THE GENETICS OF CORCHORUS (JUTE)

V. THE INHERITANCE AND LINKAGE RELATIONS OF BITTER TASTE, ANTHER AND COROLLA COLOUR

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The investigations reported here deal with the genetics of bitter taste and anther colour in *Corchorus capsularis*, and corolla and anther colour in *C. olitorius*. As the two species of jute do not hybridize the characters could not be studied in interspecies crosses. The description and occurrence of the characters reported upon here are given in the sections devoted to each of them. A number of strains were employed in these investigations; their origin and the characteristics for which the strains were used are given below:

Strain	Isolated from	Studied for	Species
G.S10	Japanese 'G'*	Bitter taste, non-branching habit, yellow corolla, yellow anther, full green (2) pigmentation	$C.\ cap sular is$
G.S12	Orissa material	Yellow corolla, light yellow anther, full green (7) pigmentation	$C.\ capsular is$
G.S14	D. 154†	Yellow corolla, yellow anther, green-coppery red pigmentation	$C.\ capsular is$
G.S19	Paichu white*	Yellow corolla, yellow anther	$C.\ capsularis$
G.S24	Sutpat deora	Pale corolla, light yellow anther	C. capsularis
G.S33	Kaila Comilla	Bitter taste	$C.\ capsularis$
G.S40	Lalpat megnal	Bitter taste	C, $capsularis$
G.S44	Chinsurah green†	Yellow corolla, yellow anther, full green pigmentation	$C.\ olitorius$
G.S60	Maniksari	Non-bitter taste, branching habit, pale corolla, light yellow anther, Maniksari red pigmentation	C. capsularis
G.S61	Chinese material*	Light yellow corolla, light yellow anther, red pigmentation	C. olitorius

* Foreign jutes.

INHERITANCE OF BITTER TASTE

The two cultivated species of jute, i.e. *C. capsularis* and *C. olitorius*, are commonly held to differ in the taste of their leaves. Chaudhury (1933) records that leaves of *C. capsularis* taste bitter, while those of *C. olitorius* do not, hence the former is known as '*Tita* (bitter) pat' and the latter as '*Mitha* (sweet) pat'; Finlow (1939) confirms this observation and says that the bitterness of *C. capsularis* is due to a glucoside which is not present in *C. olitorius*.

Our experience shows that *C. capsularis* is not invariably bitter to taste, as a *capsularis* type called *Maniksari* (G.S.-60), collected from Rangamati (Chittagong Hill Tracts), does not have bitter-tasting leaves.

To study the inheritance of bitterness in C capsularis, Maniksari was crossed to three capsularis strains having bitter leaves, viz. G.S.-10, G.S.-30 and G.S.-40. The F_1 plants had bitter leaves. In the F_2 non-bitter taste of leaves behaved as a simple recessive to bitter taste, as will be seen from the data given below.

[†] Selections of fibre section, Department of Agriculture, Bengal. The remaining jutes were collected from various Indian sources.

		. I		
Cross	Family	Bitter	Non-bitter	Total
$G.S33 \times G.S60$	S. 214/45	300	116	416
$G.S40 \times G.S60$	S. 215/45	401	138	539
$G.S10 \times G.S60$	S. 87/46	451	157	608
	S. 92/46	367	108	475
	S. 93/46	358	128	486
	S. 150/46	253	90	343
	S. 151/46	267	98	365
	Total	2397	835	3232
	Expected $(3:1)$	2424	808	3232
	$\chi^2 = 1.203$, $P = 0$	·3-0·2,		

A single-factor difference between bitter and non-bitter taste is thus established; the factor pair may be designated **Tb-tb** (Bitter-non-bitter).

Besides the taste of the leaves, the strains G.S.-10 and G.S.-60 differ from each other in their branching habit, corolla colour and anthocyanin pigmentation. Hence the F_2 families of the cross G.S.-10 × G.S.-60 were examined for these characters also, in order to investigate their linkage relationship with bitter taste.

BITTERNESS AND BRANCHING HABIT

Patel, Ghose & Sanyal (1945) have reported that branching habit in jute is controlled by a factor pair \mathbf{Br} -br (Branched-non-branched). The classification of the five F_2 families for bitterness and branching habit is given below:

*	Bitter		Non-bitter			
Family	Branched	Non-branched	Branched	Non-branched	Total	
S. 87/46	311	140	147	10	608	
S. 92/46	256	111	106	2	475	
S. 93/46	236	122	119	9	486	
S. 150/46	164	89	86	4.	343	
S. 151/46	171	96	93	5	365	
Total	1138	558	551	30	2277	
Expected $(9:3:3:1)$	1280.81	426.94	426.94	142.31	2277	

 $\chi^2 = 180.94$, P = very small.

It will be seen that there is a significant deviation from the digenic expectation of 9:3:3:1. That the single-factor ratios account for a mere fraction of the total χ^2 and that there is a large and significant component of the χ^2 corresponding to the linkage degree of freedom are seen by partitioning the χ^2 for the three degrees of freedom into its components as shown below:

, , , , , , , , , , , , , , , , , , ,	χ^2	D.F.	P
Segregation for Tb-tb	0.323	I	0.7 - 0.5
Segregation for Br-br	0.823	1	0.5 - 0.3
Toint composition	179.698	1	37 : 11
Joint segregation	180.844	3	Very small.

The families were tested for heterogeneity and were found to agree in showing linkage of the two factors concerned and also in showing good single-factor ratios. Linkage between the genes for bitterness and branching habit with $22 \cdot 2 \%$ crossing-over was established (vide table below).

	Bitter		Non-bitter			Crossing-
Family	Branched	Non- branched	Branched	Non- branched	Total	over %
S. 87/46 S. 92/46 S. 93/46 S. 150/46 S. 151/46	$311 \\ 256 \\ 236 \\ 164 \\ 171$	$140 \\ 111 \\ 122 \\ 89 \\ 96$	147 106 119 86 93	$10 \\ 2 \\ 9 \\ 4 \\ 5$	608 475 486 343 365	$25 \cdot 3$ $14 \cdot 5$ $25 \cdot 1$ $19 \cdot 8$ $20 \cdot 9$
Total (Expected on 22·2% crossing-over)	1138 1166.5 $\chi^2 = 1.543$,	558 $541 \cdot 3$ $P = 0 \cdot 5 - 0$	551 541·3 3.	30 27·9	$\frac{2277}{2277}$	22.2

BITTERNESS AND COROLLA COLOUR

Patel et al. (1945) have reported the occurrence of yellow and pale corolla in *C. capsularis*, inherited on a simple monohybrid basis, the factor pair being designated **Py-py** (Yellow-pale corolla).

The data show independent assortment of the genes for bitterness and corolla colour; vide the classification of the families given below:

	Bitter		Non-bitter			
Family	Yellow	Pale	Yellow	Pale	Total	
S. 87/46 S. 92/46	$\frac{335}{273}$	$\begin{array}{c} 116 \\ 94 \end{array}$	$\frac{106}{77}$	$\frac{51}{31}$	$\frac{608}{475}$	
S. 93/46 S. 150/46	$\frac{272}{176}$	86 77	$\frac{94}{62}$	$\frac{34}{28}$	$\frac{486}{343}$	
S. 151/46	200	67	79	19	365	
Total Expected $(9:3:3:1)$	$1256 \\ 1280 \cdot 8$	$\substack{440\\426\cdot 9}$	$418 \\ 426 \cdot 9$	$^{^{\prime\prime}}_{142\cdot4}$	$2277 \\ 2277$	
	$\chi^2 = 4 \cdot 0$	47, $P = 0.3 - 0$	2.			

BITTERNESS AND ANTHOCYANIN PIGMENTATION

The genetics of anthocyanin pigmentation have been dealt with in two papers from these laboratories by Patel, Ghose & Das Gupta (1944) and Ghose, Rao & Ghosh (1947).

C. capsularis plants fall into three groups: (1) full green, (2) green-pigmented and (3) red. The differences between and within the groups are determined by interaction of three loci, the genes concerned being:

C-c, chromogen factor pair, fundamental for the production of colour.

A^R_A^L_A-a, anthocyanin multiple allelomorphs which have no visible effect on the plant without the dominant chromogen gene. The alleles control the distribution and intensity of pigmentation.

R-r, a pigment reducer factor pair the effect of which is seen on the stem.

Strain Maniksari (G.S.-60) belongs to the red group of capsularis, and, like all the other members of this group, carries the dominant chromogen gene and the recessive reducer allele. The anthocyanin allele carried by it is definitely higher than a, A or A^L , but it is not possible to say at present whether the anthocyanin allele is A^R or some new member of the multiple allelomorphs. Phenotypically Maniksari is deeper and darker than the red associated with the allele A^R , and for the present will be referred to as Maniksari red. Strain Japanese 'G' (G.S.-10) is a full green of the constitution ccAArr. Hence, the pigmentation genes involved segregated in the F_2 generation, in the modified dihybrid ratio of 9:3:4. The joint segregation of pigmentation genes and bitterness gave a trigenic ratio of 27:9:12:9:3:4 as is shown below.

	•	Bitter	,	_	Non-bitter		
Family S. 87/46 S. 92/46 S. 93/46 S. 150/46 S. 151/46 Total Expected (27:9:12:9:3:4)	252 194 208 139 139 932 960.6	Coppery red 73 69 67 53 53 315 320·2	Green 126 104 83 61 75 449 426·9	Maniksari red 90 63 72 52 63 340 320·2	Coppery red 23 24 17 22 16 102 106.8	Green 44 21 39 16 19 139 142·3	Total 608 475 486 343 365 2277 2277
•	χ^2	=3.565, I	P = 0.7 - 0.5.			•	

The data show that the factor **Tb-tb** is independent of the chromogen factor pair **C-c** and the anthocyanin multiple alleles.

INHERITANCE OF ANTHER COLOUR

Anther colour in *C. capsularis* is either yellow or light yellow. The latter, though not so commonly occurring as the former, nevertheless is widely prevalent, and is frequently met with in all jute-growing areas.

The inheritance of anther colour was studied in three crosses, viz. G.S.-12 × G.S.-14, G.S.-19 × G.S.-24 and G.S.-10 × G.S.-60. The anthers of the F_1 generation were yellow, in the F_2 the anthers segregated in the ratio of 3 yellow to 1 light yellow (vide table below):

berow).	•		Light			70
Cross	Family	Yellow	yellow	\mathbf{Total}	χ^2	P
$G.S12 \times G.S14$	S. 153/46	395	123	518	_	
Citi, 12 / Citis, 12	S. 155/46	250	82	332		
	Total	645	205	850	0.353	0.7 - 0.5
$G.S19 \times G.S24$	S. 25/46	113	31	144		_
C.D10 X C.D22	S. 26/46	87	26	113		
•	Total	200	. 57	257	1.091	0.3 - 0.2
$G.S10 \times G.S60$	S. 87/46	441	167	608		
G.S10 × G.S00	S. 92/46	350	125	475		
	S. 93/46	366	120	486		
*	S. 150/46	238	105	343	***************************************	
	S. 151/46	279	86	365		
•	Total	1674	603	2277	2.668	0.2 - 0.1
	Grand total	2519	865	3384		· —
	Expected (3:1)		846	3384		 .
		$\chi^2 = 0.569$,	P = 0.5 - 0.3.			

In the family S. 150/46 of the cross G.S.- $10 \times$ G.S.-60, the fit to a single factor expectation is poor (P = 0.02 - 0.01), but the remaining four families show satisfactory monofactorial segregation. The evidence from other crosses and the data as a whole clearly indicate that a single factor determines the anther colour difference. The performance of a single family (S. 150/46), therefore, cannot be regarded as invalidating this conclusion. The factor pair controlling anther colour may be designated **Ay-ay** (Yellow-light yellow).

The material from the cross $G.S.-10 \times G.S.-60$ was also segregating for corolla colour, bitter taste, branching habit and anthocyanin pigmentation. Hence the plants were classified for these characters, as well, in order to investigate the linkage relationship of these with anther colour.

ANTHER AND COROLLA COLOUR

There is no difference in the expression of the colour of the anther and corolla described as yellow; but the light yellow anther, though definitely lighter in colour than the yellow

anther, is much deeper than the pale corolla, hence the light yellow anther when associated with yellow corolla is easily recognizable, but on a background of pale corolla difficulty is experienced in recognizing the light yellow anther, especially if the flower has been open for some time. The colour of the anther is best determined in freshly opened flowers.

The F_2 plants when classified for the joint segregation of anther and corolla colour fell into two phenotypes. There were no cross-overs and the plants were found to remain in their parental combination of anther and corolla colours of yellow anther-yellow corolla and light yellow anther-pale corolla (vide table below):

	Yellow a	Yellow anther		ow anther	
Family	Yellow corolla	Pale corolla .	Yellow corolla	Pale corolla	Total
S. 87/46	441			167	608
S. 92/46	350	. —		125	475
8.93/46	366		waters '	120	486
S. 150/46	238			105	343
S. 151/46	279			86	-365
Total	1674			603	2277

The data show that the two genes $\mathbf{A}\mathbf{y}$ and $\mathbf{P}\mathbf{y}$ are completely linked. This deduction is borne out from the behaviour of the two characters in the cross G.S.-19 × G.S.-24 as shown below:

	Yellow a	nther	Light yello		
Family	Yellow corolla	Pale corolla	Yellow corolla	Pale corolla	Total
S. 25/46	. 113		general and the second	31	144
S. 26/46	87			. 26	113
Total	200	**********		57	257

Yellow anther is usually found associated with yellow corolla and light yellow anther with pale corolla. In the large collection of types maintained at Dacca only in one strain (G.S.-12) has this not been found to be the case; in this strain light yellow anther is associated with yellow corolla. The combination yellow anther—pale corolla has not been met with; either this combination does not occur or it is extremely rare in nature.

ANTHER COLOUR IN RELATION TO BITTER TASTE AND BRANCHING HABIT

Since the genes for anther colour and corolla colour lie in the same chromosome, and those of bitter taste and branching habit are linked together, and it has been shown elsewhere in this paper that corolla colour is independent of bitter taste, it was expected that anther colour would also be independent of the bitter taste and branching habit genes. A study of the families for these characters confirmed this assumption (vide the tables given below):

Anther colour and bitter taste segregation

	Yellow anther		Light y		
Family	Bitter	Non-bitter	Bitter	Non-bitter	Total
S. 87/46	335	106	116	51	608
S. 92/46	273	77	94	31	475
S. 93/46	272	94	86	34	486
S. 150/46	176	62	77	28	343
S. 151/46	200	79	67	19	365
Total	1256	418	440	163	2277
Expected $(9:3:3:1)$	1280.8	426.9	426.9	142.3	2277

 $\chi^2 = 4.047$, P = 0.3 - 0.2.

Anther colour and branching habit segregation

	Yellow anther		Light yellow anther			
Family S. 87/46 S. 92/46 S. 93/46 S. 150/46 S. 151/46 Total Expected (9:3:3:1)	Branched 333 270 260 171 201 1235 1280-8	Non-branched 108 80 106 67 78 439 426-9	Branched 125 92 95 79 63 454 426.9	Non-branched , 42 33 25 26 23 149 142·4	Total 608 475 486 343 365 2277 2277	
	$\chi^2 = 4$	$\cdot 006, P = 0.3-0.$	2.			

ANTHER COLOUR AND PIGMENTATION

Elsewhere in this paper it has been shown that the difference in the pigmentation of the strains G.S.-10 and G.S.-60 is due to the different chromogen and anthocyanin multiple alleles carried by them. Since the anther and corolla colour genes are linked and the corolla colour gene has been shown to be independent of the pigmentation genes (Patel et al. 1945), as expected the anther colour factor pair was found to be independent of chromogen and anthocyanin multiple alleles—the pigmentation genes segregating in this cross (vide table below):

01035 (0000 00010 5010	, , .	Y	ellow anth	er	Ligh	t yellow au	ther	
Family S. 87/46 S. 92/46 S. 93/46 S. 150/46 S. 151/46 Total Expected (27:9:12:		red 245 190 206 128 147 916 960-6	Coppery red 69 62 68 52 57 308 320 2	Green 127 98 92 58 75 450 426.9	Maniksari red 97 67 74 63 55 356 320-2	Coppery red 27 31 16 23 12 109 106.8	Green 43 27 30 19 19 138 142-3	Total 608 475 486 343 365 2277 2277
		χ^2	=7.963,	P = 0.2 - 0.1.				

The cross G.S.- $12 \times$ G.S.-14, besides anther colour, was also segregating for anthocyanin pigmentation, the genes concerned being the chromogen factor pair and the alleles **A** and a of the multiple anthocyanin allelomorphs. The joint segregation in this cross also establishes the independence of the anther colour factor pair and the pigmentation genes (vide table below):

(viae table below).	Yellow anther			Light yellow anther			
Family S. 153/46 S. 155/46 Total Expected (27:9:12:9:3:4)	Green- coppery red 238 144 382 358-6	Green-light coppery red 73 46 119 119 6	Green 84 60 144 159·3	Green coppery red 69 47 116 119·6	Green- light coppery red 29 13 42 39.8	Green 25 22 47 53·1	Total 518 332 850 850
	X [*]	P = 3.929, P	0.7 - 0.5.				-

Inheritance of corolla colour and anther colour ($C.\ olitorius$)

In *C. capsularis* the two types of corolla and anther colour are widespread and are found in all jute-growing areas in India, though the yellow corolla and anther are more frequently met with than their respective allelomorphs pale and light yellow.

In C. olitorius, corolla and anther colour is practically confined to yellow, for, in the large number of C. olitorius types studied so far, the colour of corolla and anther was

found to be exclusively yellow, while among the foreign types only in one case was the corolla and anther colour found to be light yellow.

The light yellow corolla-anther strain (G.S.-61) was crossed to a yellow corolla-anther

strain (G.S.-44). The F_1 flowers had yellow corolla and yellow anther.

In the F_2 generation the plants were classified on the basis of corolla and anther colour as given below:

given below.	Yello	ow corolla	Light y		
Family	Yellow anther	Light yellow anther	Yellow anther	Light yellow anther	Total
S. 167/46 S. 170/46	436 512			$\begin{array}{c} 162 \\ 177 \end{array}$	598 689
Total Expected (3:1)	$948 \\ 965.25$	granous /	-	$\begin{array}{c} 339 \\ 321.75 \end{array}$	$1287 \\ 1287$
Expected (5.1)	000 20	$\chi^2 = 1.233$, $P =$	=0.3-0.2.	,	

Single-factor difference for yellow and light yellow colour of the corolla and anther is thus established. It will be noticed that the corolla and anther colour was inherited as a unit. The parental combinations of corolla—anther yellow and corolla—anther light yellow were maintained intact and there were no cross-overs. In the colour expression of yellow corolla and yellow anther there is no difference, nor in that of light yellow corolla and anther. This, along with the fact that yellow corolla is associated with yellow anther and light yellow corolla with light yellow anther in nature and that they remain associated in crosses, leads us to think that colour expression of corolla and anther in *C. olitorius* is probably controlled by the same gene; though the possibility of two completely linked genes controlling the colour expression of corolla and anther, as is the case in *C. capsularis*, cannot be ruled out.

The factor pair controlling corolla and anther colour may be designated $\mathbf{P}\mathbf{y}_{o}-\mathbf{p}\mathbf{y}_{o}$ (yellow-light yellow).

Patel et al. (1944) and Ghose et al. (1947) have shown that anthocyanin pigmentation in C. olitorius is controlled by multiple alleles $\mathbf{A^{p}}_{o}-\mathbf{A^{R}}_{o}-\mathbf{a_{o}}$ (deep red-red-green).

The cross G.S.-44 × G.S.-61 was also segregating for anthocyanin pigmentation, strain G.S.-44 being green with yellow corolla and anther, while strain G.S.-61 was red with light yellow corolla and anther. The material was consequently studied for anthocyanin pigmentation also in order to determine the linkage relationship of corolla and anther colour with anthocyanin pigmentation.

The classification of the F_2 plants on the basis of joint segregation of anthocyanin pigmentation and corolla and anther colour is given below:

Red		Green		
Yellow 337 388 725 723.9	Light yellow 113 133 246 241·3	Yellow 99 124 223 241·3	Light yellow 49 44 93 80·5	Total 598 689 1287 1287
	337 388 725 723 9	Yellow Light yellow 337 113 388 133 725 246 723.9 241.3	Yellow Light yellow Yellow 337 113 99 388 133 124 725 246 223 723.9 241.3 241.3	Yellow Light yellow Yellow Light yellow 337 113 99 49 388 133 124 44 725 246 223 93 723·9 241·3 241·3 80·5

The data show no significant deviation from the expected digenic ratio and the independence of the anthocyanin pigmentation and corolla-anther colour is established.

Discussion

The genetic basis of corolla colour and anther colour differences in the two species is apparently different. The colour difference of these two floral organs in C capsularis is caused by two different but completely linked genes, as is shown by (1) the behaviour of the cross $G.S.-12 \times G.S.-14$, where the anther colour was segregating whereas the corolla colour was not, (2) the fact that in the cross $G.S.-10 \times G.S.-60$ only segregates with parental combination of corolla and anther colour were obtained, and cross-overs were absent. In C olitorius no clear evidence has been obtained to show that corolla and anther colour are controlled by two separate factor pairs; most probably the colour expression of both these organs is controlled by a single gene. Further it may be added that while in C capsularis different combinations of corolla and anther colour occur and alternative colours to yellow are pale and light yellow for corolla and anther respectively, in C olitorius only colour combinations of yellow corolla-yellow anther and light yellow corolla-light yellow anther are found.

Banerjee (1932) has reported seven as the haploid number of chromosomes in *C. capsularis*, hence the number of linkage groups to be expected is also seven. Our knowledge of the genetics of this species of jute has now sufficiently progressed to enable us to speculate on the organization of the linkage groups and to identify some of the groups with particular genes. One of the chromosomes carries the genes for bitter taste and branching habit, and these genes have been shown, by the evidence presented in this paper, to be independent of the chromogen and anthocyanin multiple alleles, and of the corolla and anther colour genes.

Branching habit has been shown by Patel et al. (1945) to be independent of the pigment reducer factor pair, hence it is to be expected that bitter taste is not linked with the reducer gene. Bitter taste and branching habit thus form a group which is not connected with any of the genes discussed here; these include all the known capsularis genes except the stipule character factor pair (Sfl-sfl), linkage relations of which have not yet been determined.

Corolla colour and anther colour factor pairs belong to another group, which is not connected with the pigmentation or the bitter taste and branching habit genes.

Ghose (1942) has established a linkage of 8% between the chromogen and pod shape; this forms a third group and has been shown to be independent of the known genes discussed here.

The remaining genes, i.e. the anthocyanin multiple alleles and the pigment reducer factor pair, form components of two different groups.

Thus out of the possible seven linkage groups in C. capsularis, some information is now available on the organization of five.

Since sending the paper to the press Dr J. B. S. Haldane has suggested an alternative interpretation of the corolla and anther colour data. This is based on the hypothesis that the corolla-anther colour is controlled by three allelomorphs, viz.

PyA giving yellow corolla and yellow anther.

Pyª giving yellow corolla and light yellow anther.

pya giving pale yellow corolla and light yellow anther.

This interpretation gives a better explanation for the non-occurrence of pale corolla and yellow anther plants even occasionally in the crosses, and brings in line the genetic basis of corolla and anther colour in the two species.

SUMMARY

- 1. Monogenic inheritance has been established for the following characters of the jute plant:
 - (a) Bitter-non-bitter taste (**Tb-tb**) in C. capsularis.
 - (b) Yellow-light yellow anther colour (Ay-ay) in C. capsularis.
 - (c) Yellow-light yellow corolla-anther colour (Pyo-pyo) in C. olitorius,
 - 2. The following linkage relationships have been established:
- (a) Bitter taste and branching habit factor pairs are linked with $22 \cdot 2 \%$ crossing-over value.
- (b) The corolla and anther colour factor pairs in C. capsularis are completely linked, while in C. olitorius corolla colour and anther colour expression is probably controlled by the same factor pair.
- (c) The genes of C. capsularis described here have been shown to be located in five groups.
- (d) The corolla-anther factor pair in C. olitorius has been shown to be independent of the anthocyanin multiple allelomorphs.

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