

THE INHERITANCE AND LINKAGE RELATIONS OF YELLOW SEEDLING, A LETHAL GENE IN ASIATIC COTTON

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I. INTRODUCTION

THE cultivation of Asiatic cotton in China is very extensive, but the development and distribution of improved varieties has been carried out only in recent years. Since better Asiatic varieties are not very common, the varieties in cultivation have had a long history of local adaptation, in some cases over one thousand years. Environmental differences in the cotton zone of China are very marked, as cotton is grown at places the longitude or latitude of which may differ more than 20°. With such a long history and divergent environmental conditions, it is quite possible that mutations have occurred. In the past twenty years, this College and the Central Institute of Cotton Improvement of China have repeatedly collected the native varieties throughout the cotton zone. Some characters were obtained which have not been mentioned by Watt (1907) and Harland (1932). During the last decade, cotton breeding has been started in this country, and a large amount of material has been continuously selfed, and as a result, recessive mutations are frequently detected. At least seven mutations have been obtained and studied by the writer, and the lethal yellow seedling described here is one of them.

II. DESCRIPTION OF THE MUTATION

Yellow seedling commonly occurs in many different crop plants. The type described here has been observed three times in unrelated strains of cotton. Feng (1926) obtained it in both "Chicken Foot" and "Wuchang

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White Seed", and the writer recently found it in "Shaokan Long Staple". Although originating from three unrelated strains, their genetical behaviour shows that they are controlled by the same gene. The distances between the native places of the three strains in which the yellow seedling occurred are very considerable, and the three yellows must have originated independently.

The seed, which gives a yellow seedling, is not different from that which gives a normal one. The character can be seen as the cotyledons begin to appear, but becomes more distinct as they expand. At first the yellow colour is very distinct, becoming paler as the seedling grows older. The yellow seedling survives about ten days after germination. Phenotypically the heterozygote is indistinguishable from normal green, and can only be differentiated by a progeny test.

III. PREVIOUS WORK

Stroman & Mahoney (1925) and Harland (1934) studied chlorophyll deficiency and yellow seedling in New World cottons. Stroman & Mahoney concluded that there were two types of chlorophyll deficiency. In the first case the entire cotyledon was devoid of chlorophyll. This deficiency was controlled by duplicate genes, Y_1 and Y_2 . In the second type certain areas of the cotyledon contained yellow or light green colour. These they designated "pattern" or "light pattern", and the authors considered that they were controlled by independent genes, C_1 and C_2 . Harland studied chlorophyll deficiency, and concluded that there were two factors C_{ha} and C_{hb} controlling development of chlorophyll in the cotyledon. These factors were distributed differently in different cotton species. The type which the writer reports in this paper is similar to the first type reported by Stroman & Mahoney.

Harland (1932) mentioned that no chlorophyll deficiency had been described in Asiatic cotton. This was not so, as Feng (1926) had already studied yellow seedling in Asiatic cotton due to the absence of chlorophyll, and found that it was a simple completely recessive Mendelian character.

Yellow seedling is so closely linked with anthocyanin pigmentation that a brief summary of the inheritance of the latter is necessary. Many workers have studied anthocyanin pigmentation of cotton. Leake (1911) and Feng (1926), making crosses between purple and green plant colour, drew similar conclusions. They found that there was a pair of factors, R and r , controlling the presence or absence of the anthocyanin pigmentation. Hutchison (1932) studied the problem very thoroughly and

concluded that there was a multiple allelomorphous series, including six genes in all. Recently he (Hutchinson & Ghose, 1937) added to the total one more gene, discovered by the writer (Yu, 1932). Other anthocyanin genes exist, but have not yet been reported in detail. In the writer's opinion there are two series of anthocyanin allelomorphs, a spotted series and a spotless series, and evidence is being collected to show that they are very closely, but not completely linked. The interrelations of the anthocyanin allelomorphs will form the subject of a separate paper.

Linkage studies of characters in Asiatic cotton have been only rare. Hutchinson (1934) found that there was linkage between leaf shape and lint colour with a cross-over value of about 30 %. The writer (1939) obtained another linkage between curly and leaf shape with a cross-over value of about 17 %.

IV. MATERIAL AND METHODS

The yellow seedling strains used in this study included both that which was discovered by Feng and that which was newly obtained by the writer. In addition to the confirmation of Feng's conclusion (1926), special attention was paid to the correlations existing between the yellow mutation and other characters.

The following strains were used:

Characters	Sources
Sun red plant, normal leaf, heterozygous lethal, yellow corolla	Feng's selfed seeds
Sun red plant, normal leaf, heterozygous lethal, yellow corolla	The writer's strain in Shaokan cotton
Green plant, curly leaf, green seedling, white corolla	A newly mutating strain
Green plant, heterozygous lethal	Segregates from family 878

The lethal yellow is a seedling character. Thus to study it requires a much shorter time than the mature plant characters. Not only can the strain be sown at any season of the year, but also it can be grown in sand culture, in which the germination of the seed is more uniform than in heavy soil, and the seed is less susceptible to disease. The seedlings used to determine the ratio were all planted in sand, and those required for further progeny test were later transplanted into the soil, where the plants might have a better environment and give sufficient seeds.

The homozygous yellow lethal dies in two weeks, and all attempts to graft it on to normal plants failed. For linkage studies, therefore, the F_1 was backcrossed to the heterozygous lethal instead of to a homozygous double recessive. This method is less efficient than a normal backcross.

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but more efficient than an F_3 . The estimation of the cross-over value was largely supplemented by F_3 populations.

The anthocyanin pigmentation of the plant may also be distinguished in the seedling stage. The ease with which it may be scored is dependent upon the particular allelomorph involved, environment, and the age of the seedling. For instance, the sun red allelomorph hardly expresses its character in seedlings grown in the greenhouse, but under direct sunlight it shows on the hypocotyl very clearly, whilst higher allelomorphs exhibit anthocyanin whether under direct or indirect sunlight.

V. EXPERIMENTAL RESULTS AND DISCUSSION

A. *Inheritance of yellow seedling*

Owing to the lethal effect of the yellow seedling, experiments were carried out in two ways: (1) selfing of the natural heterozygous plants, and (2) crossing between the natural heterozygous plants and the normal green ones, and testing the progeny of the segregating plants.

Results are summarized in Table I.

TABLE I

Family	Green	Yellow
Feng's material selfed		
24 L1	227	95
24 L40	146	41
777	172	60
1433	219	88
Shaokan selection selfed		
c 1407	70	24
Selfed progeny of heterozygotes from crosses of natural heterozygotes × normal		
878	9021	2870
2025	3385	1107
2029	1586	493
2021a	929	297
B.C.	1393	450
Total	17148	5525
Exp. (3 : 1)	17004.75	5663.25

Planting seed from plants of the normal class in Table I, and testing their genotype, the following results were obtained:

Family	Heterozygous green	Homozygous green
2021a	42	15
1433	18	7
24 L1	35	19
24 L40	30	18
Total	134	59
Exp. (2 : 1)	128.7	64.3

Since the homozygous yellow seedling does not survive to produce gametes, it could not be used in testing the gametic ratio of heterozygotes

by the ordinary method of backcrossing. In order to avoid this difficulty, heterozygous plants were crossed with homozygous greens and the genotypes of the resulting generation were tested.

Family	Breeding true	Segregating
808	22	27
2022	25	12
3025	32	30
Total	79	69
Exp. (1:1)	74.0	74.0

From the above facts, it is clear that yellow seedling is a single Mendelian recessive.

B. Relations between yellow seedling and other characters

(1) Linkage with anthocyanin pigmentation.

The sun red-green factor pair was used. The data are divided into two parts, (a) the F_2 and F_3 families, and (b) backcross families.

(a) F_2 and F_3 : Crosses were made in both coupling and repulsion. The F_1 was sun red, normal seedling. In Table II are given distributions of F_2 families and F_3 progenies of doubly heterozygous F_2 plants.

TABLE II

Family	Sun red normal	Not sun red normal	Sun red yellow	Not sun red yellow
		Coupling F_2		
2025	524	37	38	154
2026	70	2	2	23
		Coupling F_3		
2021	192	13	14	57
2701	933	47	54	274
2705	1473	94	84	407
Total	3192	193	193	915
Exp. (cross-over value = 9.0 %)	3176	193	193	930
		Repulsion F_2		
809	215	110	112	2
810	159	66	92	1
819	314	151	137	0
878	222	115	111	1
879	167	81	69	1
880	108	48	54	1
2022	961	428	439	3
2023	820	418	392	4
2024	823	368	371	3
		Repulsion F_3		
2021	638	275	291	2
2021a	1749	785	780	4
Total	6176	2845	2848	22
Exp. (cross-over value = 9.0 %)	5959	2949	2949	24

The data indicate linkage between yellow seedling and anthocyanin pigmentation with about 9 % crossing-over.

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The normal seedlings from the F_2 families reported in Table II were transplanted and seed obtained from them for progeny tests. The genotypic constitution of the normal F_2 plants was deduced from the behaviour of their F_3 offspring. Results are summarized in Table III.

TABLE III

Anthocyanin	Chlorophyll	Observed	Expected (9 % c.o.)
Coupling: progeny of sun red normals			
Homo.	Homo.	40	40.4
Het.	Homo.	6	8.0
Homo.	Het.	9	8.0
Het.	Het.	83	81.6
Total		138	$P=0.8-0.9$
Coupling: progeny of "not sun red" normals			
Recessive	Homo.	1	0.2
Recessive	Het.	4	4.8
Total		5	
Repulsion: progeny of sun red normals			
Homo.	Homo.	0	0.3
Het.	Homo.	2	6.0
Homo.	Het.	7	6.0
Het.	Het.	64	60.7
Total		73	$P=0.3-0.5$
Repulsion: progeny of "not sun red" normals			
Recessive	Homo.	35	35.1
Recessive	Het.	7	6.9
Total		42	$P>0.0$

The data give an excellent fit to a cross-over value of 9 %.

(b) *Backcross*. As the recessive yellow seedling is lethal, it was necessary to backcross to a type recessive for anthocyanin pigmentation and heterozygous for yellow seedling. Below are given the ratios to be expected in the progeny of such a cross assuming (i) free assortment, (ii) complete coupling, and (iii) complete repulsion:

Assuming	Sun red normal	Not sun red normal	Sun red yellow	Not sun red yellow
Free assortment	3	3	1	1
Complete coupling	2	1	0	1
Complete repulsion	1	2	1	0

With only 9 % crossing-over the actual results should approach either the complete coupling or complete repulsion proportions according to the way the cross was made. Data are summarized in Table IV.

Again the data agree satisfactorily with expectation with 9 % crossing-over.

(2) *Free assortment between yellow seedling and other characters*.

Two-factor ratios for yellow seedling and corolla colour, and yellow seedling and curly leaf are summarized below. (For a description of curly leaf see Yu (1939).)

Yellow seedlings die so early that no subdivision of the yellow seedling class was possible. The expected ratio was therefore 9 : 3 : 4 in each case.

TABLE IV

Family	Sun red normal	Not sun red normal Coupling	Sun red yellow	Not sun red yellow
2025	93	62	3	33
2026	57	31	4	37
Total	149	93	7	69
Exp. (9 % crossing-over)	151.8	86.7	7.2	72.3
		Repulsion		
2022	110	192	83	4
2023	144	218	101	11
2024	105	180	100	7
Total	359	590	284	22
Exp. (9 % crossing-over)	342.0	599.3	285.5	28.2

(a) The double heterozygote for corolla colour and yellow seedling gave the following in F_2 .

Family	Yellow corolla normal	White corolla normal	Yellow seedling
2021	73	19	34
Exp. (9 : 3 : 4)	70.9	23.6	31.5

The normals were tested for yellow seedling in F_3 and gave the following:

	F_2 yellow corolla		F_2 white corolla	
	Homo. normal	Het. yellow	Homo. normal	Het. yellow
Obs.	21	52	8	11
Exp. (3 : 6 : 1 : 2)	23.0	46.0	7.7	15.3

The observed ratio agrees with expectation on free assortment.

(b) Seven families doubly heterozygous for curly and yellow seedling gave the following in F_2 :

	Normal leaf normal seedling	Curly leaf normal seedling	Yellow seedling
Obs.	1093	337	463
Exp. (9 : 3 : 4)	1064.8	354.9	473.3

Ninety-two green seedlings from one of these seven families were tested for yellow seedling in F_3 and gave the following:

	F_2 normal leaf		F_2 curly leaf	
	Homo. normal	Het. yellow	Homo. normal	Het. yellow
Obs.	20	53	9	10
Exp. (3 : 6 : 1 : 2)	23.0	46.0	7.7	15.3

Curly leaf is also independent of yellow seedling.

Assortment between yellow seedling and leaf shape, presence of nectaries, lint colour, and seed fuzz have not been directly tested, but

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these characters have been shown to be inherited independently of anthocyanin pigmentation, and are therefore presumably independent of yellow seedling.

VI. SUMMARY

1. Yellow seedling, a lethal gene in Asiatic cotton, is a simple Mendelian recessive to normal. It has been discovered three times in three unrelated varieties.

2. Yellow seedling and anthocyanin pigmentation are linked. The cross-over value is about 9 %.

3. Yellow seedling is inherited independently of curly leaf and corolla colour.

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