Host Plant Resistance in Cultivated Jute and Its Wild Relatives Towards Jute Hairy Caterpillar Spilosoma obliqua (Lepidoptera: Arctiidae)

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Host plant resistance in cultivated jute and its wild relatives towards jute hairy caterpillar *Spilosoma obliqua* (Lepidoptera: Arctiidae)

B. S. Gotyal, K. Selvaraj, P. N. Meena, and S. Satpathy*

Abstract

The oviposition, feeding behavior, and development of the jute hairy caterpillar *Spilosoma obliqua* Walker (Lepidoptera: Arctiidae) was studied on one cultivated jute species, *Corchorus olitorius* L. ('JRO-204') (Malvales: Malvaceae), and 5 wild jute species, viz., *C. tridens* L., *C. trilocularis* L., *C. pseudo-olitorius* Islam & Zaid, *C. aestuans* L., and *C. fascicularis* Lamarck under laboratory conditions with a temperature of 27 ± 2 °C and relative humidity of 80 ± 5%. These host plant species had considerable influence on oviposition, larval feeding behavior, larval survival, larval weight, pupation, pupal weight, and adult emergence. Significant differences were observed in oviposition preference based on numbers of eggs laid by the adults. The mean number of egg clusters differed significantly with 3.6 ± 0.3, 3.0 ± 0.6, 3.3 ± 0.3, 3.0 ± 0.6, 1.0 ± 0.6, and 2.0 ± 1.2 on *C. olitorius, C. fascicularis, C. trilocularis, C. pseudo-olitorius, C. tridens*, and *C. aestuans*, respectively. The *C. pseudo-olitorius* and *C. aestuans* were less preferred with the lowest mean numbers of eggs per cluster (77.2 ± 8.2 and 75.2 ± 38.8, respectively) compared with 174.0 ± 2.7 on *C. olitorius*. With respect to feeding preferences, most larvae (53.9 ± 3.4%) preferred *C. olitorius* as compared with 1.6 ± 0.02% and 7.2 ± 1.5% of larvae feeding on *C. aestuans* and *C. tridens*, respectively. Only 2 species, namely *C. trilocularis* and *C. olitorius,* supported complete larval development. The growth of 3rd instars indicated a maximum antibiosis effect by *C. tridens* and *C. aestuans* on *S. obliqua.* Total protein content in the host plants had a significant positive correlation with the larval survival, weight, pupation, and adult emergence of *S. obliqua*, whereas polyphenol oxidase and total phenol were negatively correlated. The effect of wild jute species with higher phenol and peroxidase as host plants manifested adversely on larval development, growth, survival, pupation, and adult emergence, which indicates the antibiosis mechanism of resistance.

Key Words: jute hairy caterpillar; jute species; oviposition; feeding behavior; biology; biochemical content

Resumen

Se estudiaron la oviposición, el comportamiento de alimentación y la biología del gusano peludo de Bihar, *Spilosoma obliqua* Walker (Lepidoptera: Arctiidae) sobre una especie cultivada de yute, *Corchorus olitorius* (cv 'ROJ-204'.) (Malvales: Malvaceae) y cinco especies silvestres de yute, *C. tridens, C. trilocularis, C. pseudo-olitorius, C. aestuans* y *C. fascicularis,* bajo condiciones de laboratorio de 27 ± 2 °C y 80 ± 5% humedad relativa. Estas especies de plantas hospederas mostraron una influencia considerable sobre la oviposición, el comportamiento de alimentación de las larvas, la sobrevivencia de las larvas, el peso, el estadio de pupa, el peso pupal y la emergencia de los adultos. Se observó un efecto significativo para la preferencia de oviposición basado en el número de huevos/grupo puestos por los adultos. El promedio del numero de grupos de huevos varia significantemente con 3.6 ± 0.3, 3.0 ± 0.6, 3.3 ± 0.3, 3.0 ± 0.6, 1.0 ± 0.6 y 2.0 ± 1.2 sobre *C. olitorius, C. fascicularis, C. trilocularis, C. pseudo-olitorius, C. tridens* y *C. aestuans*, respectivamente. *Corchorus pseudo-olitorius* y *C. aestuans* fueron los menos preferidos con un promedio menor del número de huevos/grupo, 77.22 ± 8.19 y 75.16 ± 38.80, respectivamente, en comparación con 173.97 ± 2.69 en *C. oliotorius*. Con respecto a las preferencias de alimentación de las larvas, la mayoria de las larvas (53.88 ± 3.38%) prefieren *C. olitorius* en comparación con 1.64 ± 0.02% y 7.22 ± 1.47% de larvas sobre *C. aestuans* y *C. tridens,* respectivamente. Solamente dos especies, *C. trilocularis* y *C. olitorius*, apoyaron el desarrollo completo de las larvas. El crecimiento de larvas del tercer estadio indica el máximo efecto de antibiosis de *C. tridens* y *C. aestuans* en *S. obliqua*. El contenido total de proteína en las plantas hospederas tenía una correlación positiva significativa en apoyar la sobrevivencia de las larvas, el peso, la pupación y la emergencia de adultos de *S. obliqua*; mientras que el polifenol oxidasa y fenol total se correlacionaron negativamente. El efecto de las especies silvestres de yute con una cantidad mayor de fenol y peroxidasa como plantas hospederas manifiesta negativamente en el desarrollo de las larvas, el crecimiento, la sobrevivencia, la pupación y emergencia de los adultos que indica el mecanismo de antibiosis de la resistencia.

Palabras Clave: gusano peludo de yute; especies de yute; oviposición; comportamiento alimentario; biología; contenido bioquímico

Jute (*Corchorus* spp.; Malvales: Malvaceae) and mesta (*Hibiscus* spp.; Malvales: Malvaceae) are natural plant fibers of commercial importance after cotton. India is the largest producer of jute goods in the world, contributing about 60% of the global production. The domestic market continues to be the mainstay of industry consuming about 87% of the total production. At the same time, India's

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export currently earns about Rs 2095 crores per annum. Intensive cultivation of high-yield, fertilizer-responsive cultivars of jute brought forth the problem of insect pests. Among them, the jute hairy caterpillar *Spilosoma obliqua* Walker (Lepidoptera: Arctiidae) is one of the major pests and highly polyphagous, infesting many economically important crop plants often causing severe economic damage (Gupta & Bhattacharya 2008). In jute, it causes yield loss up to 30% (Bandyopadhyay et al. 2014). Timely management of this pest is very important as delay may lead to complete defoliation of crop. Farmers are resorting to frequent use of toxic insecticides, and considerable levels of resistance to conventional insecticides have developed (Dhingra et al. 2007). Development of cultivars with high levels of resistance to this pest would certainly provide an effective complementary approach in integrated pest management to minimize the extent of losses.

Host plant species that slow or accelerate the development of the insect have considerable relevance to the development of management methods (Tanga et al. 2013). In co-evolution, plants and insects have evolved strategies to avoid each other's defense systems. Plants respond to herbivores through various morphological, biochemical, and molecular mechanisms to counter or offset the effects of herbivore attack. Plants confront the herbivores directly by affecting host plant preference or survival and reproductive success, and indirectly through other species such as natural enemies of the insect pests. These defenses against the herbivores are wide-ranging, highly dynamic, and mediated by biochemical mechanisms. Compounds such as terpenoids, alkaloids, anthocyanins, phenols, and quinones are the secondary metabolites, either produced constitutively or in response to plant damage, and they affect feeding, growth, and survival of herbivores (Howe & Jander 2008; Arimura et al. 2009; War et al. 2012). Among the secondary metabolites, plant phenols are a common and widespread group of defensive compounds, which play a major role in host plant resistance against herbivores, including insects (Sharma et al. 2009; Usha Rani & Jyothsna 2010). Oxidation of phenols catalyzed by polyphenol oxidase and peroxidase is a potential defense mechanism in plants against herbivorous insects. Quinones formed by oxidation of phenols bind covalently to leaf proteins and inhibit the protein digestion in herbivores (Bhonwong et al. 2009). Imbalance in digestion and utilization of plant proteins can have drastic effects on insect physiology (Gulsen et al. 2010; Usha Rani & Jyothsna 2010; Fürstenberg-Hägg et al. 2013).

Assessment of biochemical components of the host plant species would help to better understand mechanisms of host suitability (Awmack & Leather 2002). Host plant quality, particularly the variation in qualitative and quantitative amounts of secondary metabolites, is a key determinant for herbivorous insects as it affects larval survival, fecundity, growth rate, and development (Jayabalan & Murugan 1996). Therefore, development of cultivars with resistance to *S. obliqua* is an urgent need because the cultivated varieties of jute show only moderate levels of resistance (Gotyal et al. 2013b). Wild relatives of crops are useful sources of genes for resistance to biotic and abiotic stress factors when resistance within the crop species is absent (Maharijaya et al. 2012; Firdaus et al. 2013; Lucatti et al. 2013). The wild jute species *C. tridens* L. and *C. aestuans* L. significantly impair the larval growth and pupation of *S. obliqua* as compared with the cultivated species *C. olitorius* (Gotyal et al. 2013a). Detailed information on host preference mechanism and the biochemical basis of resistance in jute against *S. obliqua* is still lacking. Hence, we conducted the present study to enumerate the extent of resistance among the wild and cultivated jute species based on comparative egg laying preference and biology, and to establish the biochemical basis of resistance against jute hairy caterpillar.

Materials and Methods

Series of laboratory experiments were conducted at the Central Research Institute for Jute and Allied Fibres (CRIJAF), Kolkata, India (22°45'N, 88°26'E), during 2013 and 2014 to study the oviposition preference, feeding preference, development, and survival of *S. obliqua* on the jute species *C. tridens, C. trilocularis* L., *C. pseudo-olitorius* Islam & Zaid, *C. aestuans, C. fascicularis* Lamarck , and *C. olitorius* ('JRO-204').

HOST PLANTS

The seeds of cultivated and wild jute species were obtained from the seed bank of CRIJAF. They were sown during Mar to Aug 2013 in earthen pots (15 cm upper radius × 7.5 cm lower radius × 26 cm height). The pots were ⅔ filled up with pot soils (Soil + FYM at a 4:1 proportion). The seeds of respective species were sown and watered optimally for uniform germination. The seedlings (25 d old) were thinned out to maintain 4 healthy plants per pot. The pots were maintained in insecticide-free condition inside a glasshouse without any natural insect infestation.

INSECTS

The incipient colony of *S. obliqua* was collected from unsprayed crop at the CRIJAF Research Farm. The F_1 population was maintained on susceptible 'JRO-204' leaves in a transparent poly vinyl rearing container (13 cm height × 13 cm diameter) fitted with a removable netted cover for aeration. The feed and containers were changed every alternate day to avoid microbial infection. The progeny of laboratory-reared *S. obliqua* was used for the study.

BIOASSAYS

Development and Survival of *S. obliqua* on Jute Species

Development and survival of *S. obliqua* on 6 jute species were studied in a "detached twigs assay" under laboratory conditions with a temperature of 27 ± 2 °C and relative humidity of 80 ± 5%. Detached twigs of respective jute species (from 75-d-old plants) were washed with distilled water, air dried, inserted into water-filled conical flasks (500 mL), and placed in a plastic container (27 × 20 cm) for each jute species in a completely randomized design with 4 replications. Ten newly molted 8-d-old 3rd instars of *S. obliqua* were weighed in mini Petri plates by taring the balance (Mettler and Toledo) for recording the larval weight and released on different jute species with the help of a camel hairbrush. The jute twigs were replaced on alternate days. After 3, 5, and 9 d, larval survival, larval weight, pupal weight, and adult emergence were recorded. The data were expressed as percentage larval survival, mean weight of larvae, and percentage pupation and adult emergence.

Larval Feeding Preference

A dual-choice feeding experiment was conducted to test the differences in feeding preference of *S. obliqua* among jute species. Detached twigs were prepared as before, randomly assigned to different combinations of jute species (2 species at a time), and placed individually into dual-choice cage chambers (8 cm × 8 cm × 8 cm) of square shape prepared by using mylar sheet covered with nylon mesh. Two chambers were joined by a circular tunnel (45 cm × 15 cm) with a central rectangular small box (11 cm × 8 cm × 8 cm), the upper side covered with nylon wire mesh for larval release. Twenty 3rd instars that had been starved for 2 h were released per species combination, each replicated 4 times in a completely randomized design. After 24 h, the settlement of larvae on jute species was recorded and the percentage of consumed leaf area was estimated with the help of a graph sheet.

In a multi-choice feeding experiment, all 6 test-plant species were provided at the same time. Twigs were placed individually into 6 multi-choice cage chambers (100 cm × 76 cm × 73 cm) prepared by using polyester film sheet covered with nylon mesh. All 6 chambers were joined by using circular tunnels (45 cm × 10 cm) connected to the insect release box (11 cm × 8 cm × 8 cm). Sixty 3rd instars were released and allowed to freely move with equal probability of selection of a suitable host plant. Observations were made as in the dual-choice test.

Oviposition Preference

This experiment was carried out using no-choice (one host plant at a time) and multiple-choice tests (6 host plants at a time) in nylon-covered polyester cages (100 cm × 75 cm × 100 cm). For this experiment, the jute plants remained in pots. Oviposition preference of *S. obliqua* females was determined by counting the numbers of egg clusters and eggs per cluster laid on each jute species.

For the no-choice tests, each cage (75 cm height × 25 cm width) with a 75-d-old jute plant was infested with 2 pairs of newly emerged adult moths of *S. obliqua*. All tests were conducted with 5 replications in a completely randomized design. For the multiple-choice tests, 5 pairs of adult moths were released in an oviposition cage (100 cm × 75 cm × 100 cm) containing one plant of each of the 6 jute species. The leaves with one or more egg clusters were removed and the numbers of eggs laid in each cluster were counted at 24 h intervals for 7 d.

PLANT BIOCHEMICAL ANALYSIS

The leaf samples of the host plants were simultaneously analyzed for quantitative estimation of biochemical parameters in the Laboratories of the Division of Crop Protection, CRIJAF. Plants were selected randomly from each jute species grown in the glasshouse. Samples of deep green mature leaves from the middle part of the plants were collected at 70 to 75 d after sowing. The biochemical analysis of total protein, total phenol, and polyphenol oxidase contents were conducted as described by Lowry et al. (1951), Bray & Thorpe (1954), and Augustin et al. (1985), respectively. Each biochemical analysis was replicated 5 times.

STATISTICAL ANALYSES

Data on biological parameters such as larval survival (%), pupal weight (mg), pupation (%), and adult emergence (%) on different jute species were subjected to 1-way analysis of variance (ANOVA). Similarly, data on larval feeding preference (multiple-choice test) and adult oviposition preference were subjected to 1-way ANOVA. The significance of differences between treatments was measured by an *F*-test at $P = 0.05$. Means were separated by Duncan's multiple range test. Larval feeding preferences in the dual-choice test were compared through Yate's corrected chi-square test to determine significant differences. Simple correlations between biochemical contents (i.e., polyphenol oxidase, total phenol, and total protein) with larval survival (%), pupal weight (mg), pupation (%), and adult emergence (%) were computed through Microsoft Excel package 2010.

Results

COMPARATIVE BIOLOGY OF *S. OBLIQUA* ON CULTIVATED AND WILD SPECIES OF JUTE

Effect of Food Plants on Larval Growth and Development

Sources of resistance in cultivated and wild jute species against *S. obliqua* were determined based on antibiosis effects. Only 2 species, *C. trilocularis* and *C. olitorius*, supported complete development (Tables 1 and 2). The weights of larvae feeding on the different jute species indicated maximum antibiosis effects of *C. tridens* and *C. aestuans* (Table 1). At 5 d after feeding (DAF), the larval weight on wild species ranged from 3.3 ± 5.8 to 154.0 ± 13.1 mg and was significantly less than that on *C. olitorius* (268.6 ± 11.2 mg) (Table 1). Percent survival at 5 DAF was significantly lowest on *C. tridens* (3.3 ± 5.8%) and *C. aestuans* (13.3 ± 15.3%), and all larvae died by 9 DAF on these species (Table 1). In case of other species, the survival of larvae at 9 DAF ranged from 63.3 ± 15.3 to 33.3 ± 5.8%, with no significant difference between *C. trilocularis*, *C. fascicularis*, and *C. olitorius* (Table 1).

Of the wild jute species, only *C. trilocularis* supported pupation, which was significantly less (79.5 ± 4.1%) compared with pupation on the cultivated species *C. olitorius* (92.0 ± 1.3%) (Table 2). The mean pupal weight of the larvae fed on *C. trilocularis* was significantly less (197.3 ± 10.0 mg) than that on *C. olitorius* (285.5 ± 49.4 mg) (Table 2). The adult emergence on *C. olitorius* (72.2 ± 9.6%) was twice as high as that on *C. trilocularis* (40.0 ± 17.3%) (Table 2).

Effect of Jute Species on the Larval Feeding Behavior of *S. obliqua*

Dual-choice Test. The relative larval feeding preference of *S. obliqua* under dual-choice conditions indicated significant differences in larval feeding behavior on cultivated and wild jute species. Among the different combinations of cultivated with wild jute species, the larvae

Table 1. Effects of cultivated and wild host plants on larval survival and weight gain of *Spilosoma obliqua.*

	Larval survival (%) at different days after feeding			Larval weight (mg) at different days after feeding		
Host plant	3	5	9	3	5	9
C. tridens (WCIN-188)	70.00 ± 26.45 a	3.33 ± 5.77 a	0.00 ± 0.0 a	26.37 ± 1.26 a	3.33 ± 5.78 a	0.00 ± 0.00 a
C. trilocularis (WCIN-186)	100.00 ± 0.00 b	96.66 ± 5.77 d	63.33 ± 15.27 c	82.00 ± 13.08 d	154.00 ± 13.11 c	328.27 ± 76.15 d
C. pseudo-olitorius (WCIN-182)	93.33 ± 11.54 b	50.00 ± 10.00 b	33.33 ± 5.77 b	53.83 ± 9.70 bc	111.70 ± 18.17 b	118.03 ± 20.52 b
C.aestuans (WCIN-179)	63.33 ± 32.14 a	13.33 ± 15.27 a	0.00 ± 0.00 a	33.33 ± 9.87 ab	16.67 ± 15.28 a	0.00 ± 0.00 a
C. fascicularis (WCIN-202)	93.33 ± 11.54 b	70.00 ± 10.00 c	46.66 ± 11.54 bc	62.67 ± 8.08 cd	131.33 ± 12.47 bc	207.2 ± 23.40 c
C. olitorius ('JRO-204')	100.00 ± 0.00 b	56.66 ± 11.54 c	53.33 ± 11.54 c	117.67 ± 24.01 e	268.57 ± 11.19 d	397.77 ± 41.40 e
F-value	2.57	34.83	24.96	20.24	163.01	58.84
P-value	0.001	0.001	0.001	0.001	0.001	0.001

Means (± SEM) followed by a different letter within a column are significantly different ($P < 0.05$, Duncan's multiple range test).

Table 2. Pupation, pupal weight, and adult emergence of *Spilosoma obliqua* on different jute species.

Jute species	Pupation (%)	Weight of pupa (mg)	Adult emergence (%)
C. tridens (WCIN-188)	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
C. trilocularis (WCIN-186)	79.45 ± 4.08 b	197.33 ± 10.01 b	40.00 ± 17.32 b
C. pseudo-olitorius (WCIN-182)	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
C.aestuans (WCIN-179)	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
C. fascicularis (WCIN-202)	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
C. olitorius ('JRO-204')	92.04 ± 1.25 c	285.50 ± 49.43 c	72.16 ± 9.64 c
F-value	115.92	115.47	37.25
P-value	0.001	0.001	0.001

Means (± SEM) followed by a different letter within a column are significantly different ($P < 0.05$, Duncan's multiple range test).

showed least preference for *C. aestuans* (5 larvae, 7%) as compared with *C. olitorius* (55 larvae, 68%) ($\chi^2 = 40.01$, $n = 60$) (Table 3). Based on the proportion of total larval population choosing one species in a pairing (expressed as percentage feeding preference), significant differences among treatments were observed. Of the wild species of jute, *C. aestuans* and *C. tridens* were the least preferred hosts with 7 and 13% preference, respectively, as compared with 28, 25, and 18% for *C. pseudo-olitorius, C. fascicularis*, and *C. trilocularis*, respectively. Preference for the cultivated *C. olitorius* ranged from 52 to 87% (Table 3). Based on the leaf area consumed, larvae showed low preference for *C. tridens* and *C. trilocularis* with consumption of 0.77 and 1.74 cm^2 of leaf area, respectively; they did not feed on *C. aestuans* and consumed 10.93 cm^2 of leaf area on *C. olitorius* ($\chi^2 = 9.97$, $n = 60$) (Table 3).

Multiple-choice Test. Based on the number of larvae settled and feeding preference (%) on a particular host plant, *C. aestuans* was the least preferred (1.0 ± 0.01 larvae, 1.6 ± 0.02%) of the wild species as compared with *C. tridens* (4.3 ± 0.9 larvae, 7.2 ± 1.5%), *C. pseudo-olitorius* (6.0 ± 1.0 larvae, 10.0 ± 1.7%), *C. fascicularis* (7.3 ± 3.0 larvae, 12.1 ± 4.8%), and *C. trilocularis* (9.0 ± 0.6 larvae, 15.0 ± 1.0 %) (Fig. 1A). The cultivated species *C. olitorius* was significantly the most preferred (32.3 ± 2.0 larvae, 53.9%). We found a significant difference among host plants in the extent of leaf consumption by *S. obliqua.* The least consumption of leaves occurred on *C. aestuans* and *C. tridens* (0.21 ± 0.21 and 4.54 ± 1.92 cm^2 leaf area, respectively), whereas most consumption occurred on *C. olitorius* (92.92 ± 32.43 cm^2 leaf area) (Fig. 1B).

Table 3. Effect of jute species on *Spilosoma obliqua* larval feeding preference in dual-choice tests.

Host plant combination	No. of larvae settled[a]	Feeding preference (%)	Leaf area consumed (cm^2)
C. olitorius	43	71.66	11.25
C. pseudo-olitorius	17	28.33	7.86
χ^2	10.41	17.91	0.76
C. olitorius	52	86.66	7.23
C. tridens	8	13.33	0.77
χ^2	30.81	52.32	5.01
C. olitorius	45	52.66	11.50
C. fascicularis	15	25.00	7.96
χ^2	14.02	12.10	0.05
C. olitorius	49	81.66	8.31
C. trilocularis	11	18.33	1.74
χ^2	22.82	38.85	4.46
C. olitorius	55	67.66	10.93
C. aestuans	5	7.00	0.00
χ^2	40.01	42.01	9.98

[a]*n* = 60

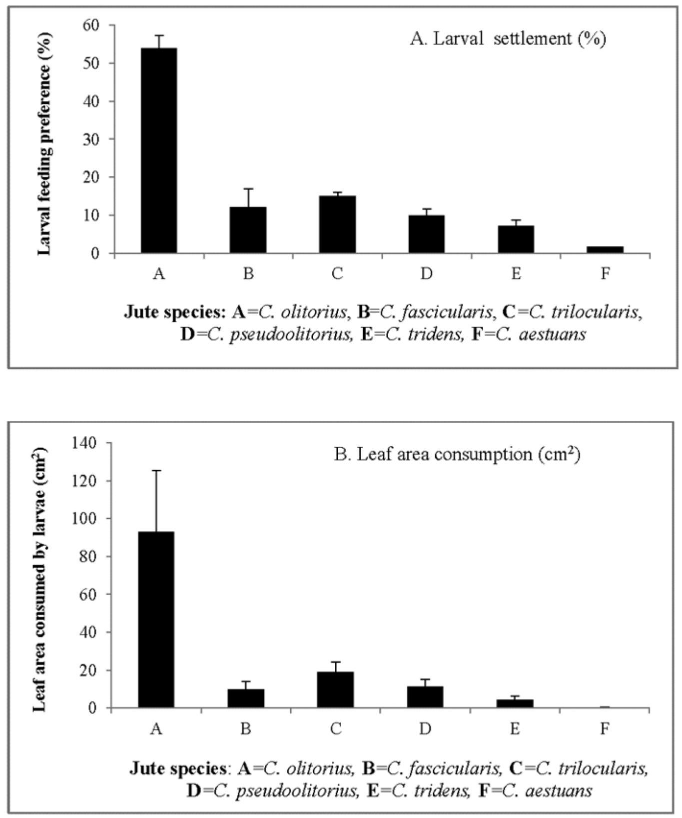

Fig. 1. Effect of cultivated and wild jute species on *Spilosoma obliqua* larvae settlement (%) (A) and leaf area consumed (cm^2) (B) after 24 h in multiple-choice tests.

Effect of Jute Species on Oviposition Preference of *S. obliqua*

No-choice Test. The mean numbers of egg clusters differed significantly on different jute species ($F = 2.296$; df = 2; $P = 0.001$) (Fig. 2A). They were 3.6 ± 0.3, 3.0 ± 0.6, 3.3 ± 0.3, 3.0 ± 0.6, 1.0 ± 0.6, and 2.0 ± 1.2 on *C. olitorius, C. fascicularis, C. trilocularis, C. pseudo-olitorius, C. tridens*, and *C. aestuans*, respectively (Fig. 2A). Similarly, we found significant differences among host plant species in oviposition preference for jute species based on numbers of eggs per cluster. The wild species *C. tridens* and *C. aestuans* were least preferred, with the smallest mean numbers of eggs per cluster (77.2 ± 8.2 and 75.2 ± 38.8, respectively) as compared with 174.0 ± 2.7 on *C. olitorius* ($F = 2.170$; df = 2; $P = 0.001$) (Fig. 2B).

Multiple-choice Test. The proportion egg laid (clusters and eggs per cluster) was greater on the cultivated than the wild jute species (Figs. 3A and B). Among the wild species, numbers of egg clusters differed

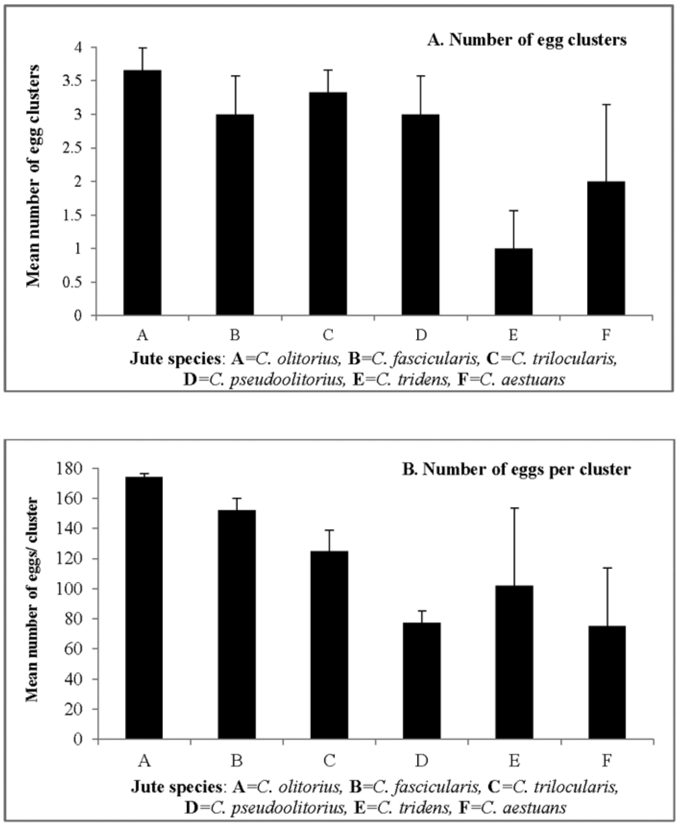

Fig. 2. Mean number of egg clusters (A) and eggs per cluster (B) laid by *Spilosoma obliqua* females on 6 jute species in no-choice tests.

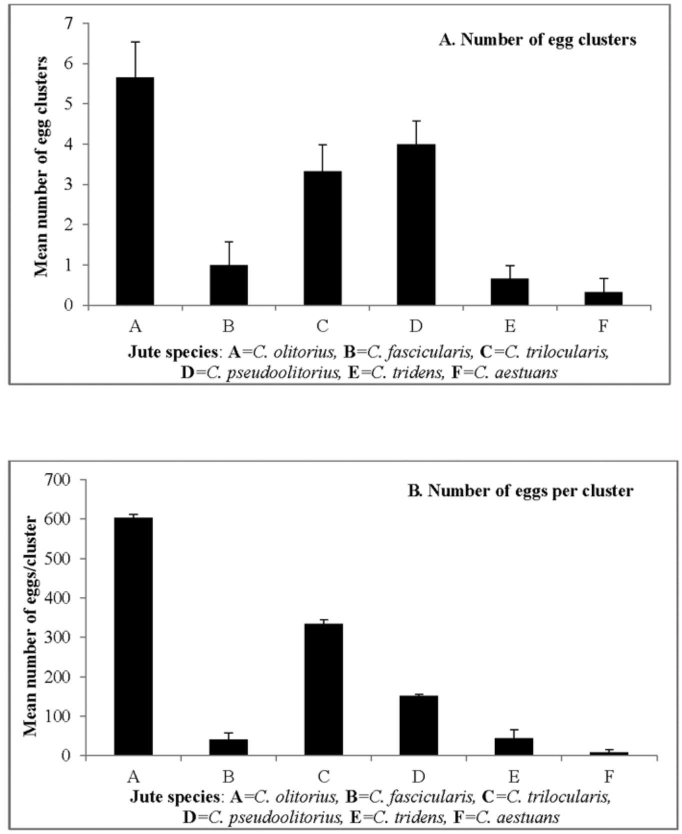

Fig. 3. Mean number of egg clusters (A) and eggs per cluster (B) laid by *Spilosoma obliqua* females on 6 jute species in multiple-choice tests.

significantly with *C. tridens*, *C. aestuans*, *C. trilocularis*, and *C. fascicularis* found to be the least preferred (with 0.7 ± 0.3, 0.3 ± 0.3, 0.3 ± 0.7, and 1.0 ± 0.6 egg clusters, respectively), *C. pseudo-olitorius* intermediate (with 4.0 ± 0.6 egg clusters), and *C. olitorius* most preferred (with 5.7 ± 0.9 egg clusters) (F = 13.23; df = 2; P = 0.001) (Fig. 3A). The total number of eggs per cluster also varied across the cultivated and wild species (F = 9.918; df = 2; P = 0.001). The least preferred were *C. aestuans* and *C. fascicularis* (with 7.7 ± 7.7 and 41.0 ± 16.3 eggs per cluster, respectively) and the most preferred was the cultivated *C. olitorius* (with 603.7 ± 8.4 eggs per cluster) (Fig. 3B).

BIOCHEMICAL ESTIMATIONS IN CULTIVATED AND WILD SPECIES OF JUTE

The biochemical content and its chemical composition differed significantly among the host plants (Table 4). The phenol content in the test species of jute varied significantly from 11.00 µg/g in *C. pseudo-olitorius* to 62.25 µg/g in *C. tridens*. The peroxidase content varied significantly from 4.17 µg/mL in *C. pseudo-olitorius* to 6.67 µg/mL in *C. trilocularis*. The protein content was the least (10.05 µg/g) in *C. tridens* and significantly the greatest in *C. olitorius* (22.00 µg/g). Biochemical content concentrations of phenol and peroxidase were greatest in the wild jute species as compared with cultivated species, whereas cultivated species possessed the greatest protein content.

CORRELATIONS BETWEEN BIOLOGICAL PARAMETERS OF *S. OBLIQUA* AND BIOCHEMICAL CONTENTS OF PLANTS

The biochemical components, i.e., polyphenol oxidase, total phenol, and total protein contents, in wild and cultivated jute species were correlated differently with biological parameters of *S. obliqua* at different days after feeding (DAF) (Table 5). The total protein content at 9 DAF had significantly positive correlations with larval survival (R^2 = 0.55), larval weight (R^2 = 0.63), pupation (R^2 = 0.61), and adult emergence (R^2 = 0.65). However, polyphenol oxidase was negatively correlated with larval survival (R^2 = −0.05), larval weight (R^2 = −0.19), pupation (R^2 = −0.51), and adult emergence (R^2 = −0.49). A similar trend was observed for total phenol content. The wild jute species with higher phenol and peroxidase contents had adverse effects on *S. obliqua* biology, feeding, and oviposition, indicating that non-preference and antibiosis mechanisms of resistance were operating in the wild species.

Discussion

Our results demonstrated significant differences in egg laying preference, extent of egg deposition, feeding, and biology of *S. obliqua* on

Table 4. Biochemical content estimation of cultivated and wild jute species.

	Biochemical contents		
Jute species	Phenol (µg/g)	Protein (µg/g)	Peroxidase (µg/mL)
C. olitorius	37.82	22.00	4.33
C. fascicularis	43.46	17.79	5.73
C. trilocularis	20.62	18.31	6.67
C. pseudo- olitorius	11.00	19.18	4.17
C. tridens	62.25	10.05	4.40
C. aestuans	55.62	14.61	5.32
Critical difference (P = 0.05)	1.92	3.07	2.03

Table 5. Correlation of biochemical contents of plants with biological parameters of *Spilosoma obliqua* on different jute species at different days after feeding (DAF).

Biochemical content	Larval survival (%)			Larval weight (mg)			Pupation (%)	Adult emergence (%)
	3 DAF	5 DAF	9 DAF	3 DAF	5 DAF	9 DAF		
Polyphenol oxidase (µg/mL)	−0.04	−0.02	−0.05	−0.29	−0.21	−0.19	−0.51	−0.49
Total phenol (µg/g)	−0.52	−0.51	−0.47	−0.34	−0.37	−0.35	−0.33	−0.25
Total protein (µg/g)	0.54	0.47	0.55	0.73	0.72	0.63	0.61	0.65

the various wild and cultivated jute species. The wild species *C. aestuans* and *C. tridens* caused significant non-preference for egg laying and larval feeding. Larval weights, pupation rates, and adult emergence were depressed on wild species of jute. Moreover, the remarkable variation in the biochemical parameters of the host plants significantly affected the biology of *S. obliqua.*

Favorable insect–host plant association requires that adult females find and accept a plant for egg laying and that larvae accept it and are able to fully develop on it. Accordingly, the acquisition of a novel plant as host, i.e., the establishment of a novel insect–plant interaction, is presumably governed by changes in behavior of adults or larvae or both (Bernays & Chapman 1994). Herbivore preference and performance are in turn strongly influenced by the quality of the host plants (Leimu et al. 2005). The plant quality for herbivores is determined by the nutrients and concentrations of secondary metabolites. The host plant plays an important role in regulating insect populations as the concentrations and proportion of nutrients differ greatly among species (Slansky & Rodriquez 1987; Schoonhoven et al. 2005). So far, there have been no studies on the mechanisms of host plant resistance towards *S. obliqua* in jute species.

Larval feeding behavior and adult oviposition preferences play important roles during the host utilization phase because the rate of feeding, number of eggs laid, and duration of feeding events are influenced by the balance of excitatory and inhibitory elements in the plant as well as the internal state of the arthropod (Miller & Strickler 1984). The effect of wild species on oviposition and feeding preference indicated the presence of secondary plant substances or poor nutritional quality of the food as the major components of resistance to *S. obliqua* in the wild relatives of jute, whereas such effects were not apparent in the cultivated species, *C. olitorius*. Similarly, the growth duration and consumption rate, utilization efficiency, development time, longevity, fecundity, and survival of *Diacrisia casignetum* Kollar (Lepidoptera: Arctiidae) were significantly different on the 4 host plants tested with respect to food quality (Roy & Barik 2012, 2013). It has been stated that plant defenses are more effective against generalist than specialist herbivores (Agrawal 1999). Antibiosis seemed to be the major component of resistance in wild relatives of jute, which may be due to presence of secondary plant substances. The most unfavorable host plants, i.e., *C. aestuans* and *C. tridens,* had the greatest phenol content of 55.62 µg/g and 66.25 µg/g, respectively, and lowest protein content of 10.05 µg/g and 14.61 µg/g, respectively.

Understanding the details of insect oviposition and larval feeding preferences is valuable for identifying resistant germplasm in a plant breeding program. Many insects have been selected naturally to oviposit on certain plant species that enhance larval development and survival by providing a suitable diet (Singer 1983; Thompson & Pellmyr 1991). Results from dual- and multiple-choice tests clearly showed that *S. obliqua* larvae preferred feeding on the cultivated jute species over wild species. Of the wild jute species, larvae preferred *C. fascicularis* > *C. trilocularis* > *C. tridens* > *C. aestuans* in the dual-choice test and *C. trilocularis* > *C. fascicularis* > *C. pseudo-olitorius* > *C. tridens* > *C. aestuans* in the multiple-choice test. The possible explanation for variation in food consumption and development of this insect may be due to significant differences in biochemical contents of the various jute species.

Several factors affect oviposition behavior of the female insect, and her choice has considerable influence on the life history of her progeny. In the present no-choice and multiple-choice tests, the females of *S. obliqua* laid significantly more eggs on the cultivated jute species than on the wild species. Oviposition on the latter occurred in descending order on *C. fascicularis, C. trilocularis, C. tridens, C. pseudo-olitorius*, and *C. aestuans* in the no-choice test and on *C. trilocularis*, *C. pseudo-olitorius*, *C. tridens, C. fascicularis*, and *C. aestuans* in the multiple-choice test.

Chemical barriers include not only antifeedant or repellent compounds to prevent colonization but also toxic compounds that delay or prevent an insect population increase (Smith & Clement 2012). The fast larval growth on the cultivated jute species observed in the present study may be due to higher protein content as compared with the wild species. Larvae also consumed a greater leaf area of the cultivated than the wild species. A possible explanation for variation in food consumption and development of *S. obliqua* may be significant differences in the plants' protein, phenol, and polyphenol oxidase contents. The growth rates of *S. obliqua* had a significantly positive correlation with protein content. Similar results were obtained with different insect–plant systems by several researchers (Endo et al. 2007; Constabel & Barbehenn 2008; Bosch et al. 2014).

Exploitation of plant defenses is already a component of integrated pest management programs, which seek to minimize insect damage. Unlike other crops, the existing varieties/cultivars of cultivated species of *Corchorus* spp. substantially lack resistance against the important insect pests. The susceptibility of the variety together with a favorable microclimate during the growing season resulted in 2 to 3 outbreaks of jute hairy caterpillar that nullified the late management approaches initiated by the farmers. So far this study, which revealed considerable resistance in the wild species *C. aestuans* and *C. tridens* will help to redefine the resistance breeding program and provide the basis for strategies in developing resistant jute varieties against the jute hairy caterpillar. The information generated on the biochemical basis of resistance will diversify and give thrust for proper selection of resistant lines. Importantly, the results will facilitate the development of truly resistant varieties for making the management of jute hairy caterpillar more handy and sustainable.

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