,,	39	0	16	55	
	39— 3	,,	37	0	13	50	
	59—12	,,	24	0	6	30	
	60— 1	,,	63	0	24	87	
	Totals	...	342	0	127	469	

TABLE XX (*continued*).

	Pedigree No. of F_3 plants	Leaf-colour	Red	Dark-red	White	Totals
(*g*)	16— 4	yellow	86	0	0	86
	16— 9	,,	31	0	0	31
	17—13	,,	31	0	0	31
	17—14	,,	34	0	0	34
	17—15	,,	33	0	0	33
	31— 5	,,	30	0	0	30
	38— 2	,,	30	0	0	30
	38— 8	,,	27	0	0	27
	39— 7	,,	118	0	0	118
	44— 1	,,	28	0	0	28
	44—10	,,	86	0	0	86
	59—11	,,	29	0	0	29
	Totals ...		563	0	0	563
(*h*)	17— 7	yellow	0	0	30	30
	56— 1	,,	0	0	44	44
	59—10	,,	0	0	25	25
	Totals ...		0	0	99	99

We may now consider some points in connection with Table XX.

(*a*) In green plants we have 34 plants with coloured and 17 with white flowers, and the ratio may be taken as 3 : 1, the deviation and the standard error being ± 4·250 and ± 3·092, respectively. Of the above 34 plants with coloured flowers 23 individuals have red and 11 dark-red ones, thus their ratio is 2 : 1, the deviation and the standard error being ± 0·333 and ± 2·450, respectively.

In yellow plants we have 13 plants with red and 3 with white flowers, and the ratio may be taken as 3 : 1, the deviation and the standard error being ± 1·000 and ± 1·732, respectively.

(*b*) In green plants, except No. 44—6, we have 207 plants with red and 106 with dark-red flowers, thus their ratio is 2 : 1, the deviation and the standard error being ± 1·667 and ± 8·340, respectively. In No. 44—6 I could find, in spite of careful observations, no green plants with red flowers, but here some yellow plants with dark-red flowers made their appearance, which were never found otherwise. This peculiar case will be the subject of my future paper.

(*c*) We have 182 plants with dark-red and 57 with white flowers, thus their ratio is 3 : 1, the deviation and the standard error being ± 2·750 and ± 6·694, respectively.

(*d*) All breed true to dark-red flowers.

(*e*) All breed true to white flowers.

(*f*) We have 342 plants with red and 127 with white flowers, thus their ratio is 3:1, the deviation and the standard error being ± 9·750 and ± 9·377, respectively.

(*g*) All breed true to red flowers.

(*h*) All breed true to white flowers.

As will be seen from above, there are some cases where the deviation is larger than the standard error, but these differences are not very large, and it may be safely concluded that the results of all these experiments are in accordance with expectation. Furthermore, from the results of F_3 and F_4 we may deduce the following facts:

1. No homozygous green plants with red flowers were found.

2. In the offspring derived from green plants with red flowers leaf-colour always segregates into green and yellow, while the segregation of flower-colour is either exactly similar to that in F_2, or different from it, in so far as no white flowers are produced.

(*e*) *Back-crossing and F_2.*

In 1916 the back-crossing of one F_1 plant ($= A \times B$) by both of the two parents was done.

The results of $F_1 \times A$ are indicated in Table XXI.

TABLE XXI.

Leaf-colour	Red	Dark-red	White	Totals
Green ...	33	0	48	81
Yellow ...	45	0	38	83
Totals ...	78	0	86	164

In this case the flower was either white or magenta as in F_1, and all coloured flowers were white-margined.

From the results in F_2 it may be *a priori* expected that the ratios of green and yellow plants, and that of red and white flowers, are 1:1 respectively. Indeed we have obtained 81 green and 83 yellow plants, thus our expectation was so perfectly fulfilled that no further comment is necessary. The ratio of plants with red and white flowers is equally 3:1, the deviation and the standard error being ± 4·000 and ± 6·043, respectively.

The results of back-cross $F_1 \times B$ are shewn in Table XXII.

In this case we should expect from the results of F_2 that leaf-colour would remain constantly green, that the ratio of plants with white-margined and fully-coloured flowers would be 1:1, and finally that the

TABLE XXII.

Green	Red ...	White-margined	25	46
		Fully-coloured	21	
	Dark-red	White-margined	10	35
		Fully-coloured	25	
	White	... ...	0	
Yellow...	...	... ...	0	

ratio of plants with red and dark-red flowers would be also 1 : 1. Let us now examine Table XXII to see whether or not our expectation is fulfilled. Firstly, all plants are green. Secondly, there are 35 plants with white-margined and 46 fully-coloured flowers, thus their ratio is 1 : 1, the deviation and the standard error being $\pm$ 5·500 and $\pm$ 4·500, respectively. Again, there are 46 plants with red and 35 plants with dark-red flowers, the deviation and the standard error being equal to those of the latter case, respectively. Thus we see that in every case the deviation is larger than the standard error, but the differences between them are not large, so that it would not be unreasonable to consider that we see in both cases segregation in the ratio 1 : 1.

The F_1 plant used in the back crosses just above mentioned was self-fertilised; and the results of the examination of the F_2 generation thus obtained, consisting of 651 individuals in all, have fully confirmed those shewn in Table I.

DISCUSSION OF RESULTS.

It will be readily seen from all the experiments above mentioned that the hereditary behaviour of leaf-colour is in exact accordance with that obtained by Takezaki (p. 61).

The results on the "hukurin" are also the same, at least in some cases, as those reported by him, and in such cases the presence of a factor for producing the "hukurin" part has been duly proven.

If we simply classify plants into those which can produce anthocyanin on the corolla, at least partially, and those which cannot, their ratio in F_2, F_3, etc., is 3 : 1. Now since, for the formation of anthocyanin, at least two factors are necessary, we may denote them by **C** and **R**, respectively. Then the dark-red colour is to be represented by **CCRR**. The white colour, as we may infer from the results of experiments, should have one of these factors; suppose the latter to be **C**, then the two parents and the F_1 hybrid are to be represented as follows, respectively:

$$\text{parent } A = \mathsf{CCrr},$$
$$,, \quad B = \mathsf{CCRR},$$
$$F_1 = \mathsf{CCRr}.$$

From these considerations it will be quite evident that the ratio of plants with coloured and white flowers is 3 : 1.

I will go now to the consideration of the interrelation existing between the hereditary behaviour of leaf-colour and dark-red flower-colour. Flowers of the latter colour never appear in yellow plants but exclusively in green ones. It was stated before that this constitutes no case of coupling or repulsion (p. 65), and the results of experiments which are now to be described led me to the conclusion that in the presence of a certain factor D, *the flower is either dark-red or of some other colour according as the green factor* G *is in either homo- or heterozygous condition (or altogether absent).*

There are many instances in which the intensity of flower-colour varies according to the homo- or heterozygous condition of the factor concerned in pigmentation. Thus the flower-colour was found to be lighter in heterozygous than in homozygous individuals, for example in *Atropa Belladonna*[1], *Datura Tatula* × *D. Stramonium*[2], *Linum usitatissimum*[3], and *Antirrhinum majus*[4]. Although our case has not to deal with the intensity of flower-colour, I think that it has to be ranked among the same class of phenomena as those above cited. Similar examples are also found in respect to the pigmentation of other plant organs, as in *Corchorus capsularis*[5], Egyptian cotton[6], Indian cotton[7], and *Phaseolus vulgaris*[8]. Saunders reported an interesting case of the connection between the factors for hoariness of leaves and flower-colour in *Stocks*[9]. Colour is due here to the presence of two factors C and R in the zygote. In certain strains of Stocks, the hoariness of the leaves has been found to depend also on the presence of two factors H and K. Between these two pairs of factors there is a certain relationship, viz.

[1] Bateson and Saunders, *Rept Evol. Com. Roy. Soc.* 1901, pp. 1—160.

[2] *L.c.*

[3] T. Tammes, *Rec. Trav. Bot. Néerl.* Vol. VIII. 3, 1911, pp. 201—288.

[4] R. S. Finlow and I. H. Burkill, *Mem. Depart. Agric. India. Bot.* Vol. IV. 4, pp. 73—92.

[5] W. L. Balls, *Journ. Agric. Sci.* Vol. II. 1908, pp. 346—379.

[6] H. de Vries, *Ber. Deut. Bot. Ges.* Vol. XVIII. 1900, pp. 83—90.

[7] H. M. Leake, *Journal of Genetics*, Vol. I. 1911, pp. 205—272.

[8] G. H. Shull, *Amer. Nat.* Vol. XVII. 1908, pp. 433—451.

[9] E. R. Saunders, *Proc. Roy. Soc.* Vol. LXXXV. B, 1912, pp. 540—545.

that the hoariness due to H and K is only manifested when C and R are both present. Hence an albino (as regards anthocyanin) may contain both H and K, and may yet be glabrous because it cannot contain at the same time both C and R. An anthocyanin form, on the other hand, which is glabrous, carries of course C and R, but can only contain either H or K, and not both; when it carries C and R, as well as H and K, it is hoary and coloured.

The relationship existing between the factor for leaf-colour and that for flower-colour in our *Convolvulus* is very similar to the last mentioned case in Stocks. The fact that the dark-red colour appears exclusively in flowers of green plants will be explained in like manner as in the case of Stocks. If we denote for example the factor for green leaf-colour by G and that for dark-red flower-colour by D, then the parents would be

$$A = \text{ggdd},$$
$$B = \text{GGDD}.$$

The F_1 hybrid is thus GgDd, so that it is heterozygous for the factor G. We will suppose that D can produce red colour but not dark-red, when G is either heterozygous or absent in the zygote.

We should have in F_2 the following plants:

Plants	Colour of leaf	Colour of flower	No. of plants
GGDD	green	dark-red	1
GGDd	,,	,,	2
GGdd	,,	white	1
GgDD	,,	red	2
GgDd	,,	,,	4
Ggdd	,,	white	2
ggDD	yellow	red	1
ggDd	,,	,,	2
ggdd	,,	white	1
Totals ...	...	... ...	16

The above zygotes may be arranged as follows:

Green leaf	dark-red flower	3
	red ,,	6
	white ,,	3
Yellow leaf	dark-red flower	0
	red ,,	3
	white ,,	1

That the theoretical expectation just mentioned is well fulfilled, may be seen from Table II (p. 63), Table VI (p. 66), and Table V (p. 65).

The offspring derived from these F_2 plants were studied in order to ascertain, whether the production of the F_2 plants with the above mentioned genotypic constitutions has been realised.

In the families containing plants which always produce white flowers, Table XI shews that α corresponds to the formula **GGdd**, β to **ggdd** and γ to **Ggdd**.

We could get no family corresponding to the formula **GGDD** in F_3, though we had some (cf. Table XIV) corresponding to the formula **GGDd**. It will be noticed here that notwithstanding the fact that there should be theoretically one **GGDD** and two **GGDd** in F_2 we had seven **GGDd** and none of **GGDD**, but this may perhaps be merely a matter of chance and without special meaning.

The results in respect to the plants of other genotypic constitutions are as follows:

Table	XVI	corresponds	to	**GgDd**.
„	XV	„	„	**GgDD**.
„	XII	„	„	**ggDD**.
„	XIII	„	„	**ggDd**.

Thus all results secured in F_3 progenies are fairly well in accordance with the theroetical expectation, except **GGDD**.

Furthermore, let us examine the results in F_4 to see whether or not our expectation is fulfilled. First of all, we have the families corresponding to **GGDD** in Table XX (*d*), and other families are similar to those in F_3. It will be noticed also here that we have had no single constant family containing green plants with red flowers till we have attained the F_4 generation, and moreover, according to our theoretical expectation it should appear neither in F_2 nor F_3. This fact alone suffices perhaps to confirm our hypothesis above mentioned that in the presence of the factor **D**, **G** will produce dark-red colour in its homozygous and red colour in its heterozygous condition.

Next I will pass on to the results of back-crossing. According to our theory the ratio of plants with dark-red and red flowers in $F_1 \times B$ should be 1 : 1, and this was really the case, as will be seen in Table XXII. In $F_1 \times A$ there should be no plant with dark-red flowers, and this is really the fact, as will be seen in Table XXI. Thus again the results of back-crosses are in perfect accordance with our expectation.

Further, I have made various crosses between some of the F_3 individuals to each other, and also between them and either one of the two original parents. The results of these experiments are shewn in the Table XXIII.

TABLE XXIII.

Crosses attempted	Leaf-colour	Flower-colour: Red	Dark-red	White	Totals	Grand totals
(10—1) × (16—9)	green	50	0	0	50	50
	yellow	0	0	0	0	
(17—7) × (17—13)	green	0	0	0	0	64
	yellow	64	0	0	64	
(22—3) × (22—4)	green	18	0	3	21	51
	yellow	27	0	3	30	
(22—3) × (22—11)	green	7	0	2	9	9
	yellow	0	0	0	0	
(31—1) × (31—5)	green	29	0	0	29	51
	yellow	22	0	0	22	
(31—10) × (31—9)	green	24	25	0	49	49
	yellow	0	0	0	0	
(44—2) × (44—10)	green	26	0	0	26	70
	yellow	44	0	0	44	
(55—15) × (38—1)	green	4	0	7	11	11
	yellow	0	0	0	0	
(56—1) × (38—1)	green	0	0	0	0	48
	yellow	27	0	21	48	
(59—10) × (16—9)	green	0	0	0	0	39
	yellow	39	0	0	39	
A × (9—4)	green	10	0	0	10	10
	yellow	0	0	0	0	
A × (16—9)	green	0	0	0	0	9
	yellow	9	0	0	9	
A × (38—1)	green	0	0	0	0	14
	yellow	8	0	6	14	
(32—5) × *B*	green	0	11	0	11	11
	yellow	0	0	0	0	

From what was above described about the results of self-fertilisation of F_3 plants it is clear that the genotypic constitutions of F_3 plants and the relative number of various kinds of the offspring as the results of their crosses are as follows:

Let us see whether the results of these experiments and our expectation are in agreement with each other.

(10—1) × (16—9): All the hybrids have the genotypic constitution **GgDd** and should be green-red.

(17—7) × (17—1): All the hybrids have the genotypic constitution **ggDd** and should be yellow-red.

TABLE XXIV.

Crosses attempted	Genotypic constitutions of the parents	Genotypic constitutions of the offspring	Ratio
(10—1) × (16—9)	GGdd × ggDD	GgDd	1
(17—7) × (17—13)	ggdd × ggDD	ggDd	1
(22—3) × (22—4)	ggDd × GgDd	GgDD, GgDd, Ggdd, ggDD, ggDd, ggdd	1:2:1:1:2:1
(22—3) × (22—11)	ggDd × GGDd	GgDD, GgDd, Ggdd	1 : 2 : 1
(31—1) × (31—5)	GgDD × ggDD	GgDD, ggDD	1 : 1
(31—10) × (31—9)	GgDD × GGDD	GGDD, GgDD	1 : 1
(44—2) × (44—10)	GgDD × ggDD	GgDD, ggDD	1 : 1
(55—15) × (38—1)	GGdd × ggDd	GgDd, Ggdd	1 : 1
(56—1) × (38—1)	ggdd × ggDd	ggDd, ggdd	1 : 1
(59—10) × (16—9)	ggdd × ggDD	ggDd	1
A × (9—4)	ggdd × GGDD	GgDd	1
A × (16—9)	ggdd × ggDD	ggDd	1
A × (38—1)	ggdd × ggDd	ggDd, ggdd	1 : 1
(32—1) × *B*	GGdd × GGDD	GGDd	1

(22—3) × (22—4): The genotypic constitution of these hybrids is very various, as will be seen in the above table. If we classify them according to leaf- and flower-colour there should be 3 green-red, 1 green-white, 3 yellow-red, and 1 yellow-white. Now according to this expectation the deviation and the standard error are ± 2·250 and ± 1·985, respectively, in green plants, and they are ± 4·500 and ± 2·371, respectively, in yellow ones. Thus the results agree almost entirely with our expectation.

(22—3) × (22—11): The genotypic constitution is here also various, as seen in the above Table. The ratio of red and white should be 3 : 1, and the experimental result 7 : 2 shews that our expectation is almost perfectly fulfilled.

(31—1) × (31—5): As the hybrids have the constitution **GgDD** and **ggDD**, the ratio of green-red and yellow-red should be 1 : 1, and the plants really obtained are 27 and 22: thus here also our expectation has been fairly well fulfilled.

(31—10) × (31—9): As the hybrids have the constitution **GGDD** and **GgDD**, all plants should be green and the ratio of red and dark-red 1 : 1, and we have had 25 red and 24 dark-red, the results being thus fairly well in accordance with our expectation.

(44—2) × (44—10): The hybrids have the constitution **GgDD** and **ggDD**, so that green-red and yellow-red should be in the ratio 1 : 1. As, however, the plants of these two kinds are 26 and 44, respectively, their ratio seems to fit somewhat badly with the expectation, but the deviation and the standard error being $\pm 9{\cdot}000$ and $\pm 4{\cdot}183$, respectively, the results may be said to be in accordance with the expectation.

(55—15) × (38—1): As the hybrids have the constitution **GgDd** and **Ggdd**, there should be 1 green-red and 1 green-white, and we have 4 green-red and 7 green-white in reality. Though the empirical numbers are very small, the deviation and the standard error are $\pm 1{\cdot}500$ and $\pm 1{\cdot}658$, respectively, and our expectation is fulfilled.

(56—1) × (38—1): As the hybrids have the constitution **ggDd** and **ggdd** all plants should be yellow, and the ratio of red and white 1 : 1, in fact we have 27 yellow-red and 21 yellow-white.

(59—10) × (16—9): The hybrids have always the constitution **ggDd**, and we have 39 yellow-red.

A × (16—4): The hybrids have the constitution **GgDd**, and we have 10 green-red.

A × (16—9): The hybrids have the constitution **ggDd**, and we have 9 yellow-red.

A × (38—1): As the hybrids have the constitution **ggDd** and **ggdd**, all plants should be yellow and the ratio of red and white 1 : 1, indeed we have 6 yellow-red and 8 yellow-white.

(32—1) × *B*: All hybrids have the constitution **GGDd**, and we have obtained 11 green-dark-red.

When we examine all the above results we find some cases which seem to fit badly with our theoretical expectation, though all these lie within the range allowed by the theory, and such cases are no doubt due to the small number of individuals included in each family. It may be noticed moreover that, on the one hand, all kinds of plants which are theoretically expected to occur in any family were found there to appear; and on the other, in no single family plants of such kinds which should not occur there according to our theoretical expectation were ever found to appear.

SUMMARY.

1. The green colour of leaves is dominant to yellow, and the segregation in F_2 takes place according to the 3 : 1 ratio.

2. The factor producing the "hukurin" is present in the parent with white flowers. This condition is dominant to full colour and in F_2 the segregation occurs according to the 3 : 1 ratio.

3. The results mentioned in 1 and 2 agree with those obtained by Takezaki.

4. If we denote the one parent by GGDD and the other by ggdd, there exists the interrelation between the factors G and D, inasmuch as in the presence of D the production of the dark-red flower-colour takes place when G is present in homozygous condition, and that of the red (magenta or scarlet) colour, when G is present in heterozygous condition or altogether absent. The hybrids F_1 (= GgDd) will thus bear always flowers of red (= magenta) colour.

EXPLANATION OF PLATE II.

Fig. 1. A dark-red flower from the one parent.

Fig. 2. A white flower from the other.

Fig. 3. A magenta flower with "hukurin" from the F_1 plant.

Fig. 4. A scarlet flower from a F_2 plant.

Fig. 5. Leaf and a portion of stem from a green plant.

Fig. 6. Leaf and a portion of stem from a yellow plant.

All figures are from water-colour drawings by Mr N. Midusima.

PLATE II

N. Midusima del.