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Effect of some antibiotic compounds in cotton on post-embryonic development of spotted bollworm (*Earias vittella* F.) and the mechanism of resistance in *Gossypium arboreum*

H C SHARMA*, R A AGARWAL and MUNSHI SINGH
Indian Agricultural Research Institute, New Delhi 110 012, India
* Present address : Sorghum Entomologist, ICRISAT, ICRISAT Patancheru P.O., 502 324, India

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Abstract. Larval survival and post-embryonic development of the spotted bollworm, *Earias vittella* was studied on 23 genotypes belonging to three cultivated species of cotton (*Gossypium arboreum, G. barbadense* and *G. hirsutum*). There were significant differences in larval survival and post-embryonic development on different genotypes. The larval survival varied from 27·1 to 93·3%, developmental period from 16·6 to 20·3 days, pupation from 60 to 100% and adult emergence from 78 to 94%. Gossypol increased the post-embryonic developmental period. Majority of the larvae entered the bolls through the thallic region, possibly, to avoid higher concentrations of gossypol in the pericarpic region. Tannin content of bolls was significantly and negatively correlated with adult emergence.

Crosses between resistant and susceptible genotypes of *G. arboreum* segregated into pigmented (red) and non-pigmented (green) plant types. The former were rich in gossypol and tannins compared to the latter. Gossypol and tannin content of bolls showed negative correlation with spotted bollworm incidence.

Keywords. *Gossypium* ; gossypol ; tannins ; spotted bollworm ; *Earias* ; antibiotic ; post-embryonic ; resistance.

1. Introduction

Cotton is an important commercial crop in Asia, Africa, America and Australia. It is damaged by over 130 different species of insect pests. Spotted bollworms (*Earias* spp.) cause serious losses to cotton in India, China, Southeast Asia, Iraq, Israel and Africa (Sohi 1964; Chang *et al* 1963; Walker 1952; Avidov and Harpaz 1969; Reed 1974). Pigment glands characterizing genus *Gossypium* (Gillham 1965) had been identified as a source of resistance against the insects feeding on cotton plant (Bottger *et al* 1964). Antibiosis, as one of the mechanisms of resistance in cotton was first demonstrated by Brazzel and Martin (1956, 1959) in *G. tomentosum* against *Pectinophora gossypiella*. Later, antibiosis was reported against *Heliothis zea* and *H. virescens* (Lukefahr *et al* 1966; Lukefahr and Houghtaling 1969; Oliver *et al* 1970, 1971; Lukefahr *et al* 1974, 1975; Meisner *et al* 1977); *Anthonomus grandis* (Douglas 1966, Bailey *et al* 1967) and *Amrasca* *biguttula biguttula* (Chakravarty and Sahni 1972). Gossypol (Lukefahr and Houghtaling 1966; Lukefahr *et al* 1966, 1975; Meisner *et al* 1977), *p-hemigossypolone* (Gray *et al* 1976), heliocides (Stipanovic *et al* 1976, 1977) and a condensed tannin (Chan and Waiss Jr. 1978) have been reported to confer resistance to insects feeding on cotton. Considering the colossal losses caused by this pest *vis-a-vis* the limitations of insecticides to control it, the host plant resistance can be used as one of the mechanisms to keep its populations at a low level. Asiatic diploid species (*Gossypium arboreum* L.) have been reported to be comparatively less damaged (Hussain and Khan 1940; Butani 1974). Singh *et al* (1972, 1976) found that within *G. arboreum*, damage by bollworms varied among different varieties and that resistance was genetically inherited. The present studies report the extent of antibiosis and the antibiotic factors affecting development of *E. vittella* in different cotton genotypes, and the mechanism of resistance in *G. arboreum*.

2. Materials and methods

The insect culture was raised in the laboratory on green cotton bolls of Bikaneri Nerma. Genotypes tested included 3 lines from *G. arboreum* (Sanguineum, Virnar and G-27), one from *G. barbadense* (Line 199-5) and 19 from *G. hirsutum*. The effect of antibiotic factors was studied on the survival of first instar larvae and the post-embryonic development. Larval survival on bolls of different genotypes was studied by releasing newly hatched larvae on green bolls (7–10 days old) in plastic boxes (15 × 15 × 5 cm). Five larvae were released on each boll. The plastic petridishes were kept inside B.O.D. incubator at 30 ± 1° C. Three days after inoculation, the bolls were dissected and the number of survivors recorded. The observations were made on 20 bolls of each genotype arranged in four sets and also on the number of larvae entering the boll through the thallic and pericarpic regions of the boll on a few genotypes.

The post-embryonic development was studied on 7–10 days old bolls of different genotypes. Food was changed every third day. The rearing was carried out at 30 ± 1° C. Observations were recorded on pupation, adult emergence, pupal weight, and larval and pupal developmental periods. Growth indices on different genotypes were calculated by the following formulae:

$$\text{Larval growth index (LGI)} = \frac{\text{Percent pupation}}{\text{Larval period (days)}}$$

$$\text{Total developmental growth index (TGI)} = \frac{\text{Per cent emergence}}{\text{Total developmental period (days)}}$$

Spotted bollworm incidence was recorded on 100 green bolls during the peak activity period (August) in 1978 on five varieties of *G. arboreum* and three F2 populations of intra-arboreum crosses involving resistant and susceptible types. The different genotypes were grown in 2 row-4 m plots. For chemical analysis, 10–15 days old bolls were collected. The bolls were dried at 40° C and powdered finely in a grinder. The gossypol content was determined by the method of Yang and Davis (1976) and tannins were estimated by indigocarmine volumetric method

(AOAC, 1975). The gossypol and tannins were expressed as per cent of dry weight of the sample taken. The data were analysed and simple correlations between the different parameters were worked out.

3. Results and discussion

The larval survival varied from 27·1 to 93·3% in different genotypes (table 1). Larval survival was minimal on SH-269, SS-265, Acala, Cocker-100A, Sanguineum, XG-15 and South Carolina. Only 27·1 to 40·7 per cent larvae survived on these lines. Comparatively, more larvae survived on PS-10, Virnar, RS-89 and 320-F (68·8 to 93·3%). This difference in survival values in different genotypes is indicative of the resistance offered by bolls of some genotypes. Larvae showed a tendency to enter the bolls through the thallic region (table 2), possibly, to avoid higher concentrations of antibiotic factors in the pericarpic region.

Table 1. Survival of first instar larvae and pupal weights of spotted bollworm (*E. vittella*) on the bolls, and amounts of gossypol and tannins in different varieties.

Variety	Larval survival (%)	Gossypol (%)	Tannins (%)	Pupal Weight (mg.)
PS-10	93·3	0·96	1·42	48·2
Virnar	76·0	0·76	1·60	66·9
320F	70·0	1·10	1·40	..
RS-89	68·7	1·04	1·40	52·4
D-33	60·4	1·12	1·35	55·3
JR-81	58·1	0·79	1·06	52·3
Ston-731N	51·6	0·79	1·63	..
Bikaneri nerma	48·8	0·92	1·22	..
Frego bract	48·3	1·00	1·49	..
M-495	47·3	1·04	1·58	50·3
H-14	47·0	1·08	1·87	43·7
G. barbadense	46·0	1·31	..	65·6
HR-26 # 8 X H.HG-6·1M	44·8	0·95	1·88	56·0
Hindiweed	43·3	1·13	1·6)	46·3
BJR	42·0	0·98	1·57	..
XG-15	40·6	1·33	1·87	45·1
South Carolina	40·6	1·11	1·15	58·5
SH-269	40·3	1·02	1·60	42·3
SS-265	40·2	1·02	1·34	57·4
Acala	39·3	0·58	1·30	56·0
Cocker-100A	34·6	0·61	1·61	45·2
Sanguineum	27·1	1·46	1·96	57·2
C.D. at 5% *t*	13·22	0·13	0·04	10·1

Table 2. Penetration behaviour of the first instar larvae of *E. vittella* into the bolls.

Variety	No. of larvae*		Gossypol (%)	
	Thallus	Pericarp	Thallus	Pericarp
Sanguineum	99	1	0·72	1·86
SH-269	72	28	0·53	1·13
XG-15	99	1	0·50	1·02
D-33	68	33	0·45	0·75

* Based on 100 larvae

Results of the experiments on post-embryonic development are given in table 3. The larvae took a minimum of 8·5 days to complete development on Virnar and nearly 11 days on SS-265. Pupal development was completed in 8·0–12·6 days on different genotypes. More than 10 days were needed to complete the pupal development when the larvae were fed on G-27 and *G. barbadense*. The development was quicker on Virnar, Empire and PS-10, while it was slower on G-27, *G. barbadense*, XG-15, SS-265 and Sanguineum. There was a difference of nearly 6 days in total developmental period between the most and the least suitable genotypes.

Per cent pupation ranged from 60 to 100% (table 4); less than 65% larvae pupated on Hindiweed, Acala, SS-265, SH-269 and XG-15, and more than 85% on Virnar, HR-26 ≠ 8XH · HG-6-IN, South Carolina and M-495. More than 90% adults emerged when the larvae were reared on South Carolina and M-495. Lower adult emergence was recorded on Sanguineum, XG-15 and Hindiweed. The growth indices based on larval period and per cent pupation, and adult emergence and total developmental period gave a fair account of the extent of antibiosis in different genotypes. Based on these growth indices, the genotypes SH-269, XG-15, Sanguineum, *G. barbadense* and Hindiweed were less suitable for the development of the insect.

The pupal weights varied considerably on different genotypes (table 1). The pupal weights are also indicative of the extent to which bolls of different genotypes were suitable for the insect development. Pupae weighed less than 50 mg when the rearing was carried out on SH-269, H-14, XG-15, Cocker 100A, Hindiweed and PS-10.

Larval survival tended to be negatively correlated with the gossypol ($r = -0 \cdot 1767$) and the tannin ($r = -0 \cdot 3104$) content of bolls. The correlation coefficients were non-significant. Evidently, some other factors also affected the larval survival on the bolls. Factors including pericarp thickness (Singh *et al* 1965) and other terpenoids in cotton bolls (*p*-hemigossypolone, gossypurin and Heliocides H_1 and H_2) might be responsible for larval mortality in addition to gossypol and tannins. Moreover, the concentration of these compounds in the whole bolls might not bear a direct relationship with larval survival. Larval penetration behaviour was significantly and negatively related with gossypol contens

Table 3. Post-embryonic development of spotted bollworm (*Earias vittella*) on some cotton genotypes.

Variety	Developmental period in days*		
	Larval	Pupal	Total developmental period
Virnar	8·50±0·08	8·33±0·35	16·67±0·67
Empire	9·00±0·83	9·33±0·82	16·67±1·66
PS-10	9·10±0·23	8·50±0·29	16·75±0·48
Ston-73IN	10·00±0·36	8·00±0·00	17·33±1·08
JR-81	8·44±0·27	9·18±0·44	17·45±0·31
HR-26 # 8 X H·HG-6-IN	9·00±0·28	9·00±0·21	17·80±0·25
D-33	9·11±0·35	9·00±0·58	18·11±0·46
H-14	10·11±0·42	8·38±0·26	18·50±1·00
SH-269	10·00±0·62	8·14±0·34	18·57±0·53
RS-89	9·11±0·24	9·69±0·22	18·75±0·30
South Carolina	9·64±0·27	9·08±0·24	18·77±0·36
M-495	9·17±0·42	9·33±0·40	18·94±0·70
Cocker-100A	9·89±0·51	9·17±0·30	19·00±0·51
Hindiweed	9·50±0·34	9·60±0·43	19·00±0·55
Frego bract	10·20±0·20	8·80±0·37	19·00±0·55
Acala	9·77±0·38	9·78±0·70	19·11±0·35
Sanguineum	10·55±0·42	9·57±0·37	19·33±0·37
SS-265	10·82±0·35	9·00±0·33	19·80±0·49
XG-15	10·36±0·18	9·72±0·32	19·93±0·43
G-27	9·75±0·96	12·57±0·99	22·22±0·51
G. barbadense	10·40±0·40	10·00±0·59	20·33±0·59

* Based on 25 larvae

Table 4. Effect of feeding on different cotton varieties on pupation and adult emergence of spotted bollworm (*E. vittella*) larvae.

Variety	No. of larvae (*n*)	Per cent Pupation	LGI*	Emergence (%)	TGI**
Virnar	50	100	11·8	..	..
HR = 26 # 8 × H·HG6-IN	40	90	10·0	81·3	4·3
South Carolina	45	87·5	9·0	93·3	5·4
M-495	30	85·7	9·4	93·8	5·0
RS-89	70	73·5	8·0	..	..
Sanguienum	75	70	6·6	77·8	4·0
G. barbadense	35	70	6·7	81·8	4·0
Hindiweed	40	63·6	6·7	78·6	4·1
Acala	65	62·5	6·4	87·5	4·6
SS-265	55	62·5	5·8	88·9	4·7
SH-269	65	60·0	6·0	..	..
XG-15	70	60·0	5·8	78·3	3·9

* Larval Growth Index (LGI) = % pupaion/Larval period

** Total Growth Index (TGI) = % Emergence/Total developmental period

($r = -0 \cdot 7638$). High concentrations of gossypol in the pericarpic region possibly deterred the larvae entering the boll through this region.

Larval period was prolonged by gossypol and tannins. Total period required for completing post-embryonic development showed a positive and significant correlation with gossypol content of bolls ($r = 0 \cdot 4974$) (table 5). The shorter developmental period on Virnar and Empire was possibly due to lower amounts of gossypol in these genotypes, while the longer developmental periods on Sanguineum, SS-265, XG-15, GH 27 and *G. barbadense* could be attributed to higher concentrations of gossypol in these varieties. Similar antibiotic factors in cotton have been reported against *P. gossypiella* (Brazzel and Martin 1956; 1959); *Heliothis* spp. (Oliver *et al* 1970, 1971); *H. virescens* (Lukefahr *et al* 1966; Meisner *et al* 1977) and *Anthonomus grandis* (Bailey *et al* 1967; Douglas 1966).

Gossypol seemed to affect pupation and adult emergence adversely, though the correlation coefficients were very low (tables 6, 7). Tannins showed significant and negative correlations with adult emergence ($r = -0 \cdot 7813$) and growth index ($r = -0 \cdot 7432$) (table 7). The regression coefficients were also significant and negative.

Gossypol incorporated in artificial diet had been found to affect the growth and survival of pink bollworm (Shaver and Parrot 1970). The larval weight had been found to be negatively correlated with gossypol content (Wilson and Shaver 1973).

Some biochemical components other than gossypol and tannins also accounted for the antibiosis expressed by different genotypes. Eagle *et al* (1950) found no correlation between cotton seed pigment glands, toxicity and extractable gossypol. Some growth inhibiting factors have recently been reported in the race stocks of *G. hirsutum*, which contained medium amounts of gossypol but were highly antibiotic against *P. gossypiella* and *Heliothis* spp. (Lukefahr *et al* 1974). These additional growth inhibiting factors were later identified as *p*-hemigossypolone (Gray *et al* 1976) and Heliocides H_1 and H_2 (Stipanovic *et al* 1976, 1977). In the present studies, some factors other than gossypol also accounted for the antibiotic effect against *E. vittella*. Major role among these factors was that of tannins. Elligar *et al* (1978) investigated the toxicity and relative importance of other terpenoids in the pigment glands and suggested that these might supplement the toxicity of gossypol but themselves are of minor importance. Gossypol reduces the nutritional quality of boll contents (Carter and Lyman, 1969; Lyman *et al* 1959). It also inhibits the activity of enzymes protease, amylase and pepsinogen (Meisner *et al* 1978; Tanksley *et al* 1970). Antibiotic effects of gossypol are possibly due to reduced nutritional quality or non-availability of nutrients or enzyme inhibition, which lead to the prolonged development and reduced growth of the insect.

Bollworm incidence on different varieties and F_2 populations of interavarietal crosses have been presented in table 8. It was observed that Daulat, CJ-73 and non-pigmented F_2 segregates had $> 75\%$ spotted bollworm incidence compared to Lohit, G-27 and pigmented F2 segregates which manifested $< 55\%$ incidence. The red pigmented segregates showed $32 \cdot 42$–$46 \cdot 87\%$ incidence whereas non-pigmented (green) segregates had $62 \cdot 50$–$80 \cdot 06\%$ bollworm incidence.

There were significant differences among different genotypes in gossypol and tannin content (table 9). The less susceptible genotypes viz., G-27 and Lohit as well as pigmented F2 segregates had comparatively higher gossypol content

Table 5. Correlations between gossypol and tannin content in bolls with post embryonic development of *E. vittella*.

	Gossypol	Tannins	Larval Period	Pupal period	Total developmental period
Gossypol	1·000				
Tannins	0·2397	1·000			
Larval period	0·3398	0·3480	1·000		
Pupal period	0·1724	−0·0725	0·0519	1·000	
Total developmental period	0·4974*	0·1491	0·7364*	0·5242*	1·000
	b_i	t value	R^2		
Y_1 Larval period					
X_1 Gossypol	0·7239	1·1745			
X_2 Tannins	0·7743	1·2208	0·1908		
Y_2 Pupal period					
X_1 Gossypol	0·4473	0·7992			
X_2 Tannins	−0·2760	0·4793	0·0434		
Y_3 Total developmental period					
X_1 Gossypol	1·9673	2·1937*			
X_2 Tannins	0·1311	0·1421	0·2483		

* Significant at $P = 0·05$

Table 6. Relationship between gossypol and tannin content of bolls with pupation and growth index.

	% Gossypol	% Tannin	% Pupation	Growth index
% Gossypol	1·000			
% Tannin	0·5095	1·000		
% Pupation	−0·2485	−0·0148	1·000	
Growth index	−0·0359	−0·0131	0·9825*	1·000
	b_i	t value	R^2	
Y_1 Pupation				
X_1 Gossypol	−19·1455	0·8255		
X_2 Tannins	8·2009	0·3830	0·786	
Y_2 Growth index				
X_1 Gossypol	− 3·8546	1·2135		
X_4 Tannins	1·7104	0·5835	0·1556	

Table 7. Relationship between gossypol and tannin content in bolls to per cent emergence and growth index.

	Gossypol	Tannins	Emergence	Growth index
Gossypol	1·000			
Tannins	0·4605	1·000		
Emergence	−0·3510	−0·7813*	1·000	
Growth index	−0·3411	−0·7432*	0·9198*	1·000

	b_i	t value	R^2
Y_1 Emergence			
X_1 Gossypol	0·3281	0·0446	
X_2 Tannins	− 17·1281	3·1635*	0·6104
Y_3 Growth index			
X_1 Gossypol	0·0027	0·0052	
X_4 Tannins	− 1·0993	2·7913*	0·5523

* Significant at $p = 0·05$

Table 8. Incidence of spotted bollworm (*E. vittella*) on *arboreum* genotypes.

Sl. No.	Genotype	Incidence/ 100 bolls
1.	Daulat	90·00
2.	CJ 73	75·00
3.	Cernuum	69·20
4.	Lohit	55·00
5.	G-27	53·00
6.	Cernuum × Lohit	
	(*a*) Non-pigmented F_2	80·00
	(*b*) Pigmented F_2	46·67
7.	Daulat × Lohit	
	Non-pigmented F_2	80·00
	Pigmented F_2	45·45
8.	Cernuum × G–27	
	Non-pigmented F_2	62·50
	Pigmented F_2	32·43
	Average for F_2 segregates	
	Non-pigmented	74·17
	Pigmented	41·52

Table 9. Gossypol and tannin content in some *G. arboreum* genotypes.

Sl. No.	Genotype	Gossypol (%)	Tannin (%)
1.	G 27	1·58 d	0·74 d
2.	Lohit	1·40 c	0·84 d
3.	* Pigmented F_2	1·20 b	0·47 c
4.	Cernuum	1·24 b	0·41 bc
5.	CJ 73	1·02 a	0·31 b
6.	* Nonpigmented F_2	0·99 a	0·17 a
	CD at 5% (*t*)	0·10	0·12

* Samples from the F_2 segregates of the cross Daulat × Lohit.

(1·20–1·58%) and were also rich in tannin content (0·41–0·84%). The spotted bollworm incidence was found to be negatively correlated with gossypol ($r = -0 \cdot 7133$) and tannin content ($r = -0 \cdot 6420$). Gossypol and tannins were also significantly associated between themselves ($r = 0 \cdot 9040$). Gossypol is the principal antibiotic compound in the cotton plant, and is also genetically inherited (Lee *et al* 1968; Rhyne and Smith 1965; Wilson and Smith, 1976).

The spotted bollworm incidence in *arboreum* varieties seems to be largely influenced by the gossypol and tannin content. On the basis of these results, it is suggested that while selecting plants resistant to spotted bollworms in F2 populations, the plant pigmentation (red-pigmented) may be used as an important character along with the gossypol and tannin content of the genotypes.

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