THE GENETICS OF COTTON. PART II. THE INHERITANCE OF POLLEN COLOUR IN NEW WORLD COTTONS.

By SYDNEY CROSS HARLAND.

(With One Colour Plate.)

CONTENTS.

Introduction.

The colour of the pollen in New World cottons varies from pale cream to rich golden yellow. In Old World cottons deep yellow is the usual colour though paler shades have been noted. Pollen of a golden yellow colour is characteristic of many other Malvaceous plants belonging to related genera, *e.g. Thespesia* and *Hibiscus*. In the cultivated *Hibiscus rosa-sinensis* a range of grades from pale cream to deep yellow is also found.

Previous investigations.

Balls (1912) studied the inheritance of anther colour, which is inseparable from pollen colour. He worked with Egyptian-Upland crosses. Upland is buff, Egyptian is golden yellow. He claimed F_1 intermediate, and F_2 segregating into a normal 1 : 2 : 1 ratio. A family of King Upland, the parent of which was pale lemon, gave 24 lemon and 8 buff.

McLendon (1912) states that in Upland-Sea Island crosses yellow by buff gave intermediate. In F_2 the expected simple Mendelian ratio was not obtained, but the parental forms reappeared in varying proportions in different crosses with continuous variation between the extremes. He states further that absolute correlation exists between petal colour and anther colour, but this has been observed by no other worker.

His ratios vary from 12·5 : 1·0, to 4·1 : 1·0, showing a deficiency of the Upland shade.

Kearney (1923) using Ridgeway's colour scale crossed Upland (pale chalcedony yellow) × Egyptian (Empire yellow). F_1 gave partial dominance of the yellow colour of Pima. Some indication of a bimodal distribution was shown by the F_2, the pale colour appearing to be a simple recessive. Kearney's results thus fall into line with those of Balls.

Grades of pollen colour.

At the outset of the experiments it was seen that a more accurate system of grading than that of previous investigators would have to be devised. Accordingly nine grades were established, and painted accurately in water-colours for reference. The paintings were frequently compared with the original types. The grades, which are reproduced on Pl. X, were as follows:

Grade	Type	Group
0	Upland, Grenadines White Pollen	Upland
0·5	Upland (0) × Bourbon Intense (1) F_1	—
1·0	Trinidad Red Leaf	Bourbon
1·5	Punjab Golden	Upland
2·0	F_1 Meade × Egyptian Pima	—
2·5	Jamaica Long Staple, Sea Island Naked (*SIN*)	Peruvian
3·0	Egyptian Pima	,,
3·5	Egyptian	,,
4·0	Caravonica	,,

Grade 0. The standard type is a variety of Upland—Superokra. Grade 0 has not been systematically subdivided but consistent variations in shade have been observed. The highest grade of 0 is found in the Peruvian type Grenadines White Pollen (G.W.P.) which comes between the standard grade and the next grade 0·5. The pollen colour of the Upland variety Meade, used in our experiments, is slightly deeper in shade than standard 0, but not so deep as that of G.W.P. Variations in grade 0 are accompanied by corresponding variations in the F_1 of crosses between 0 and 3. Thus, the cross *SIN* (2·5) by Superokra (standard 0) produces an F_1 of a grade slightly below that of *SIN* by Meade. Grade 0 is also found in the native Trinidad variety of Bourbon known as Volunteer.

Grade 0·5. The standard is Meade (0) × Bourbon intense (1), but examples are also met with in the F_2 of crosses between the Bourbon variety Cassava, and Upland.

Grade 1. The standard is the Bourbon type, Trinidad Red Leaf, but many Bourbons (Cassava, Bourbon intense, etc.) are of this shade, which has not been seen so far in the Peruvian group.

Grade 1·5. The standard is a variety of Upland known as Punjab golden, a selection from the Punjab American variety 285 *F*, which apparently consists of a mixture of yellow and white pollened plants. This shade has been seen in many commercial Upland varieties, and also in native cottons of Upland type from Guatemala.

Grade 2. Grade 2 is the heterozygote between Pima Egyptian (3) and Meade (0). The Egyptian variety Enan's Brown is apparently a homozygous type of this grade, but a sufficiently large number of plants has not yet been examined. Slight variations in this grade occur due to differences (*a*) in the type of grade 0 used in making the cross, and (*b*) when Sea Island (2·5) is used to make the cross instead of Pima a grade 2 F_1 is produced slightly below the standard grade.

Grade 2·5. The standard type is Sea Island Naked, but all Sea Island varieties so far examined belong to this grade, as well as the Peruvian types Jamaica Long Staple, Cauto and Trinidad Red Kidney.

Grade 3. The standard type is a pure line of Egyptian Pima.

Grade 3·5. This grade was made from an Egyptian plant of unknown parentage, which has since been lost. It has not been used in the present experiments.

Grade 4. The standard is the Peruvian variety Caravonica, obtained from Hawaii. This variety has not entered into the experiments. Grades 2·5 to 4 are so far known only in the Peruvian group of New World cottons.

Grades in the wild species of Gossypium. Of the so-called wild species, *G. Stocksii* has grade 0 pollen, *G. Sturtii* grade 0 pollen occasionally tinged with anthocyanin, *G. Davidsonii* grade 1 and *G. tomentosum* grade 3.

SUMMARY OF THE PRESENT RESULTS.

1. A single genetic difference is involved in all crosses between any grade of yellow and grade 0. That is, yellow and pale cream form a simple pair of factors, which may be denoted as **P** and **p**.

2. Modifying genes act on the basal gene for yellow, producing a complex series of shades from pale yellow 0·5 to deep golden 4·0. These modifying genes can be carried by grade 0, producing such minute variations in shade as are exemplified by Superokra and G.W.P.

3. **P** produces little effect when unsupported by modifiers, and the distinction between **P** and **p** is often hard to make in segregating families lacking such modifiers. It is possible that in the absence of any modifier at all, the distinction between **P** and **p** would vanish,

i.e. **P** would produce too pale a shade of yellow to observe segregation.

4. In crosses between cottons of the same class, *e.g.* inter-Peruvian or inter-Upland, segregation is usually very sharp, owing to similar modifying factors being present in a homozygous condition in both parents.

5. In the selfed back-cross (Upland × Sea Island) × Sea Island, an intensifier, **Q**, was demonstrated, having no visible effect except in presence of **P**.

The experimental data.

Segregation of yellow (**P**) *and cream* (**p**).

The ratio of **P**—all grades above 0, to **p**—grade 0, has been worked out for all the segregating families and in back-crosses and presented in Table I. The results do not demand comment, as they establish clearly

TABLE I.

A. *Segregation of families into yellow* (**P**) *and cream* (**p**).

Series	Yellow (P)	Cream (p)
1	120	39
2	798	267
3	684	248
4	369	123
5	536	157
7	338	110
8	308	104
Total	3153	1048
Expected	3150·75	1050·25

B. *Segregation in back-crosses of* **Pp** × **pp**.

Series	Yellow (P)	Cream (p)
1	816	881
2	637	811
3	317	365
Total	1770	2057
Expected	1913·5	1913·5

that the basal factor **P** producing some shade of yellow is allelomorphic to cream (grade 0). In back-crosses there is a deficiency of **p**, the reason for which will form the subject of a later communication. Grade 0 always breeds true in F_3 families or in selfed back-crosses. This statement is based on the results of many thousands of plants and it is unnecessary to present detailed figures.

Segregation of shades of yellow in different crosses.

The results of crosses between various grades of yellow and cream will now be described, and of one case of a cross between two grades of yellow.

1. The inter-Peruvian cross, Pima Egyptian (3) × Grenadines White Pollen (0).

Pima is a well-known variety of Egyptian isolated by Kearney in Arizona. Grenadines White Pollen (G.W.P.) is a variety of the Peruvian type of West Indian perennial known as Marie Galante, and, cultivated as a pedigree selection, it bred true.

The F_1 is grade 2·5, almost complete dominance being shown.

TABLE II.

Results of the cross Pima (3) × *Grenadines White Pollen* (0).

	Pollen grade					
Family	0	1·0	1·5	2·0	2·5	3·0
Pima	.	.	.	.	7[1]	5
GWP	10	.	.	.	.	.
F_1	.	.	.	.	6	.
F_2 651	.	.	.	.	2	.
653	4	.	.	.	6	3
654	2	.	.	.	6	4
655	5	.	.	.	11	6
656	8	.	.	2	8	2
657	11	.	.	4	31	7
658	0	.	.	.	6	1
659	9	.	.	2	15	4
Total	39	.	.	8	85	27

The F_2 results are shown in Table II. Segregation is sharp, and a 3 : 1 ratio of yellow to pale cream is observed:

	Yellow (P)	Cream (p)
Observed	120	39
Expected	119·25	39·75

2. The inter-Upland cross Acala (0) × Punjab Golden (1·5).

The F_1 is intermediate—grade 1.

The F_2 results will be found in Table III. All plants were examined

[1] The examination of the grades was made early in the season of 1927 when 2·5 could not be distinguished with ease from 3·0. Later examinations of other Pima families have invariably given nothing but 3·0. The distinction between 2·5 and 3·0 made in the F_2 table is similarly not absolutely to be relied on. That is, some plants classified as 2·5 are probably 3·0. The plants classified as 2·0 must be placed in grade 2 as they are lower than 2·5, but are a little above our standard 2.

TABLE III.

Results of the cross Acala × Punjab Golden.

	Pollen grade					
Family	0	1·0	1·5	2·0	2·5	3·0
Acala	*	.	.	.	.	.
Punjab Golden	.	.	*	.	.	.
F_1	.	*	.	.	.	.
F_2 501	24	12	25	15	.	.
502	26	4	33	22	.	.
Total	50	16	58	37	.	.

for **P** and **p**, while one family was picked out for detailed examination of grades. The numerical results for **P** and **p** are placed below:

	Yellow (**P**)	Cream (**p**)
Obtained	798	267
Expected	798·75	266·25

The grade of yellow in F_2 ranges from 1 to 2[1].

3. The Upland-Peruvian cross, Upland (0) × Trinidad Red Kidney (*TRK*) (2·5).

The F_1 is intermediate—grade 2 (standard).

TABLE IV.

Results of the cross Upland × Trinidad Red Kidney.

	Pollen grade					
Family	0	1·0	1·5	2·0	2·5	3·0
Upland	*	.	.	.	.	.
TRK	.	.	.	.	*	.
F_1	.	.	.	*	.	.
F_2 555	40	1	9	38	9	47
556	52	.	5	17	17	57
557	8	.	2	7	1	9
558	66	.	27	46	23	72
559	65	2	30	77	37	96
560	17	.	7	21	10	17
Total	248	3	80	206	97	298

The F_2 results are found in Table IV. The grade of yellow ranges from 1 to 3, but grade 1 is very rare—only 3 out of 684. Modes exist at grades 2 and 3.

[1] Shrivelled pollen grains were encountered very frequently in the F_2 plants, and as these pollen grains are deeper in colour than normal ones the classification of types put in grade 2 is not entirely satisfactory. It is believed, however, that many of the grade 2's are valid, and if they are correctly graded it implies that modifying factors have been brought into the cross from Upland.

The numerical results for **P** and **p** are placed below:

	Yellow (P)	Cream (p)
Obtained	684	248
Expected	699	233

4. The Upland-Peruvian cross, Upland (0) × Sea Island White (2·5).

The F_1 is grade 2, as in the last cross, but slightly lower than the standard.

In the F_2 the yellows range from 1·5 to 4, but there are only 3 plants above grade 3 out of 269. The pollen colour in these plants, is definitely more intense than grade 3. The proportion of grade 1·5 is less in this cross than in No. 3. The results are presented in Table V.

TABLE V.

Results of the cross Upland × Sea Island White Flower.

	Pollen grade							
Family	0	1·0	1·5	2·0	2·5	3·0	3·5	4·0
Upland	*	.	.	.	.	.	.	.
SIWF	.	.	.	.	*	.	.	.
F_1	.	.	.	*	.	.	.	.
F_2 547	15	.	1	17	9	19	.	.
548	47	.	5	48	18	64	.	1
549	49	.	13	64	20	44	1	1
550	2	.	.	3	1	.	.	.
552	5	.	1	13	1	8	.	.
553	5	.	2	7	1	7	.	.
Total	123	.	22	152	50	142	1	2

The numerical results for **P** and **p** are set out below:

	Yellow (P)	Cream (p)
Obtained	369	123
Expected	369	123

5. The Upland-Bourbon cross, Upland (0) × Cassava (1).

The F_1 is grade 1, showing complete dominance of yellow.

The F_2 shows a range in the yellow class from 0·5, a grade not previously recorded, to grade 2, thus transcending the limits of the parents in both directions.

Classification in this cross is complicated considerably by segregation in the time of opening of the anthers. All Bourbon cottons are "late bursters" and do not shed their pollen often till about 10.30 a.m. as against the early bursting—6 a.m. to 7 a.m. of Uplands and Peruvians. The colour of the pollen gradually darkens as it becomes older, and our grades are based on the colour at the time of opening. Thus, grade 1 becomes 1·5 by afternoon, while the higher grades show relatively little

change. For this reason it is important to grade every plant at the time of bursting but it has not been possible to do this in every case, as examination consumes an appreciable time. In this case grading has been done using flowers the grades of which were determined earlier in the morning by the chart and which are assumed to have darkened at the same rate as those under examination.

TABLE VI.

Results of the cross Upland × Cassava.

	Pollen grade				
Family	0	0·5	1·0	1·5	2·0
Upland	*	.	.	.	.
Cassava	.	.	*	.	.
F_1	.	.	*	.	.
F_2 414	84	11	107	169	16
416	34	25	59	42	2
417	15	5	33	50	.
418	37	8	23	54	2
419	26	5	37	35	.
420	39	7	46	52	.
Total	235	61	305	402	20

Three families show no plants of grade 2. The results are presented in Table VI. The numerical results for **P** and **p** are placed below:

	Yellow (P)	Cream (p)
Obtained	788	235
Expected	767·25	255·75

6. The Peruvian-Bourbon cross, Pima Egyptian (3) × Cassava (1).

The F_1 is grade 1·5, in one plant and 2 in another.

The F_2 shows a range from 1 to 3 with modes at 1·5 and 3, grade 1 occurring in 4 plants out of 50. This might indicate a bigenic difference

TABLE VII.

Results of the cross Pima × Cassava.

	Pollen grade							
Family	0	1·0	1·5	2·0	2·5	3·0	3·5	4·0
Pima	.	.	.	.	.	*	.	.
Cassava	.	*	.	.	.	.	.	.
F_1	.	.	1	1	.	.	.	.
F_2 677	.	.	2	1	.	2	.	.
678	.	1	2	.	.	1	.	.
679	.	1	6	4	1	5	.	1
680	.	1	2	.	.	.	.	.
681	.	.	2	.	.	.	.	.
684	.	1	6	1	3	7	.	.
Total	.	4	20	6	4	15	.	1

between grade 1 and grade 3. Two plants occurred with pollen of a reddish tinge, which did not exactly fit any of the grades, but was nearest to 3. The results, which do not permit of a factorial analysis, are to be found in Table VII.

7. Plant 2 (Upland × Egyptian) × Upland (**Pp**) (Grade 2).

In addition to the above crosses, which have been carried only as far as F_2, a somewhat detailed study has been made of the descendants of a single plant known as plant 2, an Upland × Egyptian F_1 heterozygous for **P**. It was back-crossed with Upland and detailed observations on pollen colour have been carried on for two or more generations, the results of which are given in Table VIII.

TABLE VIII.

Pollen colour in descendants of Plant 2 (*Upland* × *Egyptian*) × *Upland. Grade* 2, **Pp**.

Family	Parent grade	Pollen grade 0	1·0	1·5	2·0	2·5	3·0
2	2	110	20	123	107	23	65
2–8	1·5	.	.	6	3	.	.
2–14	2·5	.	.	3	9	10	11
2–15	1·5	16	.	16	6	2	5
2–16	2·0	2	.	.	3	1	.
2–20	1·5	2	.	.	3	6	.
2–28	1·5	10		6	6	5	1
2–30	3·0	.	.	.	.	1	4
2–32	.	31	.	11	23	1	37
,,	.	51	.	36	31	7	34
2–38	.	16	.	9	11	4	4
2–39	.	.	3	57	36	4	–
2–41	.	5	.	2	1	1	2
2–51	.	10	.	.	1	.	19
2–52	3·0	.	.	.	.	.	22
2–53	.	20	.	39	25	.	6
2–54	.	8	1	15	.	.	

The main points of importance are as follows:

The large family of 448 plants, progeny of plant 2, shows segregation into the usual 3 : 1 ratio as regards the main factor **P**:

	Yellow (P)	Cream (p)
Observed	338	110
Expected	336	112

In this family grades of yellow were produced from 1 to 3, but the general type of segregation is different from that in crosses 1 and 3. There are proportionally many more plants of grades 1 and 1·5.

In the next generation segregation is less complex. One case is seen (2–52) of a homozygous grade 3, identical or nearly so with Egyptian.

Family 2–51 shows segregation into grade 3 and grade 0, with only a single plant of grade 2, possibly due to vicinism. This type of segregation is practically identical with that found in the inter-Peruvian cross, No. 1, Pima × Grenadines White Pollen. It is evident that the same modifying factors accompany both **P** and **p**.

It may be supposed that the yellows have one or more modifying genes, which convert all the paler shades of yellow to grade 3, and are present in the cream class with little visible effect. Families 2–14 and 2–39 provide examples of families breeding true to yellow but with dissimilar ranges, 2–14 ranging from 1·5 to 3·0, and 2–39 from 1·0 to 2·5. A type of segregation rather like that of the inter-Upland cross 2, is seen in family 2–54 where there is practically straight segregation into 1·5 and 0.

8. (Upland (0) × Sea Island (3–2·5)) × Sea Island (3–2·5).

A number of plants in the above cross were selfed, and the pollen colour in the resulting families carefully graded. At the time of grading accurate classification into 3 and 2·5 was not yet certain. The results are presented in Table IX and show the following points of interest:

Plants of grades 3 and 2·5 show the following types of behaviour:

(*a*) breed true;
(*b*) segregate into 3 and 2;
(*c*) segregate into 3, 2·5, 2 and 1·5;
(*d*) segregate into 3, 2·5 and 0 with practically no intermediates.

Plants of grade 2 produce all grades from 3 to 0.

These results may be accounted for on the basis of one main gene **P** and an intensifying gene with no visible effect except in presence of **P**. Calling the intensifier **Q** we have for the back cross:

(**PQ**	× **pq**)	× **PQ**
(3	0)	3

giving four types of plants in equal numbers:

Type			Families	
			Obtained	Expected
1	**PQ** / **PQ**	Breeding true to 3 and 2·5	13	13·5
2	**PQ** / **Pq**	3 and 2·5 throwing lower grades of yellow	16	13·5
3	**PQ** / **pQ**	3 and 2·5 throwing 0	14	13·5
4	**PQ** / **pq**	2 throwing all grades from 3 to 0	11	13·5

TABLE IX.

Results of the selfed back-cross (Upland × Sea Island) × Sea Island.

Family	Parent	Pollen grade 0	0·5	1·0	1·5	2·0	2·5	3·0
Grades 3 and 2·5 breeding true to grade 3 and 2·5. 13 families.								
430	3	.	.	.	.	.	4	64
446	3	.	.	.	.	.	1	56
459	3	.	.	.	.	.	.	7
464	3	.	.	.	.	.	.	7
478	3	.	.	.	.	.	.	12
487	.	.	.	.	.	.	4	8
496	.	.	.	.	.	1	5	17
502	.	.	.	.	.	1	1	39
514	?	.	.	.	.	.	.	12
517	?	.	.	.	.	.	.	7
535	3	.	.	.	.	.	.	10
588	3	.	.	.	.	.	2	11
584	.	.	.	.	.	.	.	6
Grades 3 and 2·5 segregating down to 2 and 1·5. 16 families.								
423	2·5	.	.	.	.	5	3	9
424	3	.	.	.	1	16	12	39
432	.	.	.	.	3	31	7	9
433	3	.	.	.	.	5	.	11
439	.	.	.	.	.	2	8	25
443	.	.	.	.	.	5	3	64
462	2·5	.	.	.	.	1	2	2
463	3	.	.	.	.	1	.	4
486	3	.	.	.	.	1	.	6
492	3	.	.	.	.	7	7	9
519	3	.	.	.	.	2	5	11
520	?	.	.	.	.	3	1	4
521	?	.	.	.	4	11	3	7
530	3	.	.	.	.	2	.	3
554	3	.	.	.	.	3	1	4
568	.	.	.	.	.	3	3	13
Grade 3 segregating down to 0. 13 families.								
437	.	8	.	.	.	7	6	24
441	.	12	.	.	.	8	5	16
461	2·5	2	.	.	.	6	.	16
468	2·5	4	.	.	.	.	1	4
473	2·5	1	.	.	.	.	.	4
477	3	1	.	.	.	1	.	5
495	.	1	.	.	.	.	.	8
497	.	4	.	.	1	2	.	9
500	.	3	.	.	.	1	1	8
504	.	2	.	.	.	4	1	10
511	3	5	.	.	1	3	1	10
515	3	2	.	.	.	1	2	2
528	.	2	.	.	.	.	.	4
Grade 2 segregating down from 3 to 0. 12 families.								
429	2	2	.	.	.	6	1	4
434	2	2	.	.	1	1	1	3
436	2	9	.	.	4	11	3	8
440	.	6	.	.	3	6	3	4
444	.	10	.	.	3	11	6	13
466	2	3	.	.	1	4	.	5
474	2	10	.	.	.	8	.	8
482	2	3	.	.	3	2	2	1
489	2	3	.	.	.	7	2	6
490	2	3	.	.	.	.	.	2
493	2	4	.	.	.	4	.	2
460	2	2	.	.	.	.	2	5

The expectation is closely realised, though there is occasionally some difficulty in deciding the position of a family. The relative proportions of the different grades of yellow have to be taken into account. Thus, families 443, 492 and 496 are put with type 2 on account of a strong mode at 3—comparable with other members of the group, the parental grade of which is known. Families segregating into yellow and cream showing a strong mode at 3 or 2·5 are put with type 3. Where the parent grade is known, there is of course no difficulty in assigning a family to its proper class. There are variations in the type of segregation within a group: thus families 425 and 443 show very different types of segregation, probably due to the action of further minor modifying factors. It is, however, clear that one main gene is concerned with the intensification of **P**. Further evidence is provided by a classification of the back-cross itself:

	Grades 3 and 2·5	Grade 2
	PQ PQ PQ	**PQ**
	PQ Pq pQ	**pq**
Obtained	52	15
Expected	50·25	16·75

The numerical results for the segregating families are as follows:

	Yellow (P)	Cream (p)
Observed	308	104
Expected	309	103

General discussion.

The series of experiments described in this paper will illustrate admirably the fact that the sharpness of the distinction between the dominant gene **P** and the recessive **p**, depends upon the genetic background. So far the lowest grade of yellow encountered has been 0·5, and it would be almost impossible for anyone unfamiliar with the material to distinguish this grade with certainty from grade 0. By varying the genetic background the type of segregation can be correspondingly varied. By crossing a heterozygote with a 0 carrying plus modifiers, segregation can be made as clear and definite as in Pima × Grenadines White Pollen, or on the other hand, segregation can be modified to make a series of yellow down to cream which will defy analysis.

Single "point mutations" in cotton—so far, these have only been noted in Sea Island and Egyptian—comprising the types white flower, naked seed and crinkled dwarf, always segregate in a clean-cut manner when crossed with the type from which they originated. No case has

yet been encountered of segregation as clear-cut in an inter-specific cross—there is always segregation of modifiers as well. Sea Island white flower can be used for cutting out intermediate grades of yellow corolla in an interspecific cross since it has lost nothing but the main gene for yellow, **Y**, and still retains its constellation of plus modifiers. It may here be stated that species hybrids in cottons differ from varietal hybrids in the extent to which differences occur in modifying factors. In a species hybrid each main gene is apparently accompanied by a group of modifiers which have the effect of diluting the character in steps down to the recessive, and in certain cases may obscure entirely the distinction between dominant and recessive.

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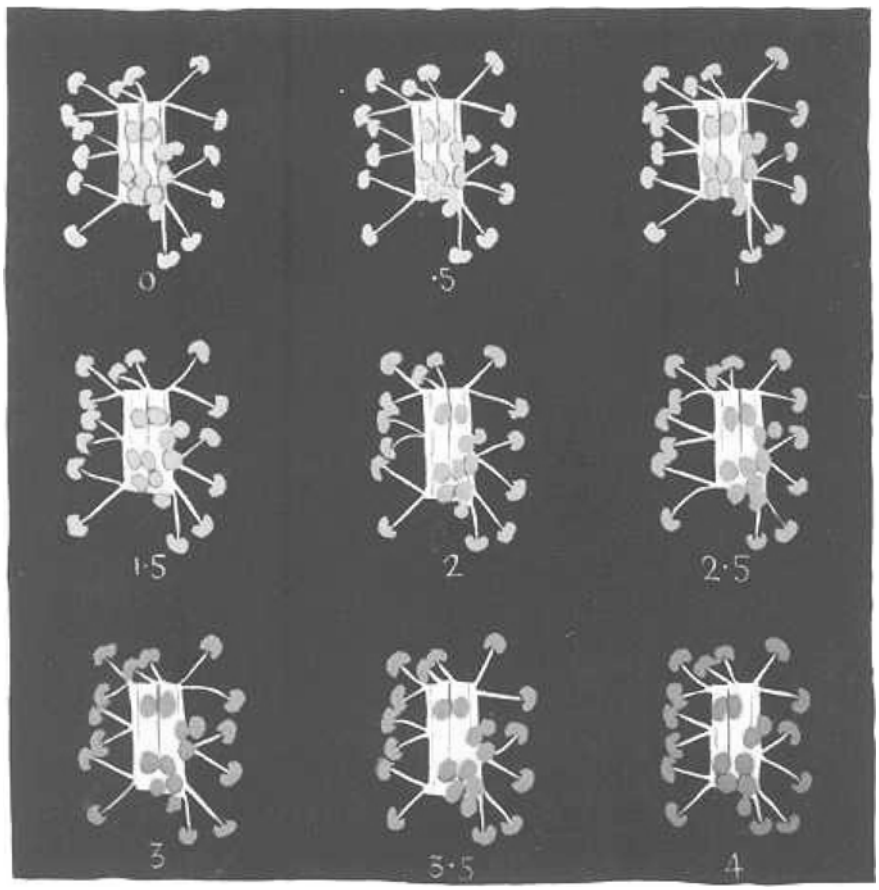
EXPLANATION OF PLATE X.

Illustrating a series of 9 grades of anther colour in cotton. For full explanation see text, p. 388.


0
·5
1
1·5
2
2·5
3
3·5
4