Behavioral Responses of a Generalist Pest, *Spilosoma Obliqua* Walker, Towards the Leaf Surface Wax Chemicals of Three Types of Jute Crop and Implications in Pest Management

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Research Article

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Abstract

Behavioral responses of a generalist pest, *Spilosoma obliqua* Walker (Lepidoptera: Arctiidae), towards the leaf surface wax chemicals of three types of jute crops (white jute, *Corchorus capsularis*, tossa jute, *C. olitorious*,, and mesta jute or kenaf, *Hibiscus cannabinus* [Malvaceae]) and their implications in pest management was studied under laboratory conditions. The GC-MS and GC-FID analyses of the jute leaf epicuticular waxes indicated the presence of 27 n-alkanes, having chain lengths from n-C_{14} to n-C_{36} and 14 free fatty acids (FFAs) having chain lengths from $C_{12:0}$ to $C_{22:0}$. Among the identified n-alkanes and FFAs of selected jute cultivars n-C_{34} (144.397±6.971 µg $leaf^{-1}$) and $C_{16:1}$ (37.034±0.848 µg $leaf^{-1}$) of tossa jute leaves were most abundant. The host preference (white jute> tossa jute > mesta jute) of *S. obliqua* was evaluated simultaneously by olfactory, visual, and tactile recognition, as valid for other lepidopteran species. For olfaction [females], oviposition [gravid females], and feeding [larvae]) in *S. obliqua*, the most stimulating combined-synthetic-mixture of epicuticular wax components was represented by 4 n-alkanes (n-C_{16}, n-C_{18}, n-C_{20}, n-C_{22}) and 5 FFAs ($C_{16:1}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$) in mixture at leaf equivalent (µg $leaf^{-1}$) amounts (195.209±2.950 µg, 119.777±1.857 µg, and 50.567±3.508 µg, respectively) in white jute, tossa jute, and mesta jute, respectively. Thus, the present study suggests that the synthetic blends of 4 n-alkanes and 5 FFAs of respective jute crops can be used as lures to develop baited trap as a part of integrated pest management (IPM) of *S. obliqua* for sustainable jute cultivation.

Introduction

Three types of jute crops (*Corchorus capsularis* [white jute], *C. olitorious* [tossa jute], and *Hibiscus cannabinus* [mesta jute or kenaf] [Malvaceae]) are the most important economic fiber crop throughout the world after cotton (Kumar et al. 2014, 2017; Mahapatra et al. 2009; Sarkar and Majumdar 2016). Presently, jute cultivation is gaining importance in India particularly in rain fed tracts of eastern transitional zones due to its increasing demand as eco-friendly green raw material for different industries (Naik and Karmakar 2016; Mazumdar et al. 2016; Roy 2015b). However, several limiting (biotic and abiotic) factors regulate agricultural production of jute throughout the world (Sarkar and Gawande 2016; Sarkar and Majumdar 2013; Rahaman and Khan 2006, 2012). Among the pests, the Bihar hairy caterpillar (BHC), *Spilosoma obliqua* Walker, syn. *Diacrisia obliqua*, (Lepidoptera, Arctiidae), is considered to be a potent pest in India including West Bengal (Gotyal et al. 2015; Mobarak et al. 2020b; Singh and Varatharajan 1999; Roy 2020). This generalist is one of the major pests on different economic crops in South East Asian countries including India (Bhaduria et al. 2001; Roy and Barik 2013; Roy 2020; Varatharajan et al. 1998). Being a sporadically occurring and polyphagous pest, its larval survival and development vary greatly on a wide range of its host plants such as oilseed crops, fibre crops, pulses, legumes, vegetables, medicinal plants, weeds, etc. (Singh and Singh 1992; Roy 2020). Their larval instars (I-VI) feed voraciously on their host leaves and the plants may be completely defoliated (Mobarak et al. 2020b; Roy 2020). The 3_{rd}-to-5_{th} instar larvae are the most damaging ones and cause a severe reduction of host yield (Mobarak et al. 2020b; Singh and Singh 1992; Roy 2020). The larvae showed a certain level of resistance to different classes of insecticides including a few biorationals and, hence, the successful control of this pest is to some extent difficult (Mohapatra and Gupta 2018; Parui and Roy 2016). Unfortunately, due to different socioeconomic attributes, still farmers are generally use broad-spectrum synthetic pesticides injudiciously (Carvalho 2017; Kumar et al. 2017). These result into secondary pest outbreak, pest resurgence, development of pesticide resistance and emergence of pest biotypes and creates ecological imbalance (Aktar et al. 2009; Kim et al., 2017; Mathew 2016). To face this ecosystem crisis, development of more sustainable methods of crop production as a part of integrated pest management (IPM) is a worldwide concern today (Kumar et al. 2014; Roy, 2020, 2021a, b).

Precise knowledge about chemical mediated plant-insect interactions between the fibre crops and the pest, *S. obliqua*, is required for their successful IPM. For many years, numerous studies have been conducted to control insect pests through plant-based semiochemicals (Mobarak et al. 2020a; Roy 2019a 2021b). Isolation and identification of semiochemical compounds responsible for triggering insect behaviour can enhance a better understanding of insect-plant interactions (Little et al. 2019; Renwick and Chew 1994; Schoonhoven et al. 2005). Herbivorous insects recognize their host plants by several physicochemical cues detected through different sensory modalities (Chapman and Bernays 1989; Lucas-Barbosa et al. 2016; Raguso and Willis 2005; Roy 2019a). They find host plants through visual (Barragan-Fonseca et al. 2020; Dahanukar et al. 2005; Goyret et al. 2007; Wadhera and Capaldi-Philips 2014), olfactory (Roy and Barik 2012b, 2014; Das et al. 2019; Mitra et al. 2017; Roy et al. 2012a), tactile (Foster and Howard 1998; Roy 2019a), and gustatory (Chapman 2003; Feng et al. 2017; Van Loon et al. 1992) cues individually or in combinations with each other (Aartsma et al. 2017; Omura et al. 1999; Roy 2019a, 2021b). Thus, the plant signals play a crucial role in the survival of most phytophagous insects, particularly in lepidopterans, because their neonates are often relatively immobile and, thus, depend on the judicious choice of the host plant by the adult females (McCallum et al. 2011; Müller and Riederer 2005). Moreover, for a polyphagous pest, a broader diet increases the risk of oviposition on the non-host or poor host along with host evaluation time in an ecological context (Chapman and Bernays 1989; Lucas-Barbosa et al. 2016; Müller and Hilker 2001).

The first physical contact between an herbivorous insect and the host plant occurs on the leaf surface and the epicuticular waxes act as volatile and structural cues towards host acceptance or rejection (Das et al. 2019; Debnath et al. 2021; Fernández et al. 2019; Eigenbrode and Espelie 1995; Jetter et al. 2000, 2006; Malik and Barik 2015; Müller 2006). The plant epicuticular waxes mainly consist of long-chain alkanes, free fatty acids (FFAs), esters, aldehydes, and primary and secondary alcohols, which composition varies widely within a species or cultivars of a species (Baker 1982; Jetter et al. 2006; Mitra et al. 2020; Roy et al. 2012a, b). The leaf epicuticular waxes play an important role in host recognition, oviposition, and feeding stimulants in different phytophagous insects (Li and Ishikawa 2006; Mitra et al. 2019; Roy 2019a, 2021b). The importance of plant leaf alkanes and FFAs as semiochemicals has been demonstrated for different insect species during the last three decades (Bernays and Champman 2000; Eigenbrode and Espelie 1995; Mitra et al. 2020; Parr et al. 1998; Roy 2021b; Sarkar et al. 2013a, b). Especially, low-volatile n-alkanes and FFAs have an important role in insect-plant interactions as an olfactory attractant (Karmakar et al. 2016; Malik et al. 2017; Mitra et al. 2019; Mobarak et al. 2020a; Roy et al. 2012a; Roy 2019a) and/or oviposition stimulant (Das et al. 2019; Li and Ishikawa 2006; Mitra et al. 2017; Parr et al. 1998; Udayagiri and Mason 1997).

To apply the chemical ecological approach, *S. obliqua* females, as well as their 5_{th} instar larvae, were tested in a series of bioassays for attraction, oviposition, and feeding preferences on the three potential host (three jute cultivars) plants in the present study. While numerous previous studies dealt with the attraction of different pest species to their host plant volatiles (Ikeura et al. 2010; Mitra et al. 2017, 2020, 2021; Mobarak et al. 2020a; Roy and Barik 2012b, 2014; Roy et al. 2012a), the comparative evidence for the complex host chemical properties used in navigation and oviposition site selection by *S. obliqua* has been scarce so far. According to Roy and Barik (2012a, 2013), Roy (2019a, 2019b, 2020), and Schoonhoven et al. (2005), polyphagous herbivores generally prefer to feed on mature leaves of their respective hosts. For this reason, epicuticular waxes of mature leaves of three fibre crops as host plants of *S. obliqua* were considered in this study. Even, there is currently no information about chemical cues mediated attraction, oviposition, and feeding preference in integration to *S. obliqua* to these host plants for an universal management strategy. The aims of the current research were (i) to identify and quantify the compositions of n-alkanes and FFAs present in the leaf epicuticular waxes of the three jute crops, (ii) to observe the variations in the composition of n-alkanes and FFAs between the fibre crops and in comparison with other crop plants, (iii) to interpret the role of leaf epicuticular wax chemistry and their analogous synthetic mixtures in short-range attraction (adult), oviposition (female), and feeding (5th instar larvae) of *S. obliqua* tested in different bioassays under laboratory conditions, (iv) to find out the most preferred n-alkanes and FFAs of leaf epicuticular wax, as well as their effective combinations in attraction, oviposition, and feeding of *S. obliqua* towards the design of a baited trap in future IPM strategies.

Materials And Methods

Plants: Three types ofjute crops such as, white jute (*Corchorus capsularis*, cv. JRC-80), tossa jute(*C. olitorious*, cv. JRO 204) and mesta jute or kenaf (*Hibiscus cannabinus*, cv. JRM 3) [Malvaceae] (Kumar et al. 2014, 2017; Mahapatra et al. 2009; Rahman and Khan 2012; Sarkar and Majumdar 2016) were cultivated in a field situated near Chinsurah Rice Research Center (CRRC), Chinsurah, 22°53' N, 88°23' E, 13 m above sea level (Hooghly, West Bengal, India) during their growing season in 2019-2021. Nine plots were prepared with an average number of plants per unit area of 30±4 plants m^{-2} where each plot was of 10 m × 10 m equipped with soil organic matter of 5.3±0.2%, pH 7.7, average relative humidity (RH) of 70±5%, and photoperiod of 13 h L : 11 h D at 30–34 °C. The cultivated varieties (cvs) or cultivars were separately germinated and grown in three side-by-side plots with a distance of 0.5 m between two plots. A distance of 1 m was kept for the cultivation of each selected jute species and all plots were maintained without any insecticide. At the pre-flowering stage (8 to 10 week old) of each crop, 2 to 3 mature leaves (14 to 20 days old) leaving 4 to 5 tender leaves from the top were collected at 6 a. m. Three separate batches of ca. 100 g of leaves of each cultivar were collected from the plants in different plots for the extraction of leaf epicuticular waxes.

Insects: Using a light trap, *S. obliqua* adults (males and females) were collected from the field of cultivated sesame plants (*Sesamum indicum* cv. Rama Pedaliaceae) (Roy 2020), similarly grown like jute plants as mentioned above in a separate field near CRRC (West Bengal, India). The adults were placed in a nylon net cage (40 × 30 × 30 cm^3) on the turgescent sesame leaves for egg-laying. Newly emerged first instar larvae (L I, F_1) were kept on the same sesame leaves for feeding at 27±1 °C, 70±10% RH and 12 h L : 12 h D photoperiod, and a light intensity of 1500 lux in a Biological Oxygen Demand (BOD) incubator (ADS, Kolkata, India) (Roy and Barik, 2013; Roy 2015a, b, 2017, 2019b, 2021a). Cut sesame leaf petioles were maintained in a moist piece of cotton wrapped with aluminium foil to prevent desiccation. Freshly cut leaves were provided replacing the wilting ones. Adults were fed with a 10% sucrose-in-tap-water solution soaked in cotton wool. Four generations (F_1–F_4) of *S. obliqua* were completed on sesame leaves to avoid any pre-adaptation to the jute plants used in bioassays. The 1 to 2 days old gravid females (F_3–F_4) were used for olfactory and oviposition bioassays, whereas 13–14-days old 5_{th} instar (L V F_4)larvae were used for feeding bioassays on jute.

Epicuticular wax analyses:

Extraction of leaf epicuticular waxes: Freshly collected mature jute leaves (14 to 20 days old) of ca. 100 g fresh weight corresponding to 1.788±0.148, 1.948±0.148, and 1.248±0.148 g $leaf^{-1}$ (mean ± SE) for white jute, tossa jute, and mesta jute, respectively (ESM Table 1), were dipped in 2 L n-hexane separately for 1 min at room temperature to extract the epicuticular wax which yielded slightly yellow extracts without traces of any chlorophyll (Mitra et al. 2020; Roy 2019a, 2021b). The crude extract was passed through filter paper Whatman No. 41 (Maidstone, UK), and hexane was evaporated at 27 °C until the sample became dry. The extraction was repeated three times, separately for each jute cultivar. The dry extract (semisolid) wax weighed 33.067±0.406, 36.333±0.636, and 28.867±0.406 mg 100 g^{-1} in white jute, tossa jute, and mesta jute leaves, respectively (ESM Table 1). Each crude extract was then dissolved in 40 ml n-hexane and divided into four equal portions (equivalent to 25 g of leaves). The first one was used for the identification and quantification of n-alkanes and FFAs, whereas the second, third, and fourth ones were purified and used for olfactory attraction, oviposition, and feeding bioassays, respectively. All solvents used were of analytical grade and purchased from E. Merck (Mumbai, India). All standard n-alkanes and FAs (> 99% purity) were purchased from Sigma-Aldrich (Darmstadt, Germany).

Identification and quantification of n-alkanes: One-half of the first portions of crude leaf extract of each jute cultivar was passed through a column of aluminum oxide (F-20 grade) and eluted with petroleum ether. The eluent was fractioned by Thin Layer Chromatography (TLC) on silica gel G (Sigma St. Louis, MO, USA) of 0.5 mm thickness by using carbon tetrachloride (CCl_4) as the mobile phase. A faint yellowish band appeared on the TLC plate and the plate was air-dried under laboratory conditions. The R_f (retardation factor) value (0.86) was compared with the R_f value of a mixture of synthetic n-alkanes between n-C_{10} to n-C_{40}. The single hydrocarbon band produced in each TLC plate was eluted from the silica gel layer with chloroform, which showed only stretching C-H bonds in IR spectroscopy (JASCO FT-IR, spectrophotometer, Tokyo, Japan). The purified alkane samples were used for gas chromatography-mass spectrometry (GC-MS) and GC-FID (flame ionization detector) for identification and quantification, respectively (Roy 2019a, 2021b). The extracts were analyzed with a Shimadzu GCMS-QP5050A (Koyeto, Japan) to produce electron ionization (EI) mass spectra using HP-5MS column for GCMS-EI analysis by using a specified oven temperature program: initially 80 °C for 2 min, then raised at 15 °C min^{-1} to 320 °C,finally held for 15 min (Roy 2019a, 2021b). The volume of the injected sample was 1 µl with a split ratio of 1 : 10. Identifications were made by comparison of spectra with library databases (NIST 2008) and also confirmed by comparison of their retention times (RTs) with those of standard n-alkanes (n-C_{10} to n-C_{40}) and the areas of each peak were converted into quantities of n-alkanes based on GC peak area of internal standard n-nonadecane (n-C_{19} at 100 ng $µl^{-1}$) (Roy 2019a, 2021b).

Identification and quantification of FFAs: The remaining half of the first portions of the crude leaf extract of each jute cultivar was mixed with diethyl ether and filtered through Whatman No. 41 filter paper. The extract was purified by TLC on silica gel G of 0.5 mm thickness by using n-butanol : acetic acid : water (4 : 1 : 5) as the mobile phase after discarding water. The band (R_f value of 0.78) was eluted from the silica gel layer with diethyl ether to get purified FFAs. Then, the purified FFAs were esterified with 3 ml BF_3-Methanol followed by warming for 5 min in a hot water bath at 50–60 °C, and then cooled to 4 °C. Hexane (40 ml) was added to this mixture followed by washing with saturated NaCl twice in a separating funnel. The aqueous layer of each sample was discarded and the hexane fraction was passed through 40 g of anhydrous Na_2SO_4. The esterified FFAs samples were used for GC-MS and GC-FID for the identification and quantification, respectively (Roy 2019a, 2021b).The extracts were analyzed with a Shimadzu GCMS-QP5050A to produce electron ionization (EI) mass spectra using an HP-5MS column for GCMS-EI analysis by setting a specified oven temperature program: initially at 120 °C for 2 min, then raised at the rate of 10 °C min^{-1} to 220 °C, and finally at 220 °C for 15 min (Roy 2019a, 2021b). The volume of the injected sample was 1 µl with a split ratio of 1:10. Identifications were made by the comparison of spectra with library databases (NIST 2008) and also confirmed by the comparison of their retention times (RTs) with those of methylated (esterified) standard FAs ($C_{10:0}$ to $C_{24:0}$). The areas of each peak were converted into quantities of FFAs based on GC peak area of internal standard methyl tricosanoate ($C_{23:0}$ at 100 ng μl^{-1}) (Roy 2019a, 2021b).

Bioassays:

*Chemicals:*Both n-alkanes and FFAs isolated from leaf epicuticular waxes of the three jute cultivars were prepared in leaf equivalent (μg^{-1} $leaf^{-1}$ ml^{-1}) amount dissolved in petroleum ether for different bioassays (olfaction, oviposition, and feeding). Petroleum ether was used as the control solvent because both adults and larvae were neither attracted nor deterred by it in preliminary bioassays. Individual synthetic n-alkanes, FFAs, and their mixtures mimicking the natural leaf wax (μg^{-1} $leaf^{-1}$ ml^{-1}) were prepared in petroleum ether. The de-waxed leaves for the bioassay were prepared by dipping freshly cut mature leaves (14 to 20 days old) in n-hexane for 1 min as described in the wax extraction paragraph above.

*Insects:*The F_3 onward generations of *S. obliqua* larvae and adults were collected from the mass rearing for different bioassays in the laboratory condition at 27±1 °C, 60±5% RH, and light intensity of 1500 lux. Newly emerged, 1-2 days old females were provisioned with water and starved for 12 h before use in the olfaction bioassay, and 10% sucrose solution was provided as food during the oviposition bioassay. Females were used in bioassay because they are responsible for finding a suitable site for oviposition by using different stimuli (visual, olfactory, tactile, and gustatory) for successful generations. The newly hatched 5_{th} instar larvae were provisioned with water and starved for 12 h before use for the feeding bioassay. Only 5_{th} instar larvae were used because they are most active and have the highest consumption rate among the instars. The larval bioassay was conducted to confirm the preference of the adult females in host plant selection to establish future generations. Females and 5_{th} instar larvae were selected and used once throughout the bioassays with three replications for each jute cultivar as described in Roy (2019a, 2021b).

Female olfaction: The effect of n-alkanes and FFAs as olfactory attractants was evaluated by different treatments under specified conditions (Roy et al. 2012a; Roy and Barik 2012b, 2014; Roy 2019a, 2021b). The behavioural responses of adult females were investigated in a Y-tube olfactometer: 10 cm long (l) stem and arms, 8 cm diameter (d), 60° Y angle (Roy 2019a, 2021b). The stem of the olfactometer was connected to a porous glass vial (d: 8.0 cm × l: 10.0 cm) in which test insects were released. Each arm of the olfactometer was connected to a glass micro kit adapter (d: 4.0 cm × l: 6.0 cm) fitted into a glass vial (d: 8.0 cm × l: 8.0 cm). The aerator producing airflow of 450 ml min^{-1}, which was first purified by passing through a charcoal filter and then adjusted to 150 ml min^{-1} in left and right glass vials through the micro kit adapters. All the connections between different parts of the setup consisted of silicon tubes. One milliliter of the solvent containing one leaf equivalent (µg $leaf^{-1}$ ml^{-1}) amount of identified n-alkanes and FFAs and their respective synthetic analogs were separately applied to Whatman no. 41 filter paper pieces (2 × 2 cm^2) as volatile sources, another one only with solvent (petroleum ether) as control, and allowed to evaporate the solvent in open space (1 min) under laboratory conditions. These filter papers were introduced into the glass vials attached to the olfactometer. One female of *S. obliqua* was introduced into the porous glass vial attached to the olfactometer (Roy 2019a, 2021b). The behavior of each female was observed for 3 min in the Y-tube. The increase in the observation time did not increase the number of responding insects. A threshold (“decision line”) was located at the middle of each arm of the Y-tube, and an individual crossing the line within 3 min from the release point with at least half the body was counted as a response. If the line was not crossed within the observation time, the run was treated as no response. To eliminate traces from previous trials, the tube was cleaned with petroleum ether followed by acetone and dried in a hot air oven at 50 ºC after 6 individuals were tested (Roy and Barik 2012b, 2014; Roy 2019a, 2021b). Each test with one volatile sample was conducted until a total of 72 (24 × 3) females had responded and after testing 12 insects while the position of the two arms was systematically changed (rotated

180°) to avoid any positional biases. The dual choice tests were conducted for the identified 20 n-alkanes (straight chain) and 14 FFAs individually in leaf equivalent (μg $leaf^{-1}$ ml^{-1}) amounts present in respective jute cultivars to find the most preferred chemicals having a minimum ≥ 70% insect response (ESM Table 2). These most preferred synthetic n-alkanes (n-C_{16}, n-C_{18}, n-C_{20}, n-C_{22}) and FFAs ($C_{16:1}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$) were used in mixture as well as in combination (4 n-alkanes + 5 FFAs) for all bioassays because they were more attractive than the individual compounds for all the jute species. Similar tests with natural n-alkanes, FFAs, their mixtures (n-alkanes + FFAs) along with mixtures of most preferred synthetic 4 n-alkanes, 5 FFAs, their combined mixture (4 n-alkanes + 5 FFAs) in leaf equivalent (μg $leaf^{-1}$ ml^{-1}) amount, were conducted in the same manner as for synthetic individual compounds with three replications in different treatments under defined conditions as follows:

Condition 1. Alkanes-treated filter paper vs. solvent with 2 treatments such as total natural n-alkanes and a mixture of the most preferred synthetic 4 n-alkanes present in the three jute cultivars (ESM Table 3, Table 3).

Condition 2. FFA-treated filter paper vs. solvent with 2 treatments such as total natural FFAs and a mixture of the most preferred synthetic 5 FFAs present in the three jute cultivars (ESM Table 3, Table 3).

Condition 3. Combined-mixture-treated filter paper vs. solvent with 2 treatments such as total natural wax (n-alkanes + FFAs) and a mixture of the most preferred synthetic wax (4 n-alkanes + 5 FFAs) mixture present in the three jute cultivars (ESM Table 3, Table 3).

Condition 4. Combined-synthetic-mixture-(4 n-alkanes + 5 FFAs)-treated leaf vs. solvent with 2 treatments such as intact leaf and de-waxed leaf of the three jute cultivars (ESM Table 3, Table 3).

The adult attraction index (AI%) was determined for the above 8 treatments under 4 conditions using the formula: $[\{(T-C)/(T+C)\} \times 100]$; where, T is the number of adult females attracted in various treatments (filter paper or jute leaf) and C is the number of adult females attracted to solvent in the control (filter paper or jute leaf) with a few modifications (Singh et al. 2011; Roy 2021b).

Female oviposition: The oviposition preference was assessed by using 3 groups of 24 pairs of newly emerged male and female *S. obliqua* (24 × 3 = 72 pairs) kept in glass chambers (40 × 40 × 40 cm^3). The natural and synthetic mixtures as in the adult olfaction bioassay were applied. The dual choice test was conducted for each treatment in the glass chambers covered with nylon net. The data were collected at a 24 h interval up to 96 h. For the choice experiments, each jute leaf or filter paper was marked separating it into vertically oriented two halves. One half was treated with the test compound and the other half was kept as a control. Each mixture was applied with a micropipette in leaf equivalent (μg $leaf^{-1}$ ml^{-1}) amount present in the respective jute cultivars and after evaporating the solvent, one pair of newly emerged adult moths (1 : 1 sex ratio) were released in each glass chamber. Each chamber was provided with 10% sucrose solution as food and kept in a BOD incubator as used for mass culture. The jute leaf or filter paper sheet of the three replicates with eggs was taken out from the glass chamber and eggs were counted at the black head stage comparing the different treatments and conditions as in female olfaction bioassay (ESM Table 4, Table 4). The oviposition preference index (OPI %) was determined for the 8 treatments under 4 conditions using the formula: $[\{(P-Q)/(P+Q)\} \times 100]$; where, P is the number of eggs laid at various treatments (leaf or filter paper) and Q is the number of eggs laid at control solvent (leaf or filter paper) with a few modifications (Singh et al. 2011; Roy 2021b).

Larval feeding: The larval feeding bioassay was conducted to trace the possible pairing between female oviposition preference and larval feeding choice. Freshly collected mature leaves of the three jute cultivars were tested for different treatments with intact vs. de-waxed leaves. The solvent on a de-waxed leaf was dried at 27 ± 1 °C before the larvae were released onto the leaves. Fifth instar (L V, F_4) larvae were selected for the experiment and placed separately in Petri dishes (9 cm in diameter) with intact and de-waxed jute leaves for different treatments. Each treatment was replicated three times and conducted with 72 (24 × 3) larvae per replication, having 24 larvae in each group for each jute species. Leaf desiccation was prevented by covering the bottom of each Petri dish with wet filter paper. Larvae were allowed to feed for 24 h and the consumed area (cm^2) was measured for 6 different treatments under 3 defined conditions (Table 5) as in adult olfaction (condition 1, 2 and 4) bioassay (ESM Table 3, Table 3). Conditions 1 and 2 were with the same treatments where filter paper were replaced by normal mature leaf of respective jute cultivars where as condition 3 were exclusively same as in adult olfaction (condition 4) bioassay (Table 5). The feeding index (FI%) was calculated for the 6 treatments under 3 conditions using the formula: $[\{(A-B)/(A+B)\} \times 100]$ where, A and B is the area consumed from the intact or de-waxed leaf treated with wax chemicals or solvent with a few modifications (Singh et al. 2011; Roy 2021b).

*Statistical analyses:*The data on total amounts of n-alkanes and FFAs were analyzed by one-way ANOVA followed by Tukey's HSD test. The data obtained for responses of *S. obliqua* to jute leaf epicuticular wax compounds and mixtures of their synthetic analogs were analyzed by Chi-squire (χ^2) test based on the null hypothesis whether the ratio of individual choosing the stimulus vs. the control differed significantly from 1 : 1 (Zar 1999). Insects that did not respond to any one of the treatments were excluded from the analyses. All the statistical analyses were conducted by using the software SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

Results

*Leaf epicuticular wax chemistry:*The n-hexane extracts of a single mature leaf (n > 52) of white jute (1.788±0.148 g, 52.148±0.847 cm^2), tossa jute (1.948±0.148 g, 58.726±0.794 cm^2), and mesta jute (1.248±0.148 g, 47.581±0.746 cm^2) yielded 1064.175±83.481 µg, 1187.578±70.683 µg, and 728.029±34.226 µg epicuticular wax, respectively (ESM Table 1). Out of the extracted waxes from a single leaf of white jute, tossa jute, and mesta jute represented by 360.628±23.779 µg, 451.570±21.825 µg, and 214.379±21.344 µg of n-alkanes and 75.741±3.594 µg, 75.766±1.763 µg, and 55.500±4.660 µg of FFAs, respectively, and remaining unidentified surface wax compounds (ESM Table 1). All the extracted n-alkanes and FFAs were differed significantly between the jute cultivars (one-way ANOVA, $F_{2,6} \geq 10.868$, $P \leq 0.010$) though their wax contents were without any significant (one-way ANOVA, $F_{2,6} = 0.243$, $P = 0.792$) differences (ESM Table 1).

*Alkanes in the leaf epicuticular waxes:*Total 27 different n-alkanes (20 straight chain + 7 branched chain) were identified having chain lengths between n-C_{14} to n-C_{36} and further expressed in leaf equivalent (µg $leaf^{-1}$) amount (Table 1). Among the 27 different n-alkanes, 25, 24, and 24 types of n-alkanes were identified from white jute, tossa jute, and mesta jute leaves, respectively (Table 1). Among them n-tetratriacontane (n-C_{34}) was predominant (144.397±6.971 µg $leaf^{-1}$) in tossa jute, whereas n-tetradecane (n-C_{14}) was in lowest amount (0.116±0.012 µg $leaf^{-1}$) in mesta jute (Table 1). All the identified amounts of n-alkanes differed significantly between the jute cultivars (one-way ANOVA, $F_{2,6} \geq 20.501$, $P \leq 0.002$; Table 1).

*FFAs in the leaf epicuticular waxes:*Total 14 different FFAs were identified having chain lengths between $C_{12:0}$ to $C_{22:0}$ and further expressed in leaf equivalent (µg $leaf^{-1}$) amount (Table 2). Out of 14 different FFAs, 14, 13, and 13 types of FFAs were identified from white jute, tossa jute, and mesta jute leaves, respectively (Table 2). Among the FFAs, trihexadecanoin acid ($C_{16:1}$) was predominant (37.034±0.848 µg $leaf^{-1}$), whereas, heptadecanoic acid ($C_{17:0}$) was detected in lowest amount (0.263±0.006 µg $leaf^{-1}$) in tossa jute (Table 2). All the identified FFAs differed significantly between the jute cultivars as in n-alkanes (one-way ANOVA, $F_{2,6} \geq 18.793$, $P \leq 0.003$; Table 2).

*Female attraction by leaf epicuticular wax compounds:*A series of olfactory bioassay (8 treatments under 4 defined conditions) were conducted to study the attraction index (AI%) of *S. obliqua* females towards leaf cuticular wax chemicals (n-alkanes and FFAs) in comparison with most preferred respective synthetic analogs (4 n-alkanes and 5 FFAs) in leaf equivalent amount (µg $leaf^{-1}$) present in the selected jute cultivars (ESM Table 3, Table 3).

Condition 1. Synthetic mixtures of the 4 n-alkanes (n-C_{16}, n-C_{18}, n-C_{20}, n-C_{22}) were more preferred than the natural n-alkanes in all kinds of jute leaves, because of the presence of less preferred n-alkanes in natural mixtures (ESM Table 3, Table 3). The AI (%) values for the synthetic mixtures at leaf equivalent (µg $leaf^{-1}$) amounts (133.508±3.727 µg, 57.526±1.836 µg, and 17.317±2.835 µg, respectively) in white jute, tossa jute, and mesta jute were 18.982±2.370%, 14.815±2.137%, and 10.648±2.095%, respectively (Table 3).

Condition 2. Synthetic mixtures of the 5 FFAs ($C_{16:1}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$) were more preferred to the natural FFAs in all kinds of jute leaves, because of the presence of less preferred FFAs in natural mixtures (ESM Table 3, Table 3). The AI(%) values for the synthetic mixtures corresponding to leaf equivalent (µg $leaf^{-1}$) amounts (61.701±2.713 µg, 62.251±1.603 µg, and 33.250±2.059

µg, respectively) in white jute, tossa jute, and mesta jute were 45.370±2.148%, 42.593±2.076%, and 38.426±2.073%, respectively (Table 3).

Condition 3. Synthetic combined mixtures (4 n-alkanes + 5 FFAs) were preferred to the naturally combined mixtures (n-alkanes + FFAs) in all kinds of jute leaves, because of less preferred n-alkanes and FFAs in natural mixtures (ESM Table 3, Table 3). The AI (%) values for the synthetic-mixtures (4 n-alkanes+5 FFAs) corresponding to leaf equivalent (µg $leaf^{-1}$) amounts (195.209±2.950 µg, 119.777±1.857 µg, and 50.567±3.508 µg, respectively) in white jute, tossa jute and mesta jute were 68.519±1.225%, 66.667±1.389%, and 62.963±2.816%, respectively (Table 3).

Condition 4. The female AI (%) were significantly ($P < 0.05$) higher for combined synthetic wax (4 n-alkanes + 5 FFAs) mixtures treated intact leaves of white jute (83.796±1.669% per 1259.384±72.213 µg wax chemicals), tossa jute (73.148±2.078% per 1307.355±66.820 µg wax chemicals), and mesta jute (77.315±4.560% per 778.596±29.359 µg wax chemicals) compared to the de-waxed leaves of respective jute cultivars (Table 3).

The attraction (%) to any of the treatments compared to the controls was always significantly higher (Chi-Square test, $\chi^2 \geq 5.480$, $df = 1$, $P < 0.05$), except for condition 1 ($\chi^2 \leq 3.571$, $df = 1$, $P > 0.05$) (Table 3). All AI (%) values were without any significant (one-way ANOVA, $F_{2,6} \leq 1.895$, $P \geq 0.230$) differences among the jute crops (Table 3). In all treatments, the AI (%) values for the jute crops can be arranged in the order of white jute> tossa jute> mesta jute, and the comparison of means by Tukey's HSD test were also differ significantly in AI (%) values ($P > 0.05$) with a few deviations (Table 3). The AI (%) depending on the conditions ranged in the order of condition 4 > condition 3 > condition 2 > condition 1 (ESM Table 3, Table 3). Among the treatments, the combined-synthetic-mixture treated intact leaves showed the highest attractiveness because of the respective amounts of wax chemicals in the jute crops (ESM Table 3, Table 3).

*Oviposition:*The oviposition bioassays were conducted in a total of 8 treatments under 4 defined conditions to determine the OPI (%) of *S. obliqua* (gravid females) as in adult olfaction for the selected jute cultivars (ESM Table 4, Table 4).

Condition 1. Synthetic mixtures of the 4 n-alkanes were more preferred than the natural n-alkanes present in the all jute crops as in adult olfaction (ESM Table 4, Table 4). OPI (%) values for the synthetic mixtures at leaf equivalent (µg $leaf^{-1}$) amounts (same as adult olfaction) in white jute, tossa jute, and mesta jute were 41.667±8.333%, 26.732±2.347%, and 37.771±6.429%, respectively (Table 4).

Condition 2. Similarly, synthetic mixtures of the 5 FFAs were more preferred than the natural FFAs present in the jute crops due to the same reasons as in adult olfaction (ESM Table 4, Table 4). OPI (%) values for the synthetic mixtures at leaf equivalent (µg $leaf^{-1}$) amounts (same as adult olfaction) in white jute, tossa jute, and mesta jute were 37.374±8.694%, 49.801±4.925%, and 23.148±6.481%, respectively (Table 4).

Condition 3. Synthetic combined mixtures (4 n-alkanes + 5 FFAs) were also more preferred than the natural wax mixture (n-alkanes + FFAs) present in the jute crops due to the same reasons as in adult olfaction (ESM Table 4, Table 4). OPI (%) values for the synthetic mixtures at leaf equivalent (µg $leaf^{-1}$) amounts (same as adult olfaction) in white jute, tossa jute, and mesta jute were 63.981±5.250%, 62.594±4.565%, and 57.879±4.077%, respectively (Table 4).

Condition 4. The OPI (%) were significantly ($P < 0.05$) higher for combined synthetic wax (4 *n*-alkanes + 5 FFAs) mixtures treated intact leaves of white jute (80.278±4.092%), tossa jute (78.307±4.132%), and mesta jute (69.167±3.632%) compared to the de-waxed leaves of respective jute cultivars at same leaf equivalent (µg $leaf^{-1}$) amounts as in adult olfaction (Table 4).

The oviposition choice (%) towards any of the treatments was always significantly higher than towards controls in condition 4 and combined synthetic wax (4 *n*-alkanes + 5 FFAs) mixtures in condition 3 (Chi-square test, $\chi^2 \geq 5.706$, $df = 1$, $P < 0.05$) (Table 4). All the OPI (%) values were without any significant (one-way ANOVA, $F_{2,6} \leq 2.243$, $P \geq 0.187$) differences between the jute crops except synthetic FFAs mixtures in condition 2 (one-way ANOVA, $F_{2,6} = 7.034$, $P = 0.027$) because all the crops were potent host plants for *S. obliqua* (ESM Table 4, Table 4). The OPI (%) values for the jute crops can be arranged in the same order (white jute> tossa jute> mesta jute) as in adult olfaction, and the comparison of means by Tukey's HSD test were also differ significantly ($P > 0.05$) in OPI (%) values with few deviations (Table 4). The OPI (%) depending on the conditions ranged in the same order (condition 4 > condition 3 > condition 2 > condition 1) as in adult olfaction (ESM Table 4, Table 4). Among the treatments, the combined-synthetic-mixture-treated intact leaves showed the highest OPI (%) because of the respective amounts of wax chemicals in the jute crops (Table 4).

*Larval feeding:*The choice test was conducted with 5^{th}-instar larvae (6 treatments under 3 defined conditions) to find the larval FI (%) towards leaf epicuticular wax chemicals (n-alkanes and FFAs) in leaf equivalent amount (μg $leaf^{-1}$) present in the selected jute crops (Table 5).

Condition 1. Synthetic mixtures of the same 4 n-alkanes (most preferred in adult olfaction and oviposition) were more preferred than natural n-alkanes present in the jute crops because of the same reasons as in adults (Table 5). Similarly, larval FI (%) for the synthetic mixtures (4 n-alkanes) at leaf equivalent amounts (μg $leaf^{-1}$) in white jute, tossa jute, and mesta jute (1197.683±15.610 μg, 1245.104±13.503 μg, and 745.346±12.610 μg wax chemicals, respectively) were 36.573±2.938%, 35.063±1.655%, and 35.779±2.220%, respectively (Table 5).

Condition 2. Synthetic mixtures of the 5 FFAs (most preferred in adult olfaction and oviposition) were more preferred than natural FFAs present in the jute crops because of the same reasons as in adults (Table 5). Similar to the results with adults, larval FI (%) for the synthetic-mixtures (5 FFAs) at leaf equivalent amounts (μg $leaf^{-1}$) in white jute, tossa jute, and mesta jute (1125.876±12.713 μg, 1249.829±11.603 μg, and 761.279±12.106 μg wax chemicals, respectively) were 37.550±3.863%, 36.382±2.773%, and 36.715±3.075%, respectively (Table 5).

Condition 3. Combined-synthetic-mixtures (4 n-alkanes + 5 FFAs) treated intact leaves were more preferred than de-waxed leaves of the jute crops due to the same reasons as demonstrated for the adults (Table 5). Similar to results obtained with adults, the larval FI (%) values for the synthetic mixtures (4 n-alkanes + 5 FAs) at same leaf equivalent (μg $leaf^{-1}$) amounts of respective jute crops as in condition 4 of adult olfaction as well as oviposition tests were 38.854±5.163%, 36.452±2.827%, and 37.952±4.276%, respectively (Table 5).

The larval feeding (%) towards all treatments were always without significant (Chi-square test, $\chi^2 \leq 3.537$, $df = 1$, $P > 0.05$) differences due to presence of potent host leaves in all treatments (Table 5). All the FI (%) values did not differ significantly (one-way ANOVA, $F_{2,6} \leq 0.270$, $P \geq 0.772$) among the jute crops (Table 5). The FI (%) values for the jute crops can be arranged in the order of white jute> mesta jute> tossa jute and the comparison of means by Tukey's HSD test were also differ significantly ($P >$ 0.05) in FI (%) values with few deviations due to different phytoconstituents of the respective jute leaves (Table 5). The FI (%) depending on the conditions ranged in the same order (condition 3 > condition 2 > condition 1) like adults (Table 5). Among the treatments, the combined-synthetic-mixture-treated intact leaves showed the highest FI (%) because of the respective amounts of preferred wax chemicals as well as other phytochemical regime in the respective jute crops (Table 5).

Considering all the above bioassays experiments (olfaction, oviposition, and larval feeding), the most stimulating synthetic combination mixture was represented by 4 n-alkanes and 5 FFAs in mature leaf equivalent (μg $leaf^{-1}$) amounts of all the selected jute cultivars.

Discussions

The leaf surface of the selected fibre crops represents different patterns of epicuticular wax deposition as in other studies (Debnath et al. 2021; Jetter et al. 2000; Kim et al. 2009; Kumari 2020; Roy et al. 2012b; Silva et al. 2017; Roy 2019a). These surface characteristics of the jute leaves were provided olfactory and tactile stimuli for suitable oviposition site selection by *S. obliqua* like other lepidopterans such as, *Amyelois transitella* Walker, *Choristoneura fumiferana* Clemens, *Ostrinia nubilalis* Hübner, *Diacrisia casignetum* Kollar, *Helicoverpa armigera* Hübner, *Spodoptera litura* Fabricius, etc. (Grant et al. 2000; Li and Ishikawa 2006; Phelan et al. 1991; Roy 2019a, 2021b; Udayagiri and Mason 1997). In total, 27 types of n-alkanes from n-C_{14} to n-C_{36} (20 straight chain + 7 branched chain) and 14 types of FFAs (11 saturated + 3 unsaturated) from $C_{12:0}$ to $C_{22:0}$ were detected in the leaf epicuticular wax of the three jute crops (white jute, tossa jute, and mesta jute) as major components with significant variations in their respective quantity (μg $leaf^{-1}$). These findings are similar to previous reports for other plants like, *Vigna radiata* (L.) R. Wilczek (Fabaceae), *Sesamum indicum* (Pedaliaceae), *Momordica charantia* (L.) (Cucurbitaceae), *M. cochinchinensi*s (Lour.) (Cucurbitaceae), *Ludwigia adscendens* (L.) H. Hara (Onagraceae), *L. octavalvis* (Jacq.) P.H. Raven (Onagraceae), *Polygonum orientale* (L.) (Polygonaceae), *Lathyrus sativus* (L.) (Fabaceae), etc. (Malik and Barik 2015; Mitra et al. 2017; Mobarak et al. 2020a; Mukharjee et al. 2014; Roy et al. 2012a; Roy, 2021b; Sarkar et al. 2013a, b). Among the identified n-alkanes and FFAs of the studied jute crops, n-C_{34} (144.397±6.971 μg $leaf^{-1}$) and $C_{16:1}$ (37.034±0.848 μg $leaf^{-1}$) of tossa jute leaf were most abundant. Previous studies suggested that various n-alkanes and FFAs were predominated in the leaf epicuticular waxes of various plant species (Das et al. 2019; Debnath et al. 2021; Karmakar et al. 2016; Li and Ishikawa 2006; Malik et al. 2015, 2017; Mukherjee et al. 2014, 2015; Mobarak et al. 2020a; Roy 2021b). Variations in the composition of leaf epicuticular wax compounds occur between plant species and even within different cultivars (Debnath et al. 2021; Jetter et al. 2000; Mitra et al. 2020; Mobarak et al. 2020a; Roy 2021b; Wang et al. 2015). Leaf surface wax of *Fatsia japonica* (Thunb.) Decne. & Planch. (Araliaceae) revealed the presence of 18 n-alkanes from n-C_{16} to n-C_{33} and 14 FFAs from $C_{9:0}$ to $C_{22:0}$, where n-C19 and C16:0, respectively, were most abundant (Li and Ishikawa 2006). Epicuticular wax of mature sunflower (*H. annuus* cv. PAC-36) leaves contained 9 n-alkanes (n-C_{24} to n-C_{33}) and 13 FFAs ($C_{12:0}$ to $C_{20:0}$) where, n-C_{29} and $C_{18:2}$, respectively were most predominant (Roy and Barik 2012b, 2014). Whereas, in *M. charantia* L. (Cucurbitaceae) 20 n-alkanes (n-C_{15} to n-C_{36}) were identified and *n*-C_{33} was predominant (Sarkar et al. 2013a). Mature leaf surface wax of *M. cochinchinensis* Spreng (Cucurbitaceae) revealed the presence of 20 n-alkanes (n-C_{15} to n-C_{35}) (Mukherjee et al. 2015). In creeping cucumber, *Solena amplexicaulis* (Lam.), leaf surface waxes revealed 18 n-alkanes (n-C_{15} to n-C_{36}) and 14 FFAs ($C_{12:0}$ to $C_{22:0}$) (Karmakar et al. 2016). Mature leaf surface waxes of *P. orientale* L. (Polygonaceae) weed revealed 19 n-alkanes (n-C_{15} to n-C_{33}) and 15 FFAs ($C_{12:0}$ to $C_{21:0}$) (Malik et al. 2015, 2017). Whereas, two rice-field weeds, *Commelina benghalensis* L. and *Murdannia nudiflora* (L.) revealed 20 n-alkanes (C_{14} to C_{36}) and 13 FFAs ($C_{12:0}$ to $C_{22:0}$) where, n-C_{15} and $C_{16:1}$ were predominant (Das et al. 2019). In the leaf surface wax of grass pea, *L. sativus* L. cv. Nirmal B-1 and BIO L 212, (Fabaceae) total, 18 n-alkanes (n-C_{15} to n-C_{36}) and 14 FFAs ($C_{12:0}$ to $C_{22:0}$) were detected where, n-C_{15} and $C_{16:1}$, respectively, were most predominant (Mitra et al. 2020). In green gram (*V. radiata* cv. PDM) 20 n-alkanes (n-C_{15} to n-C_{36}) and 13 FFAs ($C_{12:0}$ to $C_{21:0}$) were identified from their leaf cuticular wax and among them n-C_{25} and $C_{16:1}$, respectively were most abundant (Mobarak et al. 2020a). Leaf cuticular wax of sesame (*S. indicum*, cv. Savitri and Nirmala) indicated the presence of 14 n-alkanes (n-C_9 to n-C_{44}) and 12 FFAs ($C_{9:0}$ to $C_{20:0}$) where, n-C_{26} and $C_{18:1}$, respectively were most predominant (Roy 2021b). Moreover, 20 n-alkanes (*n*-C_{14} to *n*-C_{36}) and 13 FFAs ($C_{12:0}$ to $C_{21:0}$) were detected in the leaf surface waxes of three *Trichosanthes anguina* L. cultivars (MNSR-1, Baruipur Long, and Polo No.1) and among them n-C_{17} and $C_{18:0}$ were predominant (Debnath et al. 2021). Similarly, leaf surface wax of white jute (*C. capsularis* cv. Sonali [JRC-321]) contain 18 n-alkanes (n-C_{16} to n-C_{36}) and 13 FFAs ($C_{12:0}$ to $C_{20:0}$) and among them n-C_{29} and $C_{18:1}$, respectively, were most abundant (Roy 2019a). Moreover, the above-mentioned n-alkanes and FFAs can act as short-range attractants as well as other behavioural responses for different insect pests of respective host plants (Das et al. 2019; Debnath et al. 2021; Karmakar et al. 2016; Li and Ishikawa 2006; Malik and Barik 2015, 2017; Mitra et al. 2017, 2019, 2020; Mobarak et al. 2020a; Roy 2019a, 2021b)

The short-distance behavioural responses of different insects have been previously evaluated through different olfactometers (V-shaped, multi-tube, six-arm, Y-tube, etc. (Koschier et al. 2000; Mitra et al. 2020; Roy, 2019a; Turlings et al. 2004). The Y-tube olfactometer used in present bioassays revealed clear olfactory responses of *S. obliqua* females to n-alkanes and FFAs present in leaf waxes of three fibre crops. After reaching near the host plant, n-alkanes and FFAs acted as short-range attractants which also facilitated feeding induction in the larvae and oviposition in gravid females of *S. obliqua*. In other instances, two FFAs ($C_{18:1}$, $C_{18:2}$) act as host finding and oviposition cues for the navel orange worm, *Amyelois transitella* (Walker) (Lepidoptera, Pyralidae) (Phelan et al. 1991). Similarly, FFAs from $C_{8:0}$ to $C_{12:0}$, $C_{18:1}$ and $C_{18:2}$ in the epicuticular waxes of *Picea* and *Abies* spp. were also served as oviposition stimulants for the spruce budworm *Choristoneura fumiferana* (Clemens) (Lepidoptera, Tortricidae) (Grant et al. 2000). Whereas, 5 long-chain n-alkanes (n-C_{26} to n-C_{30}) present in the epicuticular wax of corn Zea *mays* L. (Poaceae) and Japanese knotweed *Fallopia japonica* (Houtt.) Ronse Decr. (Polygonaceae) leaves act as oviposition stimulants in the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera, Pyralidae) (Li and Ishikawa 2006; Udayagiri and Mason 1997). Synthetic blend of 5 n-alkanes (n-C_{18}, n-C_{23}, n-C_{24}, n-C_{28}, and n-C_{32}) and 6 FFAs ($C_{16:0}$, $C_{16:1}$, $C_{18:0}$, $C_{18:1}$, $C_{18:2}$, and $C_{18:3}$) in sunflower leaf equivalent amount attracted the arctiid moth, *D. casignetum* (Roy and Barik 2012b, 2014). A synthetic blend of 9 n-alkanes (n-

C_{19-21}, n-C_{25-26}, n-C_{28-29}, n-C_{31} and n-C_{33}) at *M. charantia* leaf equivalent amount was most attractive to the female insect, *Epilachna dodecastigma* (Wied.) (Sarkar et al. 2013a). A synthetic blend of 4 n-alkanes (n-C_{19}, n-C_{31}, n-C_{33}, n-C_{35}) and 4 FFAs ($C_{14:0}$, $C_{16:1}$, $C_{18:1}$, $C_{19:0}$) in leaf equivalent amount of *M. cochinchinensis*, respectively showed highest attraction to female *Aulacophora foveicollis* Lucas (Coleoptera: Chrysomelidae) (Mukherjee et al. 2014, 2015). Similarly, *A. foveicollis* Lucas displayed highest attraction to a synthetic mixture of n-C_{15}, n-C_{29}, $C_{16:0}$, $C_{18:0}$, $C_{18:3}$ at leaf equivalent amount of *S. amplexicaulis* (Karmakar et al. 2016). The rice-field weed, *L. adscendens* L. (Onagraceae) leaves revealed 3 prevailing saturated fatty acids (i.e., $C_{14:0}$, $C_{16:0}$, and $C_{18:0}$) in attraction of a flea beetle, *Altica cyanea* (Weber) (Coleoptera: Chrysomelidae), females at different concentrations (Roy et al. 2012a). Similarly, the flea beetle (*A. cyanea*) also showed attraction and oviposition to a synthetic blend of n-C_{16}, n-C_{18}, n-C_{20}, n-C_{23}, $C_{16:0}$, $C_{18:3}$, in 0.25 mature leaf equivalent surface waxes of *L. octovalvis* (Jacq.) Raven (Onagraceae) (Mitra et al. 2017). A synthetic blend of 10 n-alkanes (n-C_{16-18}, n-C_{20-21}, n-C_{23-24}, n-C_{26}, n-C_{28}, n-C_{31}) and 7 FFAs ($C_{12:0}$, $C_{14:0}$, $C_{15:0}$, $C_{16:1}$, $C_{17:0}$, $C_{19:0}$, $C_{20:0)}$ at leaf equivalent amount of *P. orientale* L. indicated highest attraction of the insect, *Galerucella placida* Baly (Coleoptera: Chrysomelidae) (Malik et al. 2015, 2017). Even, a synthetic blend of 4 n-alkanes (n-C_{22-23}, n-C_{25}, n-C_{27}) and 4 FFAs ($C_{13:0}$, $C_{16:1}$, $C_{18:2}$, $C_{20:0}$) in leaf equivalent amount of *C. benghalensis* and *M. nudiflora*, respectively served as short-range attractant and oviposition stimulant in *Lema praeusta* (Fab.) (Coleoptera: Chrysomelidae). (Das et al. 2019). In the grass pea, *L. sativus* L., 5 n-alkanes (n-C_{15}, n-C_{22}, n-C_{25}, n-C_{27}, n-C_{33}) and 2 FFAs ($C_{13:0}$, $C_{18:2}$) in mixture acted as attractants and stimulated the emergence of nymphs in *Aphis craccivora* Koch (Hemiptera: Aphididae) at leaf equivalent amount (Mitra et al. 2020). Even, olfactory attraction, oviposition and feeding preference of 3 generalist pests (*S. obliqua* Walker, *Helicoverpa armigera* Hübner, and *Spodoptera litura* Fabricius) were maximum towards the combined mixture of 4 n-alkanes (n-C_{16}, n-C_{22}, n-C_{24}, n-C_{26}) and 3 FFAs ($C_{12:0}$, $C_{14:0}$, $C_{18:1}$) in sesame (cv. Savitri) leaf equivalent amount (Roy, 2021b). Moreover, a synthetic blend of n-C_{17}, n-C_{20}, n-C_{26} and $C_{18:0}$ in one leaf equivalent surface wax of *T. anguina* L. (cv. MNSR-1) was acted as short-range attractants and oviposition stimulants in *Diaphania indica* (Lepidoptera, Crambidae) (Debnath et al. 2021). Whereas, a synthetic combined mixture of 4 n-alkanes (n-C_{17}, n-C_{18}, n-C_{27}, n-C_{29}) and 5 FFAs ($C_{16:0}$, $C_{16:1}$, $C_{18:1}$, $C_{18:2}$, $C_{18:3}$) in white jute (*C. capsularis* cv. Sonali [JRC-321]) leaf equivalent amount was most attractive to *D. casignetum* adults, whereas the same mixture excluding 2 n-alkanes (n-C_{27}, n-C_{29}) also caused a signi cant oviposition preference (Roy 2019a).

Similarly, in the present study, 4 n-alkanes (n-C_{16}, n-C_{18}, n-C_{20}, n-C_{22}) and 5 FFAs ($C_{16:1}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$) in a combined mixture at leaf equivalent (μg g^{-1} leaf) amounts (195.209±2.950 μg, 119.777±1.857 μg, and 50.567±3.508 μg, respectively) in white jute, tossa jute, and mesta jute, respectively acted as short-range olfactory attractants, oviposition stimulants and larval feeding stimulant in *S. obliqua*. The most stimulating synthetic combination mixture was represented by 4 n-alkanes (133.508±3.727 μg) containing n-C_{16} (27.254±1.801 μg), n-C_{18} (40.741±2.692 μg), n-C_{20} (35.993±2.378 μg), n-C_{22} (29.520±1.950 μg), and 5 FFAs (61.701±2.713 μg) containing $C_{16:1}$ (24.846±1.167 μg), $C_{16:0}$ (14.801±0.695 μg), $C_{18:0}$ (1.628±0.076 μg), $C_{20:0}$ (3.938±0.185 μg), $C_{22:0}$ (16.488±0.775 μg) at leaf equivalent (μg $leaf^{-1}$) amount present in mature white jute leaves. Moreover, this combined-synthetic-mixture (4 n-alkanes + 5 FFAs [195.209±2.950 μg $leaf^{-1}$]) treated intact white jute leaves (mature) showed highest adult AI (%), OPI (%), and larval FI (%) of 83.796±1.669%, 80.278±4.092%, and 38.854±5.163%, respectively, over the other treatments as well as other jute crops. Similarly, Mobarak et al. (2020a) recorded that females of *S. obliqua* were attracted towards a synthetic blend of 4 n-alkanes (n-C_{25}, n-C_{27}, n-C_{29}, n-C_{36} [176.7 μg]) and 3 FFAs ($C_{16:1}$, $C_{18:0}$, $C_{18:3}$ [43.2 μg]) present in the leaf surface waxes of green gram (cv. PDM). Moreover, this combined-synthetic-mixture (4 n-alkanes + 5 FFAs [195.209±2.950 μg $leaf^{-1}$]) treated intact white jute leaves (mature) showed highest adult AI (%), OPI (%), and larval FI (%) of 83.796±1.669%, 80.278±4.092%, and 38.854±5.163%, respectively, over the other treatments as well as other jute crops.

Thus, this finding can explain how the *S. obliqua* females choose oviposition sites on their potential hosts (white jute> tossa jute> measta jute) by using different sensory modalities [visual (shape and colour), olfactory (n-alkanes and FFAs as semiochemicals), tactile (leaf surface ultrastructure), and gustatory (leaf surface wax)] towards a better survival and growth of their neonates, as reported for other insects (Carlsson et al. 1999; Mitra et al. 2017, 2019, 2020; Roy 2019a, 2021b). The behavioural responsiveness of the gravid females was also comparable to that of larval feeding preferences. According to preference performance hypothesis (PPH), *S. obliqua* females maximize the population fitness by laying eggs on their preferred host plants (white jute> tossa jute> measta jute) where their offspring perform best like other butterflies and moths (Birke and

Aluja 2018; Roy 2019a; Griese et al. 2020). So, the present study suggests that the synthetic blends of 4 n-alkanes (n-C_{16}, n-C_{18}, n-C_{20}, n-C_{22}) and 5 FFAs ($C_{16:1}$, $C_{16:0}$, $C_{18:0}$, $C_{20:0}$, $C_{22:0}$) of respective jute crops can be used as lures to develop baited traps as a promising method for IPM of *S. obliqua*. Further, the study also supports to reduce indiscriminate use of any usual chemical control measures for sustainable management of *S. obliqua* for successful jute cultivation in the near future.

Declarations

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Tables

Table 1 Composition of n-alkanes (μg $leaf^{-1}$) in plant surface waxes (Mean±SE, n=3) of three selected host (white jute, *Corchorus capsularis*, tossa jute, C*. olitorius* and mesta jute, *Hibiscus cannabinus* [Malvaceae]) plants determined during their growing season in 2020-2021.

Alkanes (μg/leaf)	White Jute	Tossa Jute	Mesta Jute	$F_{2,6}$	*P*
n-Tetradecane (n-C14)	0.785±0.052^a	0.325±0.016^b	0.116±0.012^c	114.480	<0.001
n-Pentadecane (n-C15)	8.662±0.572^a	2.029±0.098^b	1.266±0.126^c	140.608	<0.001
n-Hexadecane (n-C16)	27.254±1.801^a	11.099±0.536^b	3.203±0.319^c	124.166	<0.001
n-Octadecane (n-C18)	40.741±2.692^a	17.179±0.829^b	5.305±0.528^c	118.833	<0.001
n-Eicosane (n-C20)	35.993±2.378^a	16.211±0.783^b	4.872±0.485^c	114.435	<0.001
n-Docosane (n-C22)	29.520±1.950^a	13.037±0.629^b	3.937±0.392^c	115.874	<0.001
n-Tricosane (n-C23)	2.162±0.143^a	1.166±0.056^b	0.131±0.013^c	130.268	<0.001
n-Tetracosane (n-C24)	7.696±0.509^a	1.827±0.088^b	0.220±0.022^c	174.120	<0.001
n-Pentacosane (n-C25)	23.262±1.537^a	10.072±0.486^b	3.287±0.327^c	114.393	<0.001
n-Hexacosane (n-C26) Branch	4.675±0.309^a	–	–	229.065	<0.001
n-Hexacosane (n-C26)	7.110±0.470^a	2.799±0.135^b	0.581±0.058^c	136.477	<0.001
n-Heptacosane (n-C27)	18.384±1.215^a	7.833±0.378^b	2.469±0.246^c	117.156	<0.001
n-Octacosane (n-C28) Branch	1.811±0.120^a	–	–	229.065	<0.001
n-Octacosane (n-C28)	9.481±0.626^a	11.322±0.547^b	4.495±0.447^c	41.996	<0.001
n-Nonacosane (n-C29)	13.426±0.887^a	7.250±0.350^b	2.418±0.241^c	94.419	<0.001
n-Triacontane (n-C30) Branch	3.256±0.215^a	–	–	229.065	<0.001
n-Triacontane (n-C30)	14.032±0.927^a	25.373±1.225^b	11.493±1.144^c	44.670	<0.001
n-Hentriacontane (n-C31)	9.441±0.624^a	7.359±0.355^b	3.046±0.303^c	52.565	<0.001
n-Dotriacontane (n-C32) Branch	9.438±0.624^a	3.284±0.159^b	1.649±0.164^c	114.770	<0.001
n-Dotriacontane (n-C32)	24.724±1.634^a	82.465±3.981^b	40.862±4.067^c	75.952	<0.001
n-Tritriacontane (n-C33)	7.832±0.518^a	15.840±0.765^b	7.719±0.768^a	45.087	<0.001
n-Tetratriacontane (n-C34) Branch	12.191±0.805^a	11.741±0.567^b	6.616±0.658^c	20.501	0.002
n-Tetratriacontane (n-C34)	33.082±2.186^a	144.397±6.971^b	77.921±7.756^c	82.899	<0.001
n-Pentatriacontane (n-C35) Branch	–	1.585±0.077^a	0.801±0.080^b	154.329	<0.001
n-Pentatriacontane (n-C35)	6.924±0.457^a	17.402±0.840^b	9.291±0.925^c	51.183	<0.001
n-Hexatriacontane (n-C36) Branch	–	5.796±0.280^a	3.405±0.339^b	131.776	<0.001
n-Hexatriacontane (n-C36)	8.841±0.584^a	34.199±1.651^b	19.254±1.916^c	72.320	<0.001

Note: Within rows and columns means followed by same letters (lower and upper case, respectively) are not significantly different ($P \geq 0.05$) by Tukey's HSD test.

Table 2 Composition of free fatty acids (FFAs) (µg $leaf^{-1}$) in plant surface waxes (Mean±SE, n=3) of three selected host (white jute, *Corchorus capsularis*, tossa jute, C. *olitorius* and mesta jute, *Hibiscus cannabinus* [Malvaceae]) plants determined during their growing season in 2020-2021.

Free Fatty Acids (µg/leaf)	White Jute	Tossa Jute	Mesta Jute	$F_{2,6}$	*P*
Dodecanoic acid (C12:0)	$2.679{\pm}0.126^{a}$	$0.267{\pm}0.006^{b}$	$1.200{\pm}0.100^{c}$	171.210	<0.001
Tridecanoic acid (C13:0)	$1.440{\pm}0.068^{a}$	$0.777{\pm}0.018^{b}$	$2.868{\pm}0.240^{c}$	54.999	<0.001
Tetradecanoic acid (C14:0)	$0.952{\pm}0.045^{a}$	$2.238{\pm}0.051^{b}$	$5.532{\pm}0.462^{c}$	76.726	<0.001
Pentadecenoin acid (C15:0)	$1.481{\pm}0.070^{a}$	$1.991{\pm}0.046^{b}$	$3.044{\pm}0.254^{c}$	26.628	0.001
Trihexadecanoin acid (C16:1)	$24.846{\pm}1.167^{a}$	$37.034{\pm}0.848^{b}$	$21.777{\pm}1.819^{c}$	36.242	<0.001
Hexadecanoic acid (C16:0)	$14.801{\pm}0.695^{a}$	$5.226{\pm}0.120^{b}$	$4.273{\pm}0.357^{c}$	162.635	<0.001
Heptadecanoic acid (C17:0)	$0.866{\pm}0.041^{a}$	$0.263{\pm}0.006^{b}$	$1.551{\pm}0.130^{c}$	67.443	<0.001
Trioctadecadienoin acid (C18:2)	$0.268{\pm}0.013^{a}$	–	–	452.966	<0.001
Trioctadecenoin acid (C18:1)	$0.474{\pm}0.022^{a}$	$1.581{\pm}0.036^{b}$	$0.556{\pm}0.046^{a}$	287.977	<0.001
Octadecanoic acid (C18:0)	$1.628{\pm}0.076^{a}$	$3.293{\pm}0.075^{b}$	$1.463{\pm}0.122^{a}$	116.105	<0.001
Nonadecanoic acid (C19:0)	$3.425{\pm}0.161^{a}$	$3.854{\pm}0.088^{a}$	$6.966{\pm}0.582^{b}$	30.100	0.001
Eicosanoic acid (C20:0)	$3.938{\pm}0.185^{a}$	$2.810{\pm}0.064^{b}$	$2.576{\pm}0.215^{b}$	18.793	0.003
Heneicosanoic acid (C21:0)	$2.376{\pm}0.112^{a}$	$2.485{\pm}0.057^{b}$	$0.468{\pm}0.039^{b}$	223.992	<0.001
Docosanoic acid (C22:0)	$16.488{\pm}0.775^{a}$	$13.888{\pm}0.318^{b}$	$3.161{\pm}0.264^{c}$	194.174	<0.001

Note: Within rows and columns means followed by same letters (lower and upper case, respectively) are not significantly different (P≥0.05) by Tukey's HSD test.

Table 3 Adult olfactory attraction (Mean±SE, n=72) of a generalist jute pest (*Spilosoma obliqua* Walker; Arctiidae) to plant surface wax chemicals (n-alkanes and FFAs in leaf equivalent amount [µg $leaf^{-1}$]) of three selected host (white jute, *Corchorus capsularis*, tossa jute, C. *olitorius* and mesta jute, *Hibiscus cannabinus* [Malvaceae]) plants under specified bioassay conditions.

Adult attraction conditions	White Jute		Tossa Jute		Mesta Jute		$F_{2,6}$	P
	AI (%) [μg leaf^{-1}]	**χ^2 (df=1)**	**AI (%)** [μg leaf^{-1}]	**χ^2 (df=1)**	**AI (%)** [μg leaf^{-1}]	**χ^2 (df=1)**		
Alkanes treated filter paper vs. solvent:								
Total natural n-alkanes	13.426±2.018^{a} [360.628±23.779]	2.236	10.648±2.018^{b} [451.570±21.825]	1.505	7.870±2.018^{c} [214.379±21.344]	0.905	1.895	0.230
Synthetic 4 n-alkanes mixture	18.982±2.370^{a} [133.508±3.727]	3.571	14.815±2.137^{b} [57.526±1.836]	2.330	10.648±2.095^{c} [17.317±2.835]	1.316	4.263	0.070
Free fatty acids (FFAs) treated filter paper vs. solvent:								
Total natural FFAs	32.870±2.106^{a} [75.741±3.594]	8.147	30.093±2.092^{a} [75.766±1.763]	7.039	25.926±2.104^{b} [55.500±4.660]	5.480	3.00	0.125
Synthetic 5 FFAs mixture	45.370±2.148^{a} [61.701±2.713]	20.542	42.593±2.076^{b} [62.251±1.603]	18.831	38.426±2.073^{c} [33.250±2.059]	16.311	3.00	0.125
Combined mixture treated filter paper vs. solvent:								
Total natural wax	57.870±2.117^{a} [1064.175±83.481]	30.474	53.704±2.038^{b} [1187.578±70.683]	27.704	49.537±2.116^{c} [728.029±34.226]	24.962	4.263	0.070
Synthetic wax (4 n-alknes+5 FFAs) mixture	68.519±1.225^{a} [195.209±2.950]	38.853	66.667±1.389^{a} [119.777±1.857]	37.579	62.963±2.816^{b} [50.567±3.508]	35.046	2.113	0.202
Combined synthetic mixture (4 n-alknes+5 FFAs) treated leaf vs. solvent:								
Intact leaf	83.796±1.669^{a} [1259.384±72.213]	52.262	77.315±4.560^{c} [1307.355±66.820]	47.687	73.148±2.078^{b} [778.596±29.359]	43.353	3.124	0.118
De-waxed leaf	70.370±2.016^{a} [195.209±2.950]	38.909	64.815±2.085^{b} [119.777±1.857]	35.139	62.037±2.092^{b} [50.567±3.508]	33.266	4.421	0.066

Note: Within rows means followed by same letters are not significantly different (P≥0.05) by Tukey's HSD test. AI=Attraction index.

Table 4 Oviposition preference (Mean±SE, n=72) of a generalist jute pest (*Spilosoma obliqua* Walker; Arctiidae) to plant surface wax chemicals (n-alkanes and FFAs in leaf equivalent amount [μg leaf^{-1}]) of three selected host (white jute, *Corchorus capsularis*, tossa jute, C*. olitorius* and mesta jute, *Hibiscus cannabinus* [Malvaceae]) plants under specified bioassay conditions.

Oviposition conditions	White Jute		Tossa Jute		Mesta Jute		$F_{2,6}$	P
	AI (%) [μg leaf^{-1}]	**χ^2 (df=1)**	**AI (%)** [μg leaf^{-1}]	**χ^2 (df=1)**	**AI (%)** [μg leaf^{-1}]	**χ^2 (df=1)**		
Alkanes treated filter paper vs. solvent:								
Total natural n-alkanes	34.199±9.985^a [360.628±23.779]	1.234	26.732±2.347^b [451.570±21.825]	0.744	22.540±5.643^c [214.379±21.344]	0.448	0.807	0.489
Synthetic 4 n-alkanes mixture	41.667±8.333^a [133.508±3.727]	1.833	32.778±4.339^b [57.526±1.836]	0.922	37.771±6.429^c [17.317±2.835]	1.353	1.561	0.285
Free fatty acids (FFAs) treated filter paper vs. solvent:								
Total natural FFAs	36.793±6.873^a [75.741±3.594]	2.273	26.111±3.889^b [75.766±1.763]	0.748	21.746±3.546^c [55.500±4.660]	0.625	1.273	0.346
Synthetic 5 FFAs mixture	37.374±8.694^a [61.701±2.713]	1.980	49.801±4.925^b [62.251±1.603]	2.716	23.148±6.481^c [33.250±2.059]	0.648	7.034	0.027
Combined mixture treated filter paper vs. solvent:								
Total natural wax	42.424±7.576^a [1064.175±83.481]	2.606	38.730±2.822^b [1187.578±70.683]	1.835	34.286±7.190^c [728.029±34.226]	1.524	0.426	0.672
Synthetic wax (4 n-alknes+5 FFAs) mixture	63.981±5.250^a [195.209±2.950]	6.304	62.594±4.565^a [119.777±1.857]	5.706	57.879±4.077^b [50.567±3.508]	4.285	0.472	0.645
Combined synthetic mixture (4 n-alknes+5 FFAs) treated leaf vs. solvent:								
Intact leaf	80.278±4.092^a [1259.384±72.213]	11.039	78.307±4.132^a [1307.355±66.820]	9.439	69.167±3.632^b [778.596±29.359]	8.350	2.243	0.187
De-waxed leaf	66.299±4.793^a [195.209±2.950]	7.178	65.079±4.201^a [119.777±1.857]	6.571	62.594±4.564^b [50.567±3.508]	5.706	0.174	0.844

Note: Within rows and columns means followed by same letters (lower and upper case, respectively) are not significantly different (P≥0.05) by Tukey's HSD test. OPI=Oviposition preference index (gravid female).

Table 5 Feeding preference (Mean±SE, n=72) of the 5th instar larvae of a generalist jute pest (*Spilosoma obliqua* Walker; Arctiidae) to plant surface wax chemicals (n-alkanes and FFAs in leaf equivalent amount [μg leaf^{-1}]) of three selected host (white jute, *Corchorus capsularis*, tossa jute, C. *olitorius* and mesta jute, *Hibiscus cannabinus* [Malvaceae]) plants under specified bioassay conditions.

Larval feeding conditions	White Jute FI (%) [μg leaf^{-1}]	χ^2 (df=1)	Tossa Jute FI (%) [μg leaf^{-1}]	χ^2 (df=1)	Mesta Jute FI (%) [μg leaf^{-1}]	χ^2 (df=1)	$F_{2,6}$	*P*
Alkanes treated intact leaf vs. solvent:								
Total natural n-alkanes	33.465±0.808^{a} [1424.803±19.490]	3.153	31.877±2.060^{b} [1639.148±16.847]	2.614	32.488±1.494^{ab} [942.408±18.280]	2.808	0.270	0.772
Synthetic 4 n-alkanes mixture	36.573±2.938^{a} [1197.683±15.610]	2.792	35.063±1.655^{a} [1245.104±13.503]	2.317	35.779±2.220^{a} [745.346±12.610]	2.530	0.105	0.902
Free fatty acids (FFAs) treated intact leaf vs. solvent:								
Total natural FFAs	37.307±3.645^{a} [1139.916±13.436]	3.170	35.937±2.353^{b} [1263.344±11.763]	2.670	36.322±2.704^{ab} [783.529±14.507]	2.801	0.057	0.945
Synthetic 5 FFAs mixture	37.550±3.863^{a} [1125.876±12.713]	2.713	36.382±2.773^{a} [1249.829±11.603]	2.343	36.715±3.075^{a} [761.279±12.106]	2.443	0.034	0.967
Combined synthetic mixture (4 n-alknes+5 FFAs) treated leaf vs. solvent:								
Intact leaf	38.854±5.163^{a} [1259.384±72.213]	3.537	36.452±2.827^{b} [1307.355±66.820]	2.605	37.952±4.276^{ab} [778.596±29.359]	3.149	0.084	0.921
De-waxed leaf	38.930±5.216^{a} [195.209±2.950]	3.173	36.549±2.925^{b} [119.777±1.857]	2.344	36.992±3.332^{b} [50.567±3.508]	2.477	0.103	0.904

Note: Within rows and columns means followed by same letters (lower and upper case, respectively) are not significantly different ($P \geq 0.05$) by Tukey's HSD test. FI=Feeding index (5th instar larva).

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