INHERITANCE IN *RICINUS COMMUNIS*, L. PART I.

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Introduction.

This paper presents data on the mode of inheritance of certain characters in the Castor-oil plant, *Ricinus communis*, L. As pointed out by White (1918 a), *Ricinus* is a good subject for genetic experiments. It exists in a large number of distinct and well marked varieties which readily intercross. The seeds remain viable for several years. Furthermore, back-crosses, which are so necessary for the proper study of linkage phenomena, are easily effected.

The characters which have been studied are:

1. Bloom.
2. Spines on the capsule.
3. Colour of the vegetative parts.

1. *Bloom.*

Varieties of *Ricinus* are distinguished by the presence or absence on the plant body of a waxy bloom. In varieties with bloom two main types exist:

A. Bloom on stem, petioles, and capsules.

B. Bloom on stem, petioles, capsules, and also on the under-surface of the leaf.

In class A one or more sub-types may be recognised, but so far no attention has been given to these. Type A is the only one which has been used in the experiments.

Previous Investigations.

Dr O. E. White (1918b) deals with the mode of inheritance of bloom. He states:

> Crosses of bloom × no-bloom give either complete or partial dominance of bloom in F_1. In F_2, approximately 3 with bloom : 1 no-bloom were obtained (actual

numbers being 1108 bloom : 377 no-bloom). In F_3, seeds from unguarded F_2 plants without bloom produced only plants without bloom. Seeds from unguarded F_2 plants with bloom either bred true in F_3 or gave 3 bloom : 1 no-bloom families. In one cross of bloom × no-bloom, the F_1 plants had bloom, but were only lightly covered as compared with their "bloom" parent. In F_2, the plants approximated a ratio of 3 bloom : 1 no-bloom as usual, though many of those with bloom were lightly covered as in F_1.

The present writer (1918), in a short preliminary note, put forward the results of one cross between bloom and no-bloom. The F_1 was intermediate and in F_2 331 bloom and 118 no-bloom were obtained. From these results it was considered probable that the presence and absence of bloom in *Ricinus* constitute a Mendelian pair of characters.

The Experimental Results.

Further results are presented below on the mode of inheritance of bloom, in crosses of bloom × no-bloom.

The cross St Vincent Native Type 2 × *Ricinus communis* var. *Gibsoni*.

Bloom	No-bloom

The F_1. Fourteen plants were grown. All possessed bloom, but were lightly covered in comparison with the bloom parent.

The F_2. Families were grown from all the fourteen F_1 plants. Segregation took place into bloom and no-bloom. During the examination it was established that some plants could not be classified correctly until the fruiting stage, as bloom was only present on the stem of the flowering spikes. To distinguish between the various types of bloom proved to be difficult in practice, and on this account the plants were divided only into the two broad classes, bloom and no-bloom.

Family	Bloom	No-bloom
1	27	6
2	42	16
3	55	12
4	48	10
5	69	13
6	109	23
7	26	9
8	75	25
9	67	17
10	54	15
11	21	8
12	55	9
13	35	15
14	33	10
Totals ...	716	188
Expected ...	678	226

The F_3. Of 21 families grown from F_2 plants with bloom, 10 bred true (230 plants).

11 families segregated into bloom and no-bloom.

Family	Bloom	No-bloom
2—22	26	11
3—20	63	19
3—31	16	4
6—25	33	18
8—21	39	12
9— 7	65	16
9—16	12	6
9—26	26	12
3— 1	2	3
6—28	13	6
8—24	5	1
Totals ...	300	108
Expected ...	306	102

Of 10 families grown from F_2 plants with no-bloom, all bred true (217 plants).

Back crosses of F_1 plants with the no-bloom parent.

Cross	Bloom	No-bloom
1	12	18
2	10	9
3	2	1
4	8	7
5	23	17
6	7	2
7	2	5
8	12	7
9	3	10
10	28	18
11	3	4
12	4	5
13	5	6
14	0	1
15	1	2
16	4	5
17	1	5
18	2	1
19	1	4
20	8	11
21	5	3
22	8	4
23	6	10
24	9	11
25	0	2
Totals ...	164	168
Expected ...	166	166

The conclusion previously arrived at by White and the present writer that presence and absence of bloom form a simple Mendelian pair of characters is confirmed by the above results. The symbols **B** and **b** will be used to denote presence and absence of bloom respectively. It will be noted that there is a marked excess of dominants in the F_2

families but there is no marked deviation from expectation in F_3 families or in the back-crosses.

2. *Spines on the Capsule.*

A variety of *Ricinus* devoid of spines on the capsule was collected in the Grenadines. It bred true on being grown in pedigree culture. Grisebach (1864) records this variety under the name *inermis*.

In a cross between spiny and spineless the following results were obtained :

The F_1. The fourteen F_1 plants were spiny, though the number of spines per capsule was obviously less than in the spiny parent. Spininess is therefore incompletely dominant.

The F_2. Families were grown from all the F_1 plants. The results are presented below.

Family	Spiny	Spineless
1	21	2
2	38	19
3	37	22
4	32	13
5	40	18
6	99	22
7	23	12
8	71	27
9	62	18
10	45	24
11	19	9
12	43	19
13	29	21
14	33	9
Totals ...	592	235
Expected ...	620	207
Ratio ...	2·5 :	1·0

The F_3. Of 17 families grown from F_2 plants which were spiny, 5 bred true (219 plants).

Twelve families segretated into spiny and spineless.

Family	Spiny	Spineless
3—20	29	7
3—30	56	11
6—25	45	6
6—27	32	17
6—34	29	14
8—21	37	8
9— 7	49	20
9—15	29	10
9—16	15	3
9—25	10	2
13— 9	31	6
13—10	7	5
Totals ...	369	109
Expected ...	359	120
Ratio ...	3·4 :	1·0

Three families were grown from F_2 spineless plants. All bred true (67 plants).

Back crosses of F_1 × Spineless.

Cross	Spiny	Spineless
1	55	58
2	12	8
3	46	50
4	31	30
5	68	44
6	45	34
7	41	52
Totals ...	298	276
Expected ...	287	287

Conclusion.

The above results indicate that the presence and absence of spines on the capsule are a simple pair of Mendelian characters. The factor for spines may be denoted by S, and its allelomorph by s.

3. *Colour of the Vegetative Parts.*

According to the observations of White (1918b), stem colour in *Ricinus* may be divided into five categories—bright green, green with reddish blush on sunny side, carmine or rose red, mahogany red, and purple (dark red). This author also states:

> Associated with the types of stem colouring are pigmented areas in other parts of the plant. The mahogany red stemmed plants have mahogany red leaves and fruits. The rose and red blush stemmed types have green leaves with red or reddish midribs. The dark purplish-red (mahogany bloom) stemmed plants have dark purplish-red leaves and fruits.

His experiments may be summarised thus:

1. Red-blush and green form an allelomorphic pair of characters.
2. Red-blush and mahogany are allelomorphic.
3. Rose and red-blush are allelomorphic.

The results of the present writer's experiments will now be given.

1. *The Cross Red-blush × Mahogany.*

This cross gave results similar to those obtained by White. The F_1 was rose or carmine stemmed, and in F_2 segregation occurred into 102 rose and red-blush, and 31 mahogany (expectation 103:34).

The F_3. A few families were grown in F_3.

Of 7 families grown from rose and red-blush F_2 parents, 3 bred true (25 plants).

The remaining families segregated into rose and red-blush, and mahogany.

Family	Rose and red-blush	Mahogany
1	8	2
2	7	1
3	5	4
4	12	3
Totals ...	32	10
Expected ...	32	11

Of 4 families grown from mahogany F_2 plants, 3 bred true (34 plants), while the other consisted of 15 mahogany and 3 rose and red-blush. The parent of this family was self-fertilised, but it is possible that accidental admixture of seed may have taken place.

The back-cross F_1 × mahogany.

A single back cross was made and produced seeds giving rise to 37 rose and 43 mahogany (expectation 40:40).

Conclusion.

Red-blush and mahogany are an allelomorphic pair of characters.

2. *The Cross Green × Mahogany.*

The F_1. Fourteen plants were grown. The stem colour was rose.

The F_2. Some difficulty was experienced in classifying the plants. Green and mahogany could be distinguished easily, but there appeared to be several shades of rose, grading down to red-blush. A new type was recorded which was called "tinged." The young leaves are strongly reddened, but the colour disappears as the leaves unfold, so that old leaves are practically green. The glands on the leaf stalk retain their colour, and a faint amount of colour is seen in the stem.

In an F_2 population some confusion is likely to arise in classifying the plants, owing to the fact that it is not always easy to distinguish between some of the paler types of red-blush and tinged. In practice the various shades of rose and tinged were grouped together. Grouping the plants into (*a*) rose and tinged, (*b*) mahogany, and (*c*) green the following results were obtained:

Family	Rose and Tinged	Green	Mahogany
1	19	9	9
2	41	12	6
3	44	14	13
4	37	12	14
5	64	15	22
6	98	38	32
7	75	25	16
8	93	25	26
9	61	27	16
10	59	13	19
11	27	3	8
12	50	18	8
13	56	20	14
14	43	15	12
Totals	767	246	215
Expectation on 10 : 3 : 3 basis	767	230	230

The F_3.

Family	F_2 parent	Rose	Mahogany	Green	Tinged
3—20	Rose	45	18	20	2
3—31	,,	10	1	7	2
6—34	,,	33	8	5	1
8—21	,,	33	6	12	1
9—16	,,	11	3	4	0
9—25	,,	9	3	—	—
13— 9	,,	30	7	—	—
3—30	,,	56	—	14	—
6—28	,,	37	—	15	—
9—26	,,	29	—	8	—
6—27	,,	49	—	—	—
9—15	,,	39	—	—	—
2—22	Mahogany	—	24	—	13
9— 7	,,	—	59	—	21
3—26	Green	—	—	7	1
8—16	,,	—	—	9	4
9—18	,,	—	—	30	9
13—16	,,	—	—	53	14
7— 7	Tinged	—	—	—	22
13—10	,,	—	—	1*	11

* Probable vicinist.

From these results it will be seen that rose breeds true in 2 families containing 88 plants, and segregates into rose, green, tinged, and mahogany in 5 families. Remembering the difficulty of distinguishing between rose and tinged, and classifying the plants into rose and tinged, green and mahogany, we obtain the ratio 138 : 36 : 48, with expectation 139 : 41 : 41 on a 10 : 3 : 3 basis. Rose segregates into rose and mahogany in 2 families, in the proportion of 39 rose : 10 mahogany (expectation 37 : 12 on a 3 : 1 basis). Rose segregates into rose and green in 3 families, in the proportion of 122 rose to 37 green (expectation 119 : 40 on a 3 : 1 basis).

Two families from mahogany F_2 plants segregate into mahogany and tinged in the ratio 83 : 34 (expectation 88 : 29 on a 3 : 1 basis).

Four families from green F_2 plants segregate into green and tinged, 99 : 28 (expectation 95 : 32 on a 3 : 1 basis).

Two families from F_2 plants breed true (33 plants). One family contained a green plant, which is ascribed to vicinism.

Back-crosses.

Back-crosses were made of F_1 with green, and F_1 with mahogany. The results are set forth below:

(*a*) *The Back-cross F_1 × Green.*

Cross	Rose	Green
1	70	67
2	35	31
3	50	45
4	19	44
5	54	59
6	45	37
7	60	41
Totals ...	333	324
Expected...	329	329

(*b*) *The back-cross F_1 × Mahogany.*

Cross	Rose	Mahogany
1	16	16
2	14	13
3	3	2
4	7	8
5	28	22
6	5	5
7	6	11
8	12	7
9	14	13
10	39	41
11	3	4
12	3	0
13	6	3
14	4	7
15	0	1
16	2	1
17	4	5
18	2	4
19	1	2
20	2	3
21	10	9
22	5	3
23	3	9
24	12	4
25	12	7
26	1	3
Totals ...	214	203
Expected...	209	209

Interpretation of the Experimental Results.

The results of the cross green × mahogany may be explained by the assumption that two independently inherited factor differences are concerned. The cross may be represented thus:

Parents	Green × Mahogany			
	mG	Mg		
	Rose			
F_1	Mm Gg			
F_2	9 Rose	3 Green	3 Mahogany	1 Tinged
	MG	mG	Mg	mg

It has been stated that difficulty is often experienced in distinguishing tinged from some of the shades of rose, and therefore in classification rose and tinged have been combined.

It remains now to consider to what extent the hypothesis is supported by the experimental results.

1. The expected F_2 ratio of 10 rose and tinged : 3 green : 3 mahogany is closely approximated to in the actual results.

2. Plants which were rose in F_2 should exhibit four types of behaviour in F_3:

(*a*) Breed true.

(*b*) Segregate into rose and tinged, green, and mahogany in the 10 : 3 : 3 ratio.

(*c*) Segregate into rose and mahogany in the 3 : 1 ratio.

(*d*) Segregate into rose and green in the 3 : 1 ratio.

All these types of behaviour are demonstrated in the experimental results, and the observed and expected ratios agree closely.

3. Mahogany F_2 plants should in F_3 either breed true or segregate into mahogany and tinged in the 3 : 1 ratio. No constant mahogany families were observed; both the families grown showed the ratio of 3 mahogany to 1 tinged. Had a larger number of families been grown, some would no doubt have bred true to mahogany.

4. Green F_2 plants should in F_3 either breed true or segregate into 3 green and 1 tinged. Owing probably to the small number of families grown no constant greens occurred, but four families segregated into 3 green and 1 tinged.

5. Tinged F_2 plants should breed true in F_3. This expectation was realised in two families.

6. The back-cross of $F_1 \times$ green is of the nature **Mm Gg × mG mG**, which should produce rose and green in the ratio 1 : 1. The observed results agree closely with the expected.

7. The back-cross of $F_1 \times$ mahogany is of the nature **Mm Gg × Mg Mg**, which should produce rose and mahogany in the 1 : 1 ratio. The observed results again agree with the expected.

To sum up: the hypothesis that two independently inherited Mendelian factors are concerned in the cross green by mahogany, is confirmed by the experimental results.

The two factors are:

G. The factor for green, which converts tinged into green, and

mahogany into rose. This factor can perhaps be regarded as a colour inhibitor.

M. The factor for mahogany.

Relation between the factors S (spines), and M (mahogany).

The cross green, bloom, spineless by mahogany, no bloom, spiny, is of the nature GB sm × gb SM.

Owing to the difficulty of separating rose (MG), from tinged (mg), in F_2, it was not possible to study the relation of S and M in F_2 families of this cross.

From the results of the back-cross of F_1 by double recessive sm (green spineless), placed below, it will be seen that the four phenotypes SM, Sm, sM, and sm occur in the ratio 1 : 1 : 1 : 1.

Back-crosses of Sm Sm × sm sm.

Family	SM	Sm	sM	sm
1	28	26	27	31
2	9	3	3	2
3	26	20	24	26
4	6	25	13	18
5	34	33	19	24
6	25	21	18	16
7	24	17	31	21
Totals ...	152	145	135	138
Expected ...	142·5	142·5	142·5	142·5
Ratio ...	1·1	1·0	0·9	1·0

Conclusion.

The factors S and M are independently inherited.

Relation between the factors B (bloom) and S (spines).

The relation between these two factors has been studied in a cross between Bs and bS. The F_2 results of this cross are given below.

Family	BS	Bs	bS	bs
1	17	0	4	2
2	29	11	9	7
3	31	14	6	5
4	25	10	6	3
5	40	15	10	3
6	78	18	20	4
7	44	14	16	4
8	52	19	18	7
9	48	14	13	3
10	33	20	11	4
11	13	7	6	2
12	39	15	4	5
13	18	16	12	4
14	25	7	8	2
Totals ...	492	180	143	55
Expected...	489	163	163	54

From these results it may be concluded that B and S are independently inherited.

Relation between the factors G (green), and B (bloom).

The relation of G and B was investigated in the back-cross Gg Bb × gb gb. The following were the results:

Family	GB	Gb	gB	gb
1	10	6	2	12
2	6	2	4	7
3	1	1	1	0
4	3	4	5	3
5	14	8	9	9
6	3	1	4	1
7	3	1	0	3
8	7	5	5	2
9	1	5	2	5
10	15	7	13	11
11	1	2	2	2
12	1	5	3	0
13	1	3	4	3
14	9	12	8	17
15	16	17	12	12
Totals ...	91	79	74	87
Expected ...	83	83	83	83

It will be seen from these results that GB and gb are in excess of Gb and gB. By Morgan's method of calculation the percentage of crossing over between G and B is 46·2, practically independent inheritance.

With such a small series of numbers it would be unsafe to assume that G and B are linked, but the results indicate the need for further experiments.

The relation between the factors M (mahogany), and B (bloom).

In the cross green, bloom, by mahogany, no-bloom, it was noticed that the combination green, no-bloom occurred only once among a large number of F_2 plants. Since the cross is GB m × gb M it is clear that the combination mb, *i.e.* green, no-bloom, and tinged, no-bloom should occur once in sixteen times if M and B are independently inherited. The F_2 results are placed below.

Family	BM	Bm	bM	bm
1	76	23	21	1
2	39	18	20	0
3	88	34	33	1
4	208	81	74	0
5	154	44	48	0
Totals ...	565	200	196	2

These results indicate that factors B and M are repelled, though no attempt will be made to calculate the theoretical gametic series from

the F_2 results. It is hoped to elucidate the relation of the two factors by a series of back-crosses with the double recessive.

General Summary.

This paper is concerned with the mode of inheritance of certain characters in the castor-oil plant, *Ricinus communis*, L. The experimental results may be summarised as follows:

1. The presence of bloom is partially dominant to its absence. Presence and absence of bloom behave as a pair of simple allelomorphic factors. The factor for bloom is denoted by **B**, and its allelomorph by **b**.

2. The presence and absence of spines on the capsule form another pair of allelomorphs, with spininess partially dominant. The factor for spines is denoted by **S**, and its allelomorph by **s**.

3. The experiments on the inheritance of stem colour in the cross green by mahogany indicate that two independently inherited Mendelian factors are involved:

M. The factor for mahogany.

G. The factor for green.

The four types resulting from the cross **Mg** × **mG** are:

9 MG	3 Mg	3 mG	1 mg
Rose	Mahogany	Green	Tinged

4. Experiments on the relation between the different factors show that **S** and **M**, **S** and **B**, **M** and **G**, and perhaps **G** and **B** are independently inherited. Factors **M** and **B** show repulsion in the cross **Mb** × **mB**.

REFERENCES.

Grisebach, H. R. A. 1864. *Flora of the British West Indies.*

Harland, S. C. "Notes on Castor-oil in the West Indies." *Agricultural News*, Barbados, No. 416, p. 100.

White, O. E. 1918 *a*. "Breeding New Castor Beans." *Journal of Heredity*, Vol. IX, No. 5, May—June.

—— *b*. "Inheritance Studies on Castor Beans." *Brooklyn Botanic Garden Memoirs*, I. 513—520.