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Research Article

Tapping the Latent Resistant Potential of Traditional Maize Germplasms: An Attempt to Combat the Invasive Fall Armyworm

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ABSTRACT

The fall armyworm, *Spodoptera frugiperda* (JE Smith), has invaded Africa and Asia, causing significant yield losses in maize and adversely impacting rural livelihoods in these regions. While the use of synthetic pesticides offers temporary relief, the rapid development of resistance by the pest necessitates alternative strategies. Developing cultivars that exhibit resistance to pests and diseases constitutes a crucial element of Integrated Pest Management (IPM). In this context, unexplored maize germplasm holds substantial promise for the creation of resilient cultivars, thereby fostering sustainable management of the fall armyworm. This research aims to investigate Sri Lankan maize landraces to identify potential resistance traits conducive to the development of fall armyworm-resistant maize cultivars. Sixteen open-pollinated (OP) maize landraces were collected and their responses were compared to two elite commercial maize varieties, Ruwan and Bhadra, under various conditions including field, cage and laboratory environments. Among the maize landraces studied, SEU18 and SEU21 exhibited superior traits and SEU21 had the lowest overall leaf injury rates in both field (5.61 ± 0.13) and cage studies (4.61 ± 0.13). Furthermore, these landraces demonstrated the ability to suppress larval and pupal development while significantly reducing the severity of corn cob damage (1.33 ± 0.25 and 1.76 ± 0.26, respectively). In addition, SEU18 showed a higher cob yield per plant (122.5 ± 0.74 g) compared to the commercial varieties. Hierarchical cluster analysis clearly categorized both SEU18 and SEU21 as separate entities within the germplasm tested. Our results strongly suggest that local maize landraces have significant potential for developing resistant cultivars to fall armyworm. This underscores the importance of germplasm improvement programs when pursuing sustainable and environmentally responsible pest management strategies.

Introduction

The fall armyworm (FAW) *Spodoptera fruigiperda* (JE Smith) (Lepidoptera: Noctuidae) is an alien pest recently reported in the South Asian region, initially in Karnataka, India (Sharanabasappa et al., 2018), subsequently in Sri Lanka (Perera et al., 2019) and other neighboring countries (Attaluri et al. 2022). Rural maize farmers in the dry and intermediate zones especially in the North, North-Central, Eastern, and Uva regions were severely affected as maize is the second most important cereal crop in Sri Lanka (Malaviarachchi et al., 2007). The polyphagous nature of this pest allows it to survive on over 100 host species, including rice, cotton, millet, and sorghum, in place of maize (Pogue, 2002). Among them, maize is the most vulnerable crop as larvae feed directly on immature leaves in whorls and spike tissue (Kandel and Poudel, 2020) and thereby grain yield can be reduced by 34 percent (Lima et al., 2010). However, an infestation that extends through the mid to late stages of corn cultivation could cause increased yield loss by about 15 – 73 percent (Hruska and Gould, 1997). Chemical control of the pest becomes successful to some extent and is not a sustainable way to control FAW due to its polyphagous nature, cryptic behavior, high reproductive rate and long-distance migration (Akeme et al., 2021). Farmers have mainly turned to hybrid maize because they can meet grower needs and consumer expectations by achieving a high yield per unit area (Kutka, 2011). However, most hybrids are highly susceptible to biotic (pests and diseases) and abiotic (drought and salinity) stress, considering the limited genetic diversity of cultivated maize compared to traditional varieties (Eyre-Walker et al., 1998).

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Host plant resistance (HPR) assessment of maize has been reported in the early 1900s (Hinds, 1914) and several research efforts have been undertaken in different countries to assess the HPR against several pests, including FAW. In the Midwest and the Southern United States Abel et al., (2000) using fifteen backcrossed maize lines and identified lines possessing multiple resistance traits against FAW, Southwest corn borer (*Diatraea grandiosella)* and sugarcane stalk borer (*D. saccharalis*). In addition, Ni et al*.,* (2011 and 2014) identified germplasms in the state of Mississippi and inbred lines originating from Uruguay, Cuba, and Thailand conferring resistance traits to FAW. However, most of these studies (Abel et al. 2019; Morales et al. 2021) have ended in vain, which might be due to the highly adaptive nature of the polyphagous pest. However, exploring maize germplasm is important to identify the inherent pest and disease resistance mechanisms, which could be utilized in national and global germplasm improvement programs to ensure sustainable maize production. Therefore, the present study was aimed to evaluate and identify the germplasm for resistance to FAW among maize landraces available in Sri Lanka through laboratory, cage, and field studies.

Materials and Methods

The study was conducted as three sub-experiments, *viz*., field experiment under natural infestation of FAW, cage experiment under artificial infestation and laboratory experiment to identify putative resistance of maize landraces in Sri Lanka against FAW. The laboratory experiment was conducted at the Department of Biosystems Technology, Faculty of Technology, South Eastern University of Sri Lanka. Field and cage experiments were conducted at the University Experimental Station, Malwatte, Agrotech Park (7 º18 00.3” N and 81º 51 41.8” E) in the Ampara district, which belongs to Low country dry zone (DL2b) during the 2020-2021 growing seasons.

Planting materials

Sixteen landraces were previously collected in the island-wide surveys during the main maize-growing areas in Sri Lanka (Mufeeth et al., 2020; Silwa et al., 2021). This included twelve landraces from Badulla district, in the areas of Ridimaliyadda (SEU02), Kadapoththawa (SEU09), (SEU16) and (SEU15), Udakumburegedra (SEU17) and (SEU14), Dehigama (SEU23), Baduluoya (SEU18), Nagadeepaya (SEU20), Kandaketiya (SEU26), Mapakada (SEU19) and the Waddas area in Dabana (SEU25), two from Ampara District in Padiyathalawa (SEU06) and Kirawana (SEU10), one from Pallewela, Moneragala District (SEU22) and one from Kinniya, Trincomalee District (SEU21) (Figure 1). Additionally, two open pollinated (OP) maize varieties (Ruwan and Bhadra) recommended by the Department of Agriculture (DoA) were used as checks.

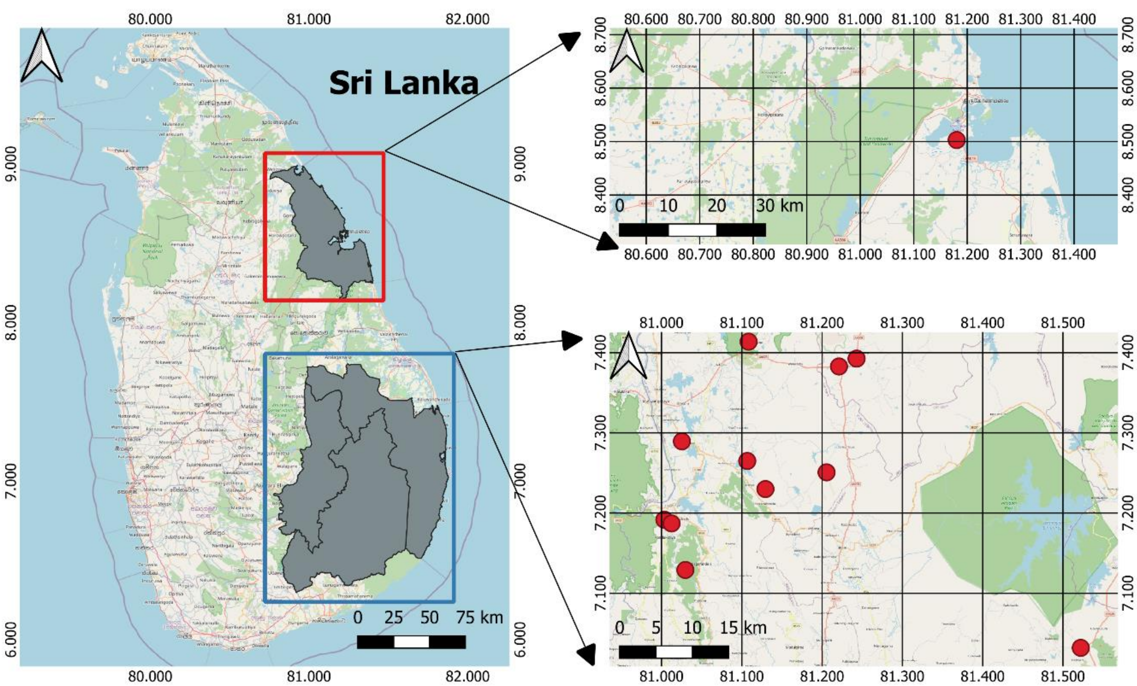

Figure 1. The geographical location of sixteen traditional maize landraces collected in Sri Lanka. The areas were mainly confined to Badulla, Moneragala, Ampara and Trincomalee districts.

Insect culture

FAW larvae were collected from infested maize fields in the Kandaketiya, Badulla district, and University Experimental Station at Agrotech Park, Malwatte. The collected larvae were reared in the laboratory under controlled conditions of the temperature 27 ± 1 ºC, 70-75% relative humidity (RH), and a photoperiod 14:10 (L: D) by feeding them natural diets according to the method described by Silwa et al., (2021). The culture was maintained using plastic bottles (D: 5 cm × H: 10 cm) from the 3rd instar larvae to pupation. After completion of 50% pupation, the pupae were collected and transferred to oviposition cages and kept until adult emergence. Adults were fed 10% sucrose solution and allowed to mate. A muslin cloth was provided as an egg-laying substrate and renewed at two-day intervals. The eggs laid were kept moist until hatching. Immature maize leaves were fed shortly after hatching and reared as masses until 3rd instar.

Field experiment

The field experiment was conducted to assess the resistance of maize landraces under the natural infestation of FAW. The experiment was conducted in a randomized complete block design (RCBD) with four replicates. Each plot (1.2 m x 3 m) consisted of 20 plants with a spacing of 60 cm x 30 cm between and within rows. The commercial maize hybrid (Pacific-999) was planted around each block to minimize the border effect. The crops were managed by the DoA recommended practices for maize cultivation in Sri Lanka, except the use of pesticides. Data recording was started 4 weeks after seed sowing and the number of infested plants in each block and leaf injury ratings (LIR) were recorded randomly selected five infested plants from each plot at weekly interval up to 7 weeks according to the Davis et al., (1995). At harvest, the mean cob yield per plant (YPP)(g) and cob damage severity (CDS) in randomly selected 5 cobs were recorded using the 1-9 Davis scale (Davis et al., 1995).

Cage experiment

The experiment was conducted to evaluate the resistance of maize landraces under artificial infestation of FAW. The experiment was carried out in semi-automated insect-proof net cages (2.5 m x 3.7 m x 4 m) at the University Experimental Station. Plants were raised in plastic plots (25 cm x 35 cm) with the media filled with a 3:2:1 ratio of topsoil: compost: sand. The experiment was set up in a completely randomized design (CRD) and replicated three times. The temperature inside the cages was maintained at 32°C using automatic misters. Subsequently, the maize plants were artificially infested with FAW neonates obtained from laboratory-reared FAW colonies. Five to six neonates per plant were introduced into the maize whorl at the V6 leaf stage using a camel's hair brush. The leaf damage rating (LIR) based on the Davis scale was recorded at weekly interval and the final cob yield per plant (YPP) and cob damage severity (CDS) were recorded.

Laboratory experiment

The laboratory bioassay in a Completely Randomized Design (CRD) with 10 replicates to assess larval and pupal development on different maize landraces was conducted. Third instar larvae obtained from the FAW culture introduced individually into each plastic bottles (5x10 cm). At the V3-V4 leaf stage, leaf discs (D: 2 cm) were obtained from each landrace and the larvae were fed daily *ad libitum* till pupation. The maize leaf samples were taken from additionally managed plants in the insect-proof net cages. To retain ideal conditions, a wet tissue paper was placed at the bottom of the plastic bottles and the residues were removed daily. Leaf area consumption (LAC) (cm^2) using a portable leaf area meter (AM350), larval weight (LWt) (mg) at 3-day interval, pupal weight (PWt) (mg), larval duration (LD) (days) and the final dry weight of the fecal materials (DWF) (mg) were recorded.

Leaf trichome density and thickness

Leaf discs (1 cm^2) were collected from the fully unfolded leaves, avoiding margins and midribs at the V6 stage of each landrace (n=10). The number of trichomes on the leaf discs was counted using a stereotype microscope (Optica LAB 20, manufactured by Italy; 25X). Similarly, leaf thickness was measured using a micrometer gauge (thimble scale 0.01 mm) (n=20).

Data analysis

Cob yield per plant, leaf, and cob damage scores from field and cage experiments were compared using analysis of variance (ANOVA) conforming to single factor landrace in a randomized complete block design and completely randomized designs, respectively. The larval duration, pupal weight, fecal weight, weight gain, and leaf area consumption in the laboratory bioassay were compared using ANOVA. The significant means were separated at a significance level of 0.05 using Tukey's HST test. A principal component analysis (PCA) was performed to identify the contribution of traits to variation, and a cluster analysis was performed for the most contributory traits to identify similar resistant landraces. All statistical analyzes were performed with SPSS (version 22).

Results

Cage experiment

Results showed a significant difference among landraces for leaf injury rates in both 5th ($F_{17, 114} = 1.83$, $p<0.05$) and 6th ($F_{17, 114} = 4.982$, $p<0.01$) weeks after sowing and the leaf injury score varied from 4.50 ± 0.18 (SEU21) to 6.57 ± 0.29 (SEU17) and 4.44 ± 0.33 (Bhadra) to 7.14 ± 0.26 (SEU14) 5th and 6th weeks respectively (Table 1). However, overall leaf damage was significantly lower in SEU21, further revealing a non-significant difference with the commercial checks, Bhadra and Ruwan. The mean cob damage severity (CDS) scale of the landraces showed that they scored less than 3 and the lowest was exhibited in the check Bhadra. The highest mean yield per plant was consistently found in check Bhadra (116.34 ± 5.49 g), SEU15, SEU18, SEU16, and SEU22, which differed significantly from the lowest yield possessed by SEU21, SEU06, SEU10, SEU26 and Ruwan (Table 1).

Table 1. Leaf and cob injury rates and cob yield of maize landraces under artificial FAW infestation

Entry	LIR @5 Mean ± SE	LIR@6 Mean ± SE	OLD Mean ± SE	CDS Mean ± SE	YPP (g) Mean ± SE
SEU02	5.88±0.48^{ab}	7.11±0.26^{a}	6.50±0.31^{ab}	2.55±0.55^{ab}	86.27±10.32^{abcd}
SEU06	5.00±0.69^{ab}	5.71±0.71^{abcd}	5.35±0.68^{abc}	1.42±0.20^{abc}	73.76±11.26^{bcd}
SEU09	5.50±0.26^{ab}	6.75±0.36^{ab}	6.12±0.27^{abc}	2.62±0.77^{a}	77.00±16.98^{abcd}
SEU10	5.66±0.50^{ab}	6.55±0.37^{abc}	6.11±0.35^{abc}	1.14±0.14^{abc}	59.48±9.42^{cd}
SEU14	6.28±0.52^{ab}	7.14±0.26^{a}	6.71±0.35^{a}	1.83±0.30^{abc}	75.10±14.81^{abcd}
SEU15	5.62±0.26^{ab}	5.77±0.27^{abcd}	5.68±0.24^{abc}	1.11±0.11^{bc}	113.23±7.61^{ab}
SEU16	6.00±0.44^{ab}	6.37±0.26^{abc}	6.16±0.35^{abc}	1.37±0.18^{abc}	107.74±11.53^{ab}
SEU17	6.57±0.29^{a}	6.22±0.27^{abcd}	6.42±0.22^{ab}	1.12±0.12^{bc}	77.122±12.33^{abcd}
SEU18	5.25±0.31^{ab}	5.22±0.40^{bcd}	5.37±0.30^{abc}	1.77±0.22^{abc}	105.55±4.93^{ab}
SEU19	5.77±0.22^{ab}	6.22±0.32^{abcd}	6.00±0.26^{abc}	1.55±0.24^{abc}	84.78±4.92^{abcd}
SEU20	6.11±0.30^{ab}	6.66±0.23^{abc}	6.38±0.24^{ab}	2.22±0.22^{abc}	82.14±4.61^{abcd}
SEU21	4.50±0.18^{b}	4.88±0.30^{cd}	4.81±0.16^{c}	2.00±0.23^{abc}	59.11±3.13^{d}
SEU22	5.85±0.40^{ab}	6.28±0.28^{abcd}	6.07±0.33^{abc}	1.22±0.14^{abc}	100.80±5.30^{abc}
SEU23	5.33±0.21^{ab}	5.75±0.59^{abc}	5.83±0.24^{abc}	1.88±0.30^{abc}	97.68±6.65^{abcd}
SEU25	5.71±0.35^{ab}	5.87±0.58^{abcd}	6.07±0.22^{abc}	1.11±0.11^{bc}	97.47±4.22^{abcd}
SEU26	4.88±0.26^{ab}	5.55±0.24^{abcd}	5.22±0.16^{abc}	1.44±0.17^{abc}	60.01±4.71^{cd}
RUWAN	5.75±0.31^{ab}	6.11±0.30^{abcd}	6.06±0.23^{abc}	1.77±0.27^{abc}	63.16±2.10^{cd}
BHADRA	5.62±0.37^{ab}	4.44±0.33^{d}	5.00±0.31^{bc}	1.00±0.00^{c}	116.34±5.49^{a}
$F_{(17, 114)}$	1.830	4.982	3.050	3.070	5.414
P	0.038	0.000	0.000	0.000	0.000

The table indicated the data, LIR @5 and LIR@6: plant leaf injury rates at 5th and 6th weeks after seed sowing., OLD: overall leaf damage scores of 5th and 6th weeks, CDS: Cob damage severity, YPP: Yield per plant. SE: Standard error of the mean (n = 9), Superscript letters within the column indicate the significant differences among the entities at p = 0.05 significant level on Tukey's post hoc test.

Field experiment

The result of the field experiment showed that the leaf injury rates varied significantly among the landraces during 4th ($F_{17,3}$ = 4.953, p<0.001), 5th ($F_{17,3}$ = 8.104, p<0.001) and 6th ($F_{17,3}$ = 20.828, p<0.01) weeks after sowing. In the 4th week, Bhadra had the significantly the lowest injury rate, while SEU21 showed the lowest injury rate in the 5th and 6th weeks. Similarly, the trend of overall leaf damage score was significantly lowest in SEU21, which differed significantly from the commercial variety Bhadra. Maize cob injury varied from 1.10 ± 0.26 (SEU22) to 3.23 ± 0.59 (SEU02) and yield per plant was significantly the highest in SEU18 (122.50 ± 7.49 g), followed by SEU17 (102.53 ± 8.35 g), SEU15 (90.26 ± 6.38) and SEU16 (91.98 ± 8.16) were superior to check varieties (Bhadra and Ruwan) (Table 2).

According to the standardized data best performing, four landraces were selected from each experiment. Under cage experiments, SEU18, SEU15, SEU21, and SEU06 and in the field trial SEU21, SEU25, SEU18, and SEU26 showed the best performance in terms of fewer leaf and ear injuries and a high yield per plant. Therefore, the landraces of SEU21 and SEU18 were performing well and were selected under both conditions.

The result of the principal component analysis revealed that components 1, and 2 cumulatively explained 82.83% of the variation in the cage experiment, including 53.45% of component 1 by the traits LIR@5, LIR@6, and OLD and the rest 29.38% was determined by CDS and YPP of component 2. The field experiment results showed that overall 92.06% of the variation was explained, including 49.56% (component 1) explained by LIR@5, LIR@6, and OLD, 23.38% (component 2) from CDS and 19.10% (Component 3) from LIR@4 and YPP.

According to the cluster analysis, at 40%> similarity level four distinct groups were found in the cage experiment and the best performing landraces were grouped in the same groups as SEU21 and SEU06 (G1), SEU18 and SEU15 (G4) while the commercial cultivar Bhadra stood his own. According to the field experiment, 4 distinct groups were at a similarity level of 40%> while SEU21 stood alone, however, the best performing landraces were SEU25 and SEU26, grouped in G3 next to SEU18, in G4 and Bhadra in G2. In addition, it was found that SEU02 and SEU10 differ significantly compared to the remaining entities (Figure 2).

Table 2. Leaf and cob injury rates and cob yield of maize landraces under natural infestation of FAW in field

Entry	LIR@4 Mean ± SE	LIR@5 Mean ± SE	LIR@6 Mean ± SE	OLD Mean ± SE	CDS Mean ± SE	YPP (g) Mean ± SE
SEU02	5.31 ± 0.23^{abc}	7.45 ± 0.18^{a}	7.55 ± 0.19^{a}	6.91 ± 0.13^{a}	3.23 ± 0.59^{a}	17.85 ± 7.15^{f}
SEU06	4.20 ± 0.25^{bcde}	6.55 ± 0.18^{abcd}	6.10 ± 0.19^{bcd}	5.84 ± 0.13^{bcdef}	2.50 ± 0.37^{ab}	71.39 ± 7.51^{bcde}
SEU09	4.18 ± 0.23^{bcde}	6.95 ± 0.18^{abc}	7.15 ± 0.19^{a}	6.29 ± 0.13^{abc}	1.95 ± 0.26^{ab}	73.72 ± 6.88^{bcde}
SEU10	5.04 ± 0.25^{abcd}	6.75 ± 0.18^{abcd}	7.00 ± 0.19^{ab}	6.39 ± 0.13^{ab}	2.23 ± 0.46^{ab}	42.11 ± 9.53^{ef}
SEU14	4.45 ± 0.23^{bcde}	6.25 ± 0.18^{bcd}	5.50 ± 0.19^{de}	5.46 ± 0.13^{ef}	2.22 ± 0.28^{ab}	83.74 ± 6.89^{abcde}
SEU15	4.25 ± 0.23^{bcde}	7.15 ± 0.18^{ab}	6.65 ± 0.19^{abc}	6.15 ± 0.13^{bcd}	2.34 ± 0.27^{ab}	90.26 ± 6.38^{abc}
SEU16	4.04 ± 0.25^{de}	6.30 ± 0.18^{bcd}	6.50 ± 0.19^{abc}	5.83 ± 0.13^{bcdef}	1.77 ± 0.31^{ab}	91.98 ± 8.16^{abc}
SEU17	5.05 ± 0.23^{abcd}	7.05 ± 0.18^{abc}	6.75 ± 0.19^{ab}	6.37 ± 0.13^{ab}	1.69 ± 0.38^{b}	102.53 ± 8.35^{ab}
SEU18	5.00 ± 0.20^{abcd}	6.55 ± 0.18^{abcd}	5.30 ± 0.19^{de}	5.61 ± 0.13^{cdef}	1.33 ± 0.25^{b}	122.50 ± 7.49^{a}
SEU19	5.00 ± 0.20^{abcd}	7.10 ± 0.18^{abc}	5.35 ± 0.19^{de}	5.81 ± 0.13^{bcdef}	1.49 ± 0.29^{b}	74.83 ± 8.59^{bcde}
SEU20	5.55 ± 0.20^{a}	6.15 ± 0.18^{cd}	5.05 ± 0.19^{e}	5.58 ± 0.13^{def}	1.72 ± 0.27^{ab}	76.35 ± 7.87^{bcde}
SEU21	4.50 ± 0.20^{abcde}	5.32 ± 0.19^{e}	4.10 ± 0.19^{f}	4.61 ± 0.13^{g}	1.76 ± 0.26^{ab}	46.61 ± 7.48^{def}
SEU22	5.25 ± 0.20^{ab}	7.35 ± 0.18^{a}	5.45 ± 0.19^{de}	6.01 ± 0.13^{bcde}	1.10 ± 0.26^{b}	70.05 ± 7.48^{bcde}
SEU23	5.25 ± 0.20^{ab}	6.75 ± 0.18^{abcd}	5.35 ± 0.19^{de}	5.78 ± 0.13^{bcdef}	1.17 ± 0.28^{b}	86.16 ± 8.09^{abcd}
SEU25	4.55 ± 0.20^{abcde}	6.25 ± 0.18^{bcd}	5.45 ± 0.19^{de}	$5.41 \pm 0.13d^{ef}$	1.20 ± 0.29^{b}	75.24 ± 8.58^{bcde}
SEU26	4.50 ± 0.20^{abcde}	5.95 ± 0.18^{de}	5.45 ± 0.19^{de}	5.30 ± 0.13^{f}	1.67 ± 0.29^{ab}	58.14 ± 8.59^{cdef}
RUWAN	5.00 ± 0.20^{abcd}	6.36 ± 0.20^{bcd}	4.80 ± 0.19^{ef}	5.29 ± 0.13^{f}	1.77 ± 0.28^{ab}	61.38 ± 8.08^{bcde}
BHADRA	3.78 ± 0.23^{e}	6.60 ± 0.18^{abcd}	5.65 ± 0.19^{cde}	5.49 ± 0.13^{def}	2.18 ± 0.24^{ab}	79.01 ± 7.04^{bcde}
$F_{(17, 3)}$	4.953	8.104	20.828	14.557	2.369	6.372
P	0.000	0.000	0.001	0.000	0.002	0.000

The table indicated the data LIR@4, LIR@5 & LIR@6: Plant leaf injury rates at the 4th, 5th, and 6th week after seed sowing., OLD: overall leaf damage scores of 4th, 5th, and 6th weeks, CDS; Cob damage severity, YPP: Cob yield per plant and SE: Standard error of the mean (n = 20), Superscript letters within the column indicate the significant differences among the entities at p = 0.05 significant level of Tukey's post hoc test.

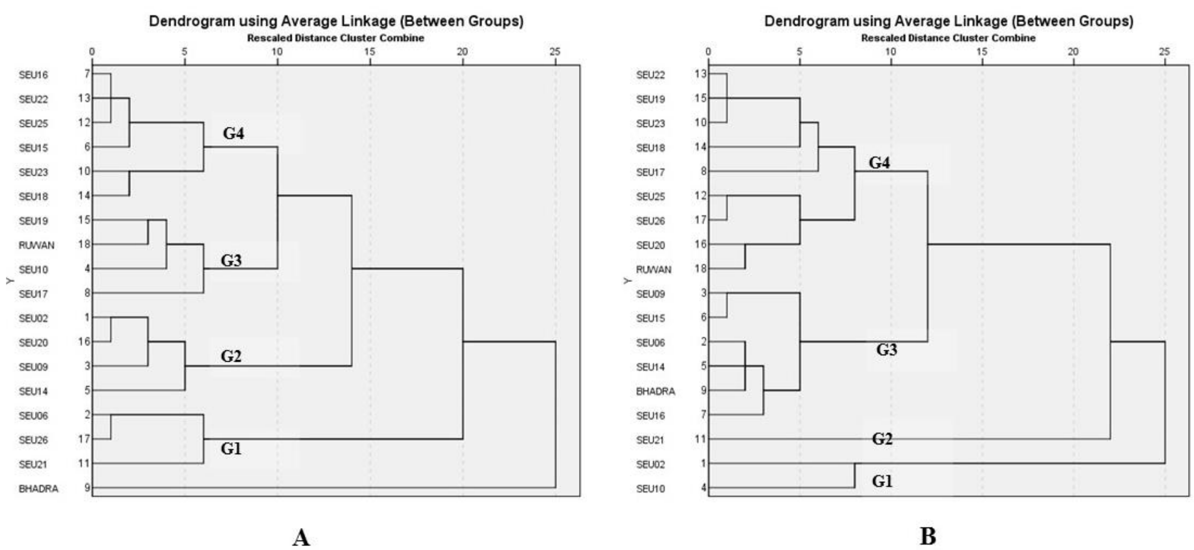

Figure 2. Clustering groups of maize landraces under cage (A) and field (B) experiments using squared Euclidean distance

Laboratory bioassay

The laboratory bioassay was performed to evaluate the effect of maize landraces on larval and pupal developmental traits and revealed that larval weight varied significantly ($F_{17, 162} = 5.931$, $p<0.01$) among landraces three days after feeding. The mean larval weights varied between 96.40 ± 13.37 mg (SEU19) - 219.20 ± 5.04 mg (SEU06). In addition, it was found that weight gain after 3 days was the lowest for SEU20 and SEU19. The pupal weight varied significantly among landraces ($F_{17, 162} = 3.35$, $p<0.01$), the lowest weight was found on SEU18 and SEU22. Larval duration ranged from 6.00 - 8.66 days and also varied significantly ($F_{17, 162} = 6.656$, $p<0.01$) among the landraces (Table 3). Leaf area consumed during the larval period varied significantly ($F_{17, 71} = 3.756$, $p<0.001$) where SEU25 had the lowest consumption and differed significantly from SEU15 and SEU10 (Figure 3).

Table 3. Larval and pupal development traits of FAW among the landraces

Entry	LWt (mg) Mean ± SE	PWt (mg) Mean ± SE	LD(Days) Mean ± SE	DWF (mg) Mean ± SE	WG (mg) Mean ± SE
SEU02	182.00±20.09^{ab}	173.33±12.41^{ab}	8.33±0.66^{a}	584.66±86.76^{ab}	141.00±28.57^{ab}
SEU06	219.20±5.04^{a}	161.00±6.5^{ab}	7.66±0.33^{ab}	362.88±7.30^{def}	182.86±4.93^{a}
SEU09	180.40±17.88^{ab}	170.33±8.64^{ab}	8.33±0.33^{a}	288.33±6.97^{def}	136.73±24.44^{ab}
SEU10	144.00±14.73^{bcd}	150.00±9.86^{ab}	8.66±0.33^{a}	383.33±7.75^{cde}	123.00±13.00^{abc}
SEU14	167.00±34.21^{abcd}	178.66±7.53^{a}	8.66±0.33^{a}	448.33±9.35^{bcd}	141.33±29.23^{ab}
SEU15	172.20±16.67^{abc}	168.00±13.61^{ab}	8.33±0.33^{a}	357.66±4.85^{def}	152.80±15.92^{a}
SEU16	154.60±32.46^{abcd}	170.33±0.33^{ab}	8.00±0.00^{ab}	724.66±5.74^{a}	136.60±32.46^{ab}
SEU17	132.20±21.61^{bcd}	166.66±3.28^{ab}	8.66±0.33^{a}	523.66±8.29^{bc}	116.86±22.19^{abcd}
SEU18	96.60±7.66^{d}	134.00±4.96^{b}	6.60±0.60^{ab}	261.40±3.16^{ef}	52.80±6.27^{cde}
SEU19	96.40±13.37^{d}	150.40±5.41^{ab}	7.20±0.73^{ab}	254.40±19.79^{ef}	47.000±8.99^{e}
SEU20	97.00±14.37^{d}	139.00±9.62^{ab}	7.20±0.58^{ab}	245.00±21.72^{ef}	39.80±9.61^{e}
SEU21	126.50±13.33^{bcd}	148.75±9.34^{ab}	6.00±0.00^{b}	234.25±8.20^{ef}	57.00±13.22^{cde}
SEU22	104.40±9.03^{cd}	134.00±8.83^{b}	6.40±0.40^{ab}	216.80±10.84^{ef}	58.00±5.47^{cde}
SEU23	110.60±3.55^{bcd}	148.40±4.50^{ab}	6.00±0.00^{b}	203.60±5.26^{f}	36.20±11.38^{e}
SEU25	117.50±1.55^{bcd}	141.00±4.60^{ab}	6.00±0.00^{b}	219.75±11.18^{ef}	56.00±12.12^{cde}
SEU26	118.80±5.77^{bcd}	145.80±5.66^{ab}	6.00±0.00^{b}	238.40±3.47^{ef}	60.80±4.01^{cde}
RUWAN	116.20±7.53^{bcd}	145.00±6.97^{ab}	6.00±0.00^{b}	195.20±5.70^{f}	77.00±5.77^{bcde}
BHADRA	157.20±17.12^{abcd}	167.60±8.41^{ab}	8.66±0.33^{a}	717.66±9.38^{a}	145.53±17.43^{ab}
F(17,162)	5.931	3.356	6.656	7.051	11.036
P	0.000	0.000	0.000	0.000	0.000

The table indicated data, Lwt: Larval weight after 3 days (mg), PWt: Pupal weight (mg), LD: larval duration (days), Dwt; dry weight fecal materials in the larval phase (mg), WG; larval weight gains after 3 days (mg) and SE: Standard error of the mean (n=10), Superscript letters indicate significant differences among the entries tested at p=0.05 significant level of Tukey's post hoc test

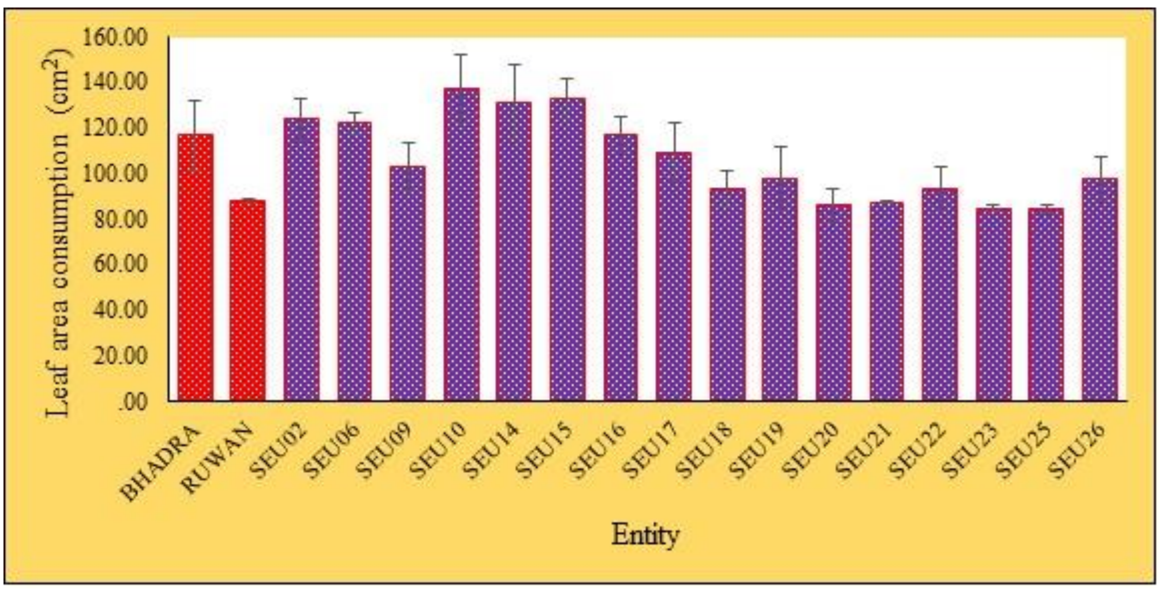

Figure 3. Leaf area consumption (cm^2) by FAW larvae among the maize landraces
(Error bars indicate the standard error, n=10)

Leaf trichome density and thickness

Leaf trichome density was significantly ($F_{17, 135}$) = 17.60, p<0.001) different among maize landraces, the lowest trichome density was found in Ruwan, SEU23, SEU18 and leaves with many trichomes were found in SEU02 (Figure 4). The leaf thickness of the maize landraces did not significantly ($F_{17, 58}$ = 1.172, p > 0.05) varied (data were not presented).

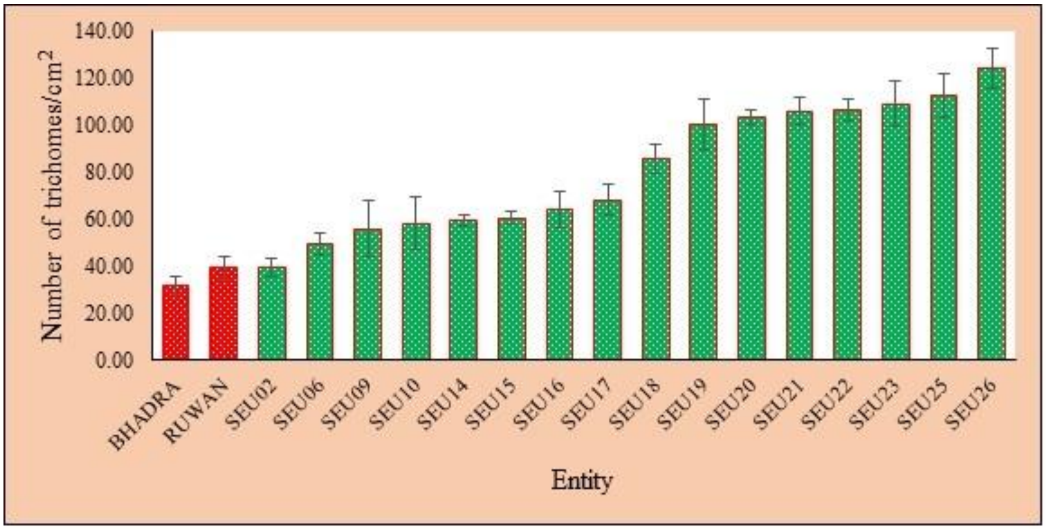

Figure 4. The number of trichome density/cm^2 variations among landraces (error bars indicate the standard error, n =10).

Discussion

The present study rigorously evaluated sixteen OP maize landraces collected from farmer fields in major maize growing areas for their potential resistance to FAW. The assessment was reconfirmed by in vitro (antixenosis and antibiosis), field (natural infestation), and cage (artificial infestation) experimental conditions. Ultimately, we found that SEU18 and SEU21 exhibited comparatively high potential resistance traits when challenged naturally and artificially infestation with FAW. According to Prasanna et al., (2018), CIMMYT identified some promising maize inbred lines with foliar damage scores between 2.0 - 6.0. Similar results were observed in our study, where SEU18, SEU15, SEU06, SEU23, SEU21, and SEU26 reported a mean leaf damage score of less than 6, while SEU18 and SEU15 reported high yield per plant, thereby these landraces were selected as the best performing landraces under artificial infestation. According to the natural infestation results, SEU06, SEU14, SEU16, SEU23, SEU25, SEU21, SEU18, SEU19, SEU20, and SEU26 showed an overall leaf damage rating of less than 6. Regarding the yield potential of natural infestation conditions, SEU18, SEU17, SEU15, and SEU14 showed the highest yield per plant with lower cob damage ratings. In contrast, SEU21 exhibited the lowest yield per plant due to its inherent low yield potential. In addition, an in vitro study identified a significant difference in leaf area consumed by larvae after their 3rd instar and a significant difference in trichome density on top of the leaf layer.

However, we could not find any relationships between trichome density and leaf area consumption. In addition, it was found that the leaf consumed by the larvae was not associated with body weight and larval duration. However, SEU21 and SEU18 showed significantly superior properties of antibiosis and antixenosis (Table 3) as thses landraces consistently showed low growth of larval and pupal development. This may be due to the antibiosis that occurs in maize plants as a resistance mechanism when the deleterious consequences of a resistant plant affect the biology of the insect pest that uses the plant as a host due to the presence of morphological or chemical plant defenses (Smith, 2005). Antixenosis is alter the behavior of an insect typically expressed as non-preference of the host plant (Seifi et al., 2012; Smith, 2005). Several authors reported that transgenic Bt maize genotypes affect FAW larval and pupal developmental traits more than conventionally by reducing larval weight (Ligia et al., 2016), lowering pupal weight (Fernandes et al., 2003), and the Bt genotypes with the ability to synthesize crystal proteins further prolong the larval lifespan, impairing larval digestibility (Mendes et al., 2011). In addition, Morales et al., (2021) on the effects of antibiosis of six maize cultivars grown by farmers in Kenya by laboratory bioassay by reducing FAW larval pupa weight. Similarly, based on the available knowledge, we observed significantly lower larvae and pupae weight when fed with SEU21 and SEU18.

Typically, two types of plant defense mechanisms against herbivores are reported, namely constitutive and induced defenses. The induction defense is common to all plants that induce metabolic pathways, *ie*. Jasmonate, salicylic acid, hydrogen peroxide, oligogalacturonic acid, and herbivore-induce volatile plant matter through which trytropic interactions arise to resist the herbivores, while constitutive defenses are species-specific, accumulating proteins and insecticidal compounds (Gatehouse, 2002). Insect adaptations to offset the effects of plant defenses can also be defined as constitutive and induced. Insect species with a limited host range tend to rely on constitutive adaptation mechanisms that can be tailored to the specific host(s), while others rely on induced plant defenses against insecticidal and protein compounds (Gatehouse, 2002). The success of polyphagous insects such as FAW can successfully counter their host plant's defense strategies and survive. At the same time, morphological or physical leaf traits are also important to mediate the interaction between host plants and phytophagous insects (dos Santos et al., 2020).

Morphological factors such as leaf fiber content (Hedin et al., 1996), silica content (Reynolds et al., 2009), leaf thickness and toughness (Davis et al., 1995), and leaf trichome density (Moya-Raygoza, 2016: Paul et al., 2020) cause avoidance behavior in insects. However, the reported trichome density is unrelated to the feeding preferences of FAW (Morales et al., 2021). According to Yang et al., (1993) showed that FAW larvae gained more weight and developed faster when fed leaves from which cuticular lipids had been removed. In addition, Chen et al., (2015) plant nutrient levels and the presence of toxic metabolites often impair host suitability and resistance to herbivores. Based on our findings, SEU18 and SEU21 possess the best overall resistance traits, allowing these two OP landraces can be suggested for future crop improvement programs to develop resistant varieties against FAW.

Conclusion

The results of the study allow the conclusion that the landrace of SEU18 and SEU21 are comparatively resistant to both natural and artificial infestation with FAW. Therefore, these landraces could be used in future breeding programs to develop FAW-resistant maize varieties.

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