



Insights into the biochemical basis of ovipositional preference of *Earias vittella* (Fabricius) in *Abelmoschus* species

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ABSTRACT: The present study investigated the ovipositional preference of okra shoot and fruit borer, *Earias vittella* (Fabricius) (Order: Lepidoptera; Family: Noctuidae) in relation to host plant biochemical traits independently and also through combining with host plant morphological traits in different wild and cultivated *Abelmoschus* species. Correlation studies revealed a significant positive relationship between the number of eggs laid by *E. vittella* to total protein (P, $r = 0.17$) and a significant negative relationship with total phenols (TP, $r = -0.57$), total flavonoids (TF, $r = -0.38$), total sugar (TS, $r = -0.57$) and total reducing sugars (TRS, $r = -0.64$). Path co-efficient analysis revealed that total phenols, flavonoids, and total reducing sugars appear to be particularly important, as they, directly and indirectly, affect *E. vittella* egg-laying choice. Multiple step-wise regression analyses of the number of eggs laid by *E. vittella* on different *Abelmoschus* species with host plant biochemical traits together explained the variability in the egg laying to the tune of 54% ($R^2 = 0.54$; $Y = 26.71 - 0.30_{TP} + 0.32_{TF} - 1.39TS - 4.41_{TRS} + 8.29_p$; $R^2 = 0.54$; VIF = 2.19). Further, combining the significant biochemical traits (TRS and P) with significant morphological traits (FL: fruit length, FW: fruit width, T: trichomes) based on r/SE explained the variability in the number of eggs laid by *E. vittella* to the tune of 78%; $Y = 7.15 + 1.35_{FL} - 3.64_{FW} + 0.05_T - 2.00_{TRS} + 1.66_p$; $R^2 = 0.78$; VIF = 4.56.

Keywords: Correlation, cultivated species, egg laying, okra, multiple linear regression, shoot and fruit borer, wild species.

INTRODUCTION

The survival and development of phytophagous lepidopteran insects primarily rely on their selection of appropriate oviposition sites on their host plants. The decisions made by gravid females in choosing suitable oviposition sites significantly influence the performance and survival of their offspring, ultimately impacting the species' reproductive success (García-Barros and Fartmann, 2009). The process of host plant selection for laying their eggs is influenced by a variety of factors, including morphological (such as the size of the plant or plant parts, shape, color, leaf hairs, cuticle thickness), (Keerthi *et al.*, 2023) and biochemical traits etc. (Carrasco *et al.*, 2015). Insects have evolved to detect and assess these traits that support their reproductive success, leading to positive preference-performance relationships (Beck, 1965; Kessler and Baldwin, 2002; Sharma, 2007; Dhillon and Sharma, 2004; War *et al.*, 2012; Da Silva *et al.*, 2021; Ali *et al.*, 2019; Coapio *et al.*, 2018; Thakur *et al.*, 2017). Okra shoot and fruit borer, *Earias vittella* (Fabricius) (Lepidoptera: Nolidae), is an economically important oligophagous pest that feeds on numerous host plants of Malvaceae. In okra, gravid female moths of *E. vittella* lay eggs singly on shoot

tips, flower buds and tender fruits. The neonate larvae bore into delicate terminal shoots during the vegetative phase and fruit formation; they bore into flower buds and young fruits (Qasim *et al.*, 2018). Damaged shoots wilt and dry out, and infested fruits have a distorted look and contain larval excrement, rendering them unfit for consumption, and crop losses often range from 3.5 to 90 percent (Hafeez *et al.*, 2019; Mandal *et al.*, 2006).

In the case of *E. vittella*, our earlier studies revealed that host plant morphological traits, namely number of branches (NB), stem diameter (SD), leaf length (LL), fruit length (FL), fruit width (FW) and trichomes density (T) significantly influenced the female moth egg laying choice. Step-wise linear regression equations showed that a combination of these morphological traits could explain the variability in the number of eggs laid by *E. vittella* to the tune of 79% ($y = 17.29 - 0.61NB - 8.17SD + 0.48LL + 1.16FL - 5.73FW + 0.11T$, $R^2 = 0.79$). Of these traits, fruit traits (fruit length, fruit width, and trichomes on fruit) were found to impact the egg-laying choice of moths exclusively. Further, consideration of only the fruit length (FL) alone was found to explain the maximum variability in egg laying choice of female moth *E. vittella* ($R^2 = 0.72$) (Krishna Kumar *et al.*,

2023). However, in addition to the morphological traits, several studies revealed that biochemical traits such as phenols, flavonoids, sugars, etc. also found to influence the host plant preference of *E. vittella* during the egg laying, feeding vis-a-vis progeny fitness (Manju *et al.*, 2021; Kumar *et al.*, 2021; Sandhi *et al.*, 2017; Gautam *et al.*, 2013; Koujalagi *et al.*, 2009). The presence or absence of specific host plant biochemical traits can determine whether the particular host plant is preferred or avoided by insects (War *et al.*, 2012; Painter, 1951); understanding the potential host plant biochemical traits that are underlying the oviposition preference of *E. vittella* will serve as ready reckoners during host plant resistance breeding programs. Therefore, an attempt was made to explore the association of different host-plant biochemical traits with the oviposition preference of *E. vittella*, in wild and cultivated species of *Abelmoschus*.

MATERIALS AND METHODS

The present study was conducted at the Division of Crop Protection, ICAR-Indian Institute of Horticultural Research (ICAR-IIHR), Bengaluru, India (12°58'N, 77°35'E, 890 m above sea level) during 2021–2022. Seeds of selected wild species of *Abelmoschus*, viz., *Abelmoschus tetraphyllus* (Roxb. ex Hornem.) Hochr., *Abelmoschus tuberculatus* Pal & Singh and *Abelmoschus angulosus* Wall. ex-Wight & Arn. (var. *grandiflorus*) along with the cultivated species (*Abelmoschus esculentus* L. (Moench) cv. Arka Anamika) were procured from the Division of Vegetable Crops, ICAR-IIHR, Bengaluru. The host plants were grown in polybags (6 x 8") containing a standard pot mixture (Red soil 40%; Coco peat 30%; Farm yard manure 30%) without any pesticide application (Agboyi *et al.*, 2019). Regular water sprays were given at frequent intervals to avoid insect pest infestation.

Insect culture maintenance

Okra fruits infested with *E. vittella* larvae were collected from the experimental fields of ICAR-IIHR. The larvae were reared by providing fresh immature okra fruits in plastic containers (13.63 × 8.25 × 4.88 cm) until pupation. The emerged adult moths were collected and released into net cages (1 × 1 × 1 m) for mating. The gravid females were separated and used for ovipositional preference studies.

Oviposition assays

Choice and no-choice oviposition assays with different host plants provide clues about the insect host plant's preference for egg-laying. The above-selected

host plants were arranged randomly in a net cage and exposed to *E. vittella* (@ 2 moths/plant) for 48 hrs. In the no-choice assay, a single species of each of the six host plants was arranged randomly (N = 6) in net cages. The plants were exposed to gravid females of *E. vittella* (@ 2 moths/plant) for 48 hrs. Observations were recorded on the number of eggs laid on each host plant. Each assay was replicated six times at different times (Uzun *et al.*, 2015).

Biochemical traits

Observations on different biochemical traits were recorded, namely, total phenols (TP) (Singleton *et al.*, 1999), total flavonoids (TF) (Zhishen *et al.*, 1999), total and reducing sugar (TS& TRS) (Somogyi, 1952), total protein (P) (Lowry *et al.*, 1951), total free amino acids (FA) (Moore and Stein, 1954) and total antioxidants (AO) (Benzie and Strain, 1996) using double beam UV-visible spectrophotometer. For this investigation, 10-day-old okra fruits were utilized from a 55-day-old plant.

Morphological traits

Data on different morphological traits of host plants namely plant traits [plant height (PH, cm), number of branches/ plant (NB) and stem diameter (SD, cm)], leaf traits [number of leaves/ plant (NL), leaf length (LL, cm), petiole diameter (PD, cm)], fruit traits [number of fruits/ plant (NF), fruit length (FL, cm), fruit width (FW, cm), trichomes density on fruits (T, cm²)] as per our earlier studies (Krishna Kumar *et al.*, 2023) was used.

Statistical analysis

Data on biochemical and morphological traits and the number of eggs laid were subjected to correlation analysis, and the correlation coefficient values were plotted in Corplot using R 4.2.0. Path-coefficient analyses were also carried out between the plant traits and the number of eggs laid. To get further insights, a step-wise regression procedure (Ryan, 1997) was employed to select the most crucial plant traits (based on r/SE , a stringent criterion for identifying significant variables for regression analysis) influencing the variability in the egg-laying choice of *E. vittella*. This technique identified, stage by stage, trait(s) significantly related to egg-laying choice (y). Further, as a measure of the goodness-of-fit of the models developed, values pertaining to the Coefficient of Determination (R²) (Agostid'no and Stephens, 1986) were calculated. The Variance Inflation Factor (VIF) was computed to test the multi-collinearity of variables.

Table 1. Descriptive statistics of biochemical traits of different *Abelmoschus* genotypes

Host plants	Total Phenols (mg GAE/100g)	Total Flavonoids (mg CE/100g)	Total sugar (g /100g)	Reducing Sugar (g/100g)	Protein (mg BSA/ 100g)	Free amino acids (mg/ 100g)	Antioxidant (mg AEAC/ 100 g)
<i>A. angulus</i>	111.50±10.28 ^a (89.3-147.8)	51.38±1.46 ^a (46.8-56.5)	11.46±0.55 ^a (9.9-13.1)	2.92±0.44 ^a (1.9-3.9)	3.56±0.24 ^{abc} (3.2-4.5)	3.02±0.26 ^a (2.1-3.7)	68.5±1.15 ^c (64.2-72.4)
<i>A. tetraphyllus</i>	78.52±4.77 ^b (71.2-88.2)	36.04±1.15 ^b (32.1-39.6)	12.31±1.26 ^a (11.8-13.2)	2.65±0.19 ^{ab} (2.4-3.4)	3.68±0.07 ^{ab} (3.5-3.8)	1.30±0.13 ^d (1.0-1.8)	39.33±0.73 ^{cd} (37.3-42.4)
<i>A. tuberculatus</i>	80.75±0.87 ^c (38.1-43.1)	19.63±0.61 ^f (17.9-22.1)	7.54±1.22 ^{bc} (7.1-8.2)	2.66±0.29 ^{ab} (2.0-3.4)	2.29±0.11 ^g (1.9-2.5)	2.78±0.20 ^{ab} (2.1-3.3)	34.03±0.91 ^c (31.8-38.2)
Arka anamika	40.52±2.86 ^{dc} (33.2-61.3)	24.85±0.84 ^{dc} (22.6-28.1)	6.13±0.31 ^{de} (5.3-6.9)	1.80±0.21 ^c (1.1-2.4)	3.31±0.06 ^{bcd} (3.2-3.5)	2.07±0.14 ^c (1.7-2.5)	46.39±3.03 ^b (40.1-59.6)
ACC 1685	40.11±2.32 ^{dc} (34.6-46.2)	20.31±1.18 ^f (17.5-25.9)	8.54±0.58 ^b (6.5-9.6)	2.06±0.30 ^{bc} (1.0-2.9)	2.81±0.20 ^f (2.4-3.4)	2.21±0.26 ^{bc} (1.6-2.9)	37.48±1.45 ^{cde} (32.2-41.8)
IIHR 356	56.64±4.89 ^e (61.2-69.3)	31.11±0.66 ^e (29.9-34.3)	5.60±0.31 ^{de} (4.9-6.7)	1.01±0.01 ^d (1.0-1.1)	3.90±0.05 ^a (3.7-4.0)	1.17±0.13 ^d (0.8-1.6)	65.16±1.13 ^a (60.8-69.5)
IIHR 358	39.83±2.36 ^e (34.1-48.1)	19.68±0.28 ^f (18.3-20.2)	5.58±1.51 ^{de} (4.2-7.1)	1.38±0.14 ^{cd} (1.0-1.9)	3.23±0.14 ^{cde} (2.9-3.7)	1.78±0.24 ^{cd} (1.1-2.6)	36.54±0.95 ^{cde} (32.2-38.6)
IIHR 379	55.29±1.26 ^{cd} (51.3-58.6)	25.66±1.79 ^{dc} (22.1-34.2)	5.19±2.09 ^e (4.9-5.4)	1.64±0.22 ^{cd} (1.2-2.5)	3.10±0.05 ^{def} (3.0-3.2)	2.08±0.32 ^c (1.0-3.0)	41.29±2.75 ^c (31.9-52.8)
IIHR 394	46.67±4.12 ^{dc} (39.6-61.9)	22.49±1.19 ^{ef} (20.1-28.1)	6.62±0.74 ^{cd} (4.1-8.3)	1.60±0.20 ^{cd} (1.0-2.2)	3.06±0.12 ^{def} (2.7-3.4)	2.78±0.27 ^{ab} (2.0-3.7)	38.49±1.84 ^{cde} (30.6-44.1)
IIHR 402	38.14±1.45 ^e (34.8-43.1)	18.76±1.36 ^f (14.8-24.6)	7.83±1.53 ^{bc} (6.4-9.6)	1.45±0.22 ^{cd} (1.0-2.1)	3.08±0.26 ^{ef} (2.5-3.7)	3.10±0.06 ^a (2.9-3.3)	34.86±1.44 ^{dc} (30.8-39.8)
<i>F</i> (9,50)	46.53	81.01	44.88	9.96	13.94	15.31	52.33
<i>P</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
C D (0.05)	15.18	3.31	1.25	0.71	0.39	0.63	5.02

Figures in parentheses show the range of values; *P* = significance at 5% level; CD (0.05) = critical difference at 5% level

RESULTS AND DISCUSSION

Among all the host plant biochemical traits studied, significantly higher amounts of total phenols (mg GAE/100g) were observed in the wild species *A. angulosus* var. *grandiflorus* (111.50±10.28 mg GAE/100g) and the lowest was found in cultivated line namely IIHR 402 (38.14±1.45 mg GAE/100g) [$F_{(9,50)} = 46.53$; $P < 0.0001$; CD = 15.18]. Similarly, the total flavonoid content was observed to be the highest in wild species *A. angulosus* var. *grandiflorus* (51.38±1.46 mg CE/100g) and lowest in the cultivated line namely IIHR 402 (18.76±1.36 mg CE/100g) [$F_{(9,50)} = 81.01$; $P < 0.0001$; CD = 3.31]. Higher amounts of total sugars were observed in *A. tetraphyllus* (12.31±1.26 g /100g) and the lowest were noticed in IIHR 379 (5.19±2.09 g /100g) [$F_{(9,50)} = 44.88$; $P < 0.0001$; CD = 1.25]. Higher amounts of reducing

sugar significantly were observed in *A. angulosus* var. *grandiflorus* (2.92±0.44 g /100g) and lowest in IIHR 356 (1.01±0.01 g /100g) [$F_{(9,50)} = 9.96$; $P < 0.0001$, CD = 0.71]. Observations on total protein content among the host plants revealed significantly higher amounts in *A. tetraphyllus* (3.68±0.07 mg BSA /100g) and low protein in *A. tuberculatus* (2.29±0.11 mg BSA /100g) [$F_{(9,50)} = 13.94$; $P < 0.0001$; CD = 0.39]. Significantly, the highest amounts of total free amino acids were observed in IIHR 402 (3.10±0.06 mg/ 100g) and the lowest in IIHR 356 (1.17±0.13 mg/ 100g) [$F_{(9,50)} = 15.31$; $P < 0.0001$; C. D. = 0.63]. Significantly, the highest total antioxidant content was observed in *A. angulosus* (68.5±1.15 mg/100g) and the lowest in *A. tuberculatus* (34.03±0.91 mg/100g) [$F_{(9,50)} = 52.33$; $P < 0.0001$; CD = 5.02] (Table 1).

Variations in host plant traits, including nutritional

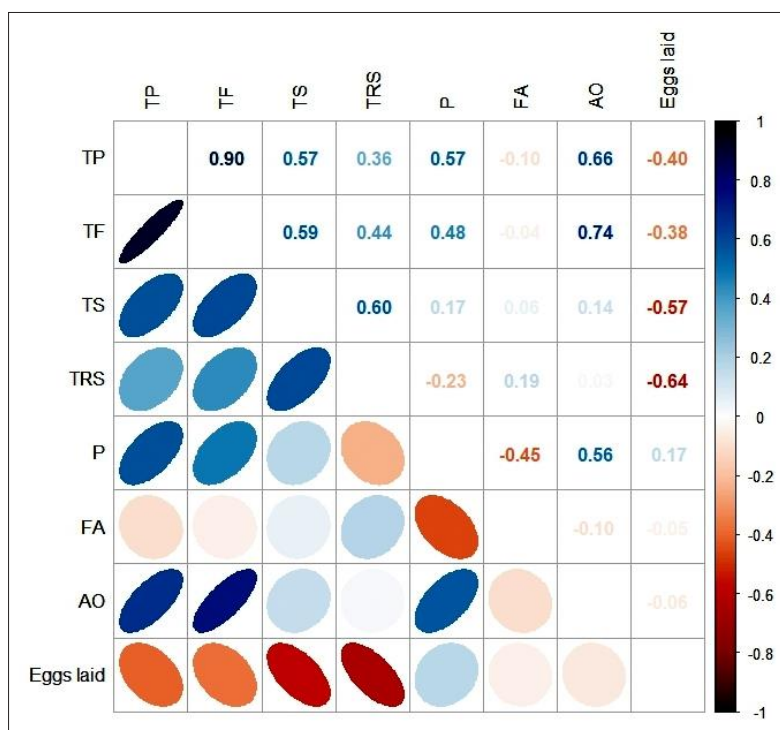


Fig. 1. Correlation analysis of oviposition preference of *E. Vittella* and biochemical traits of *Abelmoschus* species. The correlation matrix shows that the lower left to high right ellipse shows a positive relationship; lower right to higher left shows a negative correlation. Thin ellipse size shows higher correlation coefficient value; the thicker one shows lower the value. Total phenols, TP; Total flavonoids, TF; Total sugar, TS; Total reducing sugar, TRS; Total protein, P; Total free amino acids, FA; Total antioxidant, AO.

quality and defensive characteristics, significantly impact plant resistance against pests (Birke and Aluja, 2018). Ecological, physiological, and behavioral factors also influence insect oviposition preferences and offspring fitness (Balagawi *et al.*, 2013; Birke *et al.*, 2015). The relationship between female oviposition preference and offspring performance is strongly associated with their dietary habits and the absence of adverse effects from host plant biochemistry, crucial for maximizing offspring fitness (Hafsi *et al.*, 2016; Gripenberg *et al.*, 2010; Clark *et al.*, 2011). Thus, the initial phase of insect oviposition choice relies heavily on the diverse morphological and biochemical traits of host plants (Beck, 1965; War and Sharma, 2014).

Correlation analysis

Biochemical traits namely, total phenols (TP; $r=-0.40$; $p<0.0001$), total flavonoids (TF; $r=-0.38$; $p<0.0001$), total sugar (TS; $r=-0.57$; $p<0.0001$) and total reducing sugar (TRS; $r=-0.64$; $p<0.0001$) exhibited a significant negative correlation and a significant positive correlation was obtained from total protein (P; $r=0.17$; $p=0.0138$) with the number of eggs laid by *E. vittella*. Other traits such as total free amino acids (FA) and total antioxidants (AO) did not show any significant correlation (Figure 1).

Data analysis of biochemical traits indicates that higher levels of total phenols, total flavonoids, total sugars, and total reducing sugars in host plants negatively affect the oviposition behaviour of the okra shoot and fruit borer, *E. vittella*. In this study, wild species such as *A. tetraphyllus*, *A. angulosus* var. *grandiflorus*, and *A. tuberculatus* exhibited higher concentrations of phenols, flavonoids, total sugars, and reducing sugars compared to cultivated *A. esculentus* lines. Previous research on different *Abelmoschus* spp. also demonstrated that *A. tetraphyllus* and *A. angulosus* var. *grandiflorus* possess significant resistance to *E. vittella* due to their higher levels of total phenols, total sugars, and reducing sugars, while *A. tuberculatus* exhibited moderate field resistance with moderate levels of these compounds (Sandhi *et al.*, 2017; Doshi, 2004).

Most insects are negatively affected by phenolic compounds due to their toxic nature (Palial *et al.*, 2018; Dreyer and Campbell, 1987). Studies by Kumar *et al.* (2021), Halder *et al.* (2015), and Gautam *et al.* (2013) revealed that the presence of phenols in okra fruits has a detrimental effect on *E. vittella* infestation. Similarly, Sultani *et al.* (2011) reported that higher total sugar content reduces the ovipositional preference of

Table 2. Step-wise linear regression models to estimate *E. vittella* ovipositional preference using biochemical traits of *Abelmoschus* species

Variables	Model	R ²	VIF
TP	Y= 37.26-0.20 _{TP}	0.16	-
TF	Y= 37.53-0.44 _{TF}	0.14	-
TS	Y= 46.47-2.71 _{TS}	0.33	-
TRS	Y= 44.81-9.92 _{TRS}	0.41	-
P	Y= 12.91+4.00 _P	0.03	-
TP+TF	Y= 37.70-0.17 _{TP} -0.09 _{TF}	0.16	1.19
TP+TS	Y= 47.35-0.05 _{TP} -2.42 _{TS}	0.34	1.51
TP+TRS	Y=48.33-0.10 _{TP} -8.81 _{TRS}	0.44	1.78
TP+P	Y=3.33-0.38 _{TP} +13.77 _P	0.40	1.68
TF+TS	Y= 47.05-0.07 _{TF} -2.55 _{TS}	0.33	1.50
TF+TRS	Y= 47.05-0.14 _{TF} -9.09 _{TRS}	0.42	1.72
TF+P	Y=10.76-0.70 _{TF} +10.59 _P	0.31	1.44
TS+TRS	Y=50.29-1.42 _{TF} -7.10 _P	0.46	1.86
TS+P	Y=27.61-2.94 _{TS} +6.47 _P	0.41	1.69
TRS+P	Y=42.64-9.82 _{TRS} +0.62 _P	0.41	1.68
TP+TF+TS	Y=46.93-0.11 _{TP} +0.15 _{TF} -2.49 _{TS}	0.34	1.52
TP+TF+TRS	Y=47.54-0.22 _{TP} +0.32 _{TF} -9.34 _{TRS}	0.45	1.82
TP+TF+P	Y=3.02-0.40 _{TP} +0.04 _{TF} +13.81 _P	0.40	1.68
TP+TS+TRS	Y=51.03-0.05 _{TP} -1.18 _{TS} -7.06 _{TRS}	0.47	1.88
TP+TS+P	Y=16.26-0.24 _{TP} -1.87 _{TS} +11.68 _P	0.50	2.01
TP+TRS+P	Y=25.48-0.23 _{TP} -6.09 _{TRS} +7.88 _P	0.45	1.97
TF+TS+TRS	Y=50.29+0.001 _{TF} -1.42 _{TS} -7.11 _{TRS}	0.46	1.86
TF+TS+P	Y=23.05-0.33 _{TF} -2.23 _{TS} +9.03 _P	0.45	1.81
TF+TRS+P	Y=34.76-0.30 _{TF} -7.52 _{TRS} +4.21 _P	0.44	1.77
TS+TRS+P	Y=39.51-1.77 _{TS} -5.86 _{TRS} +3.47 _P	0.48	1.93
TP+TF+TS+TRS	Y=50.30-0.18 _{TP} +0.36 _{TF} -1.25 _{TS} -7.56 _{TRS}	0.49	1.94
TP+TF+TS+P	Y=15.32-0.32 _{TP} +0.22 _{TF} -1.96 _{TS} +11.81 _P	0.51	2.04
TP+TF+TRS+P	Y=25.46-0.33 _{TP} +0.27 _{TF} -6.63 _{TRS} +7.65 _P	0.50	2.00
TP+TS+TRS+P	Y=26.68-0.18 _{TP} -1.33 _{TS} -3.88 _{TRS} +8.53 _P	0.53	2.13
TF+TS+TRS+P	Y=35.11-0.18 _{TF} -1.59 _{TS} -4.89 _{TRS} +5.33 _P	0.49	1.97
TP+TF+TS+TRS+P	Y= 26.71-0.30 _{TP} +0.32 _{TF} -1.39 _{TS} -4.41 _{TRS} +8.29 _P	0.54	2.19

TP = Total phenols; TF = Total flavonoids; TS = Total sugar; TRS = Total reducing sugar; P = Total protein.

E. vittella. However, research by Sundararaj and David (1987) suggested that higher quantities of reducing sugars, particularly from immature fruit parts, may be favourable for *E. vittella*. Unlike the current study focusing on ovipositional preference, Sundararaj and David (1987) primarily examined larval food quality and reproductive biology. Furthermore, the present study indicates that higher total protein content in the host plant facilitates greater egg laying by female *E. vittella* moths, showing a significant positive correlation. Interestingly, cultivated *A. esculentus* lines exhibited higher protein content compared to wild species. Previous studies have also shown that higher total protein content from okra and cotton plants enhances fecundity in *E. vittella* (Basker *et al.*, 2014; Sundararaj and David, 1987).

The high levels of various biochemical parameters in wild species and their negative correlation with *E. vittella* egg laying suggest that a combination of these parameters rather than a single one influences ovipositional non-preference. Literature indicates that biochemical traits influence lepidopteran pests' egg-laying choices, serving as a significant factor in selecting suitable host plants for offspring fitness (Kogan and Ortman, 1978). In the case of *Abelmoschus* species, as observed in this study, biochemical traits such as phenols, flavonoids, and sugars play a crucial role in positively impacting ovipositional non-preference against the okra shoot and fruit borer, *E. vittella*.

Table 3. Step-wise linear regression models to estimate *E. vittella* ovipositional preference using a combination of host-plant (*Abelmoschus* species) morphological and biochemical traits

Variables	Model	R ²	VIF
FL+TRS	Y= 4.90+1.20 _{FL} -1.92 _{TRS}	0.73	3.70
FL+P	Y= -3.76+1.33 _{FL} +4.19 _P	0.75	4.08
FW+TRS	Y= 32.06+7.30 _{FW} -7.25 _{TRS}	0.50	1.99
FW+P	Y= -7.11+12.93 _{FW} +6.06 _P	0.40	1.67
T+TRS	Y= 35.87+0.11 _T -10.06 _{TRS}	0.51	2.05
T+P	Y= 12.10+0.09 _T +1.77 _P	0.10	1.11
FL+FW+TRS	Y= 15.94+1.42 _{FL} -3.83 _{FW} -1.81 _{TRS}	0.74	3.89
FL+FW+P	Y= -1.44+1.49 _{FL} -2.79 _{FW} +3.77 _P	0.76	4.19
FL+T+TRS	Y= 12.46+1.09 _{FL} +0.06 _T -2.71 _{TRS}	0.76	4.19
FL+T+P	Y= -3.68+1.30 _{FL} +0.03 _T +3.35 _P	0.76	4.24
FL+TRS+P	Y= -0.81+1.28 _{FL} -0.76 _{TRS} +3.92 _P	0.76	4.10
FW+T+TRS	Y= 27.18+5.82 _{FW} +0.09 _T -7.91 _{TRS}	0.57	2.31
FW+T+P	Y= -6.51+12.30 _{FW} +0.04 _T +4.95 _P	0.41	1.71
FW+TRS+P	Y= 19.44+8.28 _{FW} -6.39 _{TRS} +3.12 _P	0.51	2.05
T+TRS+P	Y= 43.61+0.12 _T -10.48 _{TRS} -2.52 _P	0.52	2.09
FL+FW+T+TRS	Y= 13.49+1.33 _{FL} -4.18 _{FW} +0.06 _T -2.62 _{TRS}	0.78	4.49
FL+FW+T+P	Y= -0.86+1.49 _{FL} -3.38 _{FW} +0.04 _T +2.70 _P	0.77	4.42
FL+FW+TRS+P	Y= 1.73+1.43 _{FL} -2.82 _{FW} -0.81 _{TRS} +3.48 _P	0.76	4.22
FL+T+TRS+P	Y= 3.22+1.17 _{FL} +0.05 _T -1.78 _{TRS} +2.47 _P	0.77	4.34
FW+T+TRS+P	Y= 26.99+5.84 _{FW} +0.09 _T -7.89 _{TRS} +0.05 _P	0.57	2.31
FL+FW+T+TRS+P	Y= 7.15+1.35 _{FL} -3.64 _{FW} +0.05 _T -2.00 _{TRS} +1.66 _P	0.78	4.56

FL = Fruit Length; FW = Fruit Width; T = Trichomes density; TRS = Total reducing sugar; P = Total protein.

Regression analysis

Based on r/SE (a stringent criterion for identifying significant variables for regression analysis), the biochemical traits *viz.*, total phenols (TP), total flavonoids (TF), total sugars (TS), total reducing sugar (TRS) and total protein (P) were further considered for multiple regression analysis. Step-wise regression analysis of all significant host-plant biochemical traits explained the variability in the number of eggs laid by *E. vittella* in the range of 16-54 per cent with lower VIF values (1.19-2.19, <10.0) suggesting that multicollinearity might not be a significant concern in these models. The regression equation that involved all the host plant biochemical traits explained a maximum of 54 per cent of the variability in the number of eggs laid by *E. vittella* ($Y = 26.71 - 0.30_{TP} + 0.32_{TF} - 1.39_{TS} - 4.41_{TRS} + 8.29_P$; $R^2 = 0.54$; $VIF = 2.19$) (Table 2).

Multiple linear regression analysis conducted to further understand the relationship between the biochemical traits (TP, TF, TS, TRS & P) and the number of eggs laid by *E. vittella* could explain 54% of the variability in the moth egg laying choice. The study also considered the combined effect of both morphological and biochemical traits of the host plants in a step-wise regression model which revealed that together these traits could explain a substantial variability of 78% in the number of eggs laid by *E. vittella*. This suggests that combining both morphological (fruit length, fruit width, trichome density) and biochemical traits (total reducing sugars and total protein), could not improve the R^2 value significantly when compared to morphological traits (fruit length, fruit width, trichome density) alone was used ($R^2 = 76\%$; Krishna Kumar *et al.*, 2023). Therefore, as demonstrated by Krishna Kumar *et al.* (2023), host plant morphological traits, such as leaf length, stem diameter, number of branches, fruit characteristics (e.g., length, width, and trichomes density) might play a substantial role in shaping the ovipositional preference of *E. vittella* over biochemical traits that were explored in the present study.

The biochemical traits alongside previously generated morphological traits (the morphological trait data utilized in this study were sourced from the research conducted by Krishna Kumar *et al.*, 2023) namely, fruit length (FL), fruit width (FW), trichomes (T), total reducing sugar (TRS) and total protein (P) were considered for multiple regression analysis. Step-wise regression analysis of all significant host-plant morphological and biochemical traits (based on r/SE) explained the variability in the number of eggs laid in the range of 41-78 per cent with acceptable VIF values (1.11-4.56, <10.0; indicating a

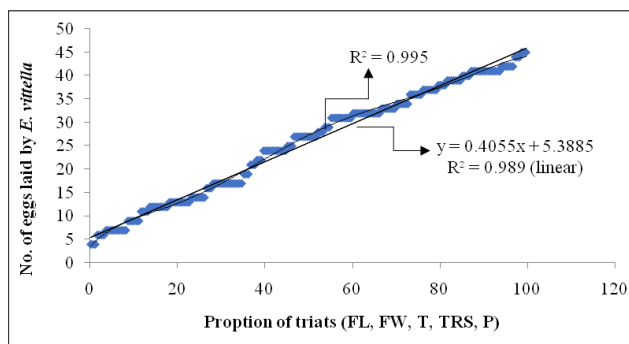


Fig. 2. Relationship between the proportion of host plant morphological and biochemical traits and number of eggs laid by *E. vittella*. Total phenols, TP; Total flavonoids, TF; Total sugar, TS; Total reducing sugar, TRS & Total protein, P.

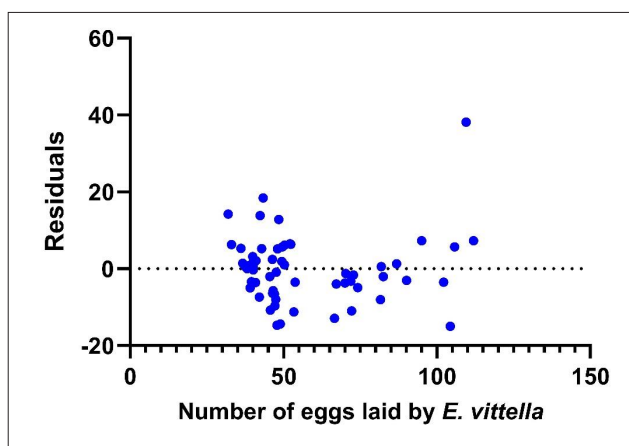


Fig. 3. Plot of the residuals against the egg laying of *E. vittella* with selected host plant (*Abelmoschus* species) morphological and biochemical traits as independent variables

lack of multi-collinearity). A total of 78 per cent of the variability in the number of eggs laid by *E. vittella* was explained by combining all the host plant morphological and biochemical traits ($Y = 7.15 + 1.35_{FL} - 3.64_{FW} + 0.05_{T} - 2.00_{TRS} + 1.66_P$; $R^2 = 0.78$; $VIF = 4.56$; Table 3).

The results of the polynomial models of different orders [(2), (3), (4), (5) and (6)] with all significant traits like fruit length, fruit width, trichomes, total reducing sugar and total protein increased the coefficient of determination to the maximum of 99% [$R^2 = 0.9930$, $R^2 = 0.9937$, $R^2 = 0.9943$, $R^2 = 0.9948$, for polynomial model orders (2), (3), (4) and (5) respectively] and the linear model explained to the tune of 98% variability in egg laying (Figure 2). Plotting the residuals observed and the estimated number of eggs laid by *E. vittella* using the host plant traits (FL, FW, T, TRS and P) showed a random dispersal of points across the x-axis (Figure 3).

Table 4. Direct and indirect effects of host plant (*Abelmoschus* species) biochemical traits on eggs laid by *E. vittella*

Pathways of association	Direct effects	Indirect effects
1. Total phenols		
a. Direct effect	0.86	
b. Indirect effect via		
Total flavonoids		0.86
Total sugar		0.58
Total reducing sugar		0.47
Total Protein		0.55
2. Total flavonoids		
a. Direct effect	-0.91	
b. Indirect effect via		
Total phenols		-0.91
Total sugar		-0.60
Total reducing sugar		-0.48
Total Protein		-0.58
3. Total sugar		
a. Direct effect	-0.04	
b. Indirect effect via		
Total phenols		-0.03
Total flavonoids		-0.03
Total reducing sugar		-0.03
Total Protein		-0.01
4. Total reducing sugar		
a. Direct effect	0.76	
b. Indirect effect via		
Total phenols		-0.42
Total flavonoids		-0.40
Total sugar		-0.63
Total Protein		0.16
5. Total Protein		
a. Direct effect	0.05	
b. Indirect effect via		
Total phenols		0.03
Total flavonoids		0.03
Total sugar		0.01
Total reducing sugar		-0.01

With data support from Krishna Kumar *et al.*, 2023

Table 5. Direct and indirect effects of host plant (*Abelmoschus* species) morphological and biochemical traits on eggs laid by *E. vittella*

Pathways of association	Direct effects	Indirect effects
1. Fruit length (cm)		
a. Direct effect	0.96	
b. Indirect effect via		
Fruit width (cm)		0.92
Trichomes density (cm ²)		0.24
Total reducing sugar		-1.13
Total Protein		-0.03
2. Fruit width (cm)		
a. Direct effect	-0.23	
b. Indirect effect via		
Fruit length (cm)		-0.18
Trichomes density (cm ²)		-0.04
Total reducing sugar		0.15
Total Protein		0.04
3. Trichomes density (cm ²)		
a. Direct effect	0.06	
b. Indirect effect via		
Fruit length (cm)		0.01
Fruit width (cm)		0.01
Total reducing sugar		0.002
Total Protein		0.03
4. Total reducing sugar		
a. Direct effect	0.20	
b. Indirect effect via		
Fruit length (cm)		-0.17
Fruit width (cm)		-0.13
Trichomes density (cm ²)		0.01
Total Protein		-0.04
5. Total Protein		
a. Direct effect	0.18	
b. Indirect effect via		
Fruit length (cm)		-0.004
Fruit width (cm)		-0.03
Trichomes density (cm ²)		0.08
Total reducing sugar		-0.04

With data support from Krishna Kumar *et al.*, 2023

Path co-efficient analysis

To reveal direct and indirect associations between biochemical traits and number of eggs laid by *E. vittella*, further analyses were carried out under path-coefficient analysis. The results showed that total phenols have a strong positive direct effect with a high magnitude (0.86). Total phenols also have positive indirect effects via total flavonoids (0.86), total sugar (0.58), total reducing sugar (0.47) and total protein (0.55). Total flavonoids have a strong negative direct effect (-0.91) and negative indirect effects via total phenols (-0.91), total sugar (-0.60), total reducing sugar (-0.48) and total protein (-0.58) with maximum magnitude. A weaker negative direct effect was observed with total sugar (-0.04) and its indirect effects also showed a negative effect of a very weak magnitude via total phenols (-0.03), total flavonoids (-0.03), total reducing sugar (-0.03) and total protein (-0.01). Total reducing sugar has a strong positive direct effect with high magnitude (0.76) and indirect effects via total phenols (-0.42), total flavonoids (-0.40), total sugar (-0.63) and positive indirect effects via total protein (0.16). Total protein has a weak positive direct effect with lesser magnitude (0.05) and total protein has very weak positive indirect effects via total phenols (0.03), total flavonoids (0.03), total sugar (0.01) and negative indirect effects via total reducing sugar (-0.01) (Table 4).

In the case of morphological and biochemical traits combined together, fruit length has a positive direct effect of 0.96 and significant positive indirect effects via fruit width (0.92) and relatively weaker indirect effects via trichomes density (0.24), total reducing sugar (-1.13) and total protein (-0.03). Fruit width has a negative direct effect with reasonable magnitude (-0.23) and negative indirect effects via fruit length (-0.18), trichomes density (-0.04), total reducing sugar (0.15) and total protein (0.04). Trichomes density has a positive direct effect with lesser magnitude (0.06) and has very weak indirect effects via fruit length (0.01), fruit width (0.01), total reducing sugar (0.002) and total protein (0.03). Total reducing sugar has a positive direct effect (0.20) and has negative indirect effects via fruit length (-0.17), fruit width (-0.13), trichomes density (0.01), and total protein (-0.04). Total protein has a positive direct effect (0.18); indirect negative effect via fruit length (-0.004), fruit width (-0.03), total reducing sugar (-0.04) and indirect positive effect via trichomes density (0.08) (Table 5).

In path-coefficient analysis, biochemical traits such as total phenols and total flavonoids showed strong positive and negative direct effects on *E. vittella* egg laying respectively. This suggests that they are closely

related and may have a synergistic or antagonistic effect on *E. vittella*'s ovipositional preference. Total reducing sugars stood out with strong positive direct and negative indirect effects on *E. vittella* egg laying via total phenols, total flavonoids, and total sugars. These results revealed that biochemical traits such as total phenols and total flavonoids seem to be particularly important, as they have strong direct and indirect effects that might influence *E. vittella*'s ovipositional preference. When combining the morphological and biochemical traits of *Abelmoschus* species to understand their effects on the ovipositional preference of *E. vittella*, a strong direct effect by fruit length and total reducing sugars on egg laying was noticed indicating that these traits are highly influencing the egg laying choice of *E. vittella*. Other morphological traits like trichome density have weaker direct effects on *E. vittella* egg-laying choice. The variables namely fruit length and fruit width have reciprocal negative indirect effects on *E. vittella* egg laying. Additionally, both total reducing sugars and total protein were found to have positive and negative indirect effects on *E. vittella* egg laying. Thus, fruit length and total reducing sugars appear to be important traits, with strong direct and indirect effects on moth egg laying. This suggests that these variables may play a significant role in determining the attractiveness of host plants to *E. vittella*. In other words, the present study reveals that longer fruit length with higher total protein content is associated with increased oviposition, while greater fruit width with higher levels of total reducing sugars is associated with decreased oviposition. The present study also endorses previous findings which identified fruit length and total protein content as potential host-plant traits that positively influenced the egg-laying behaviour of *E. vittella* (Muthukumaran and Ganesan, 2017; Sundararaj and David, 1987). Conversely, studies also reported that fruit width and higher levels of total reducing sugars had an adverse effect on the number of eggs laid by *E. vittella* (Anitha and Karthika, 2018; Sultani *et al.*, 2011).

In conclusion, the present study clearly indicated that host plant morphological traits outweigh the host plant biochemical traits in the oviposition site selection process of *E. vittella*, in spite of the latter having a significant association with moth egg-laying choice. However, detailed studies including diverse germplasm might help to attain a more comprehensive understanding of the host plant traits that shape oviposition preference in okra fruit and shoot borer, *E. vittella*.

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