Laboratory Evaluation of Host Plant Resistance on Sri Lankan Maize Landraces to Fall Armyworm (*Spodoptera frugiperda* Smith) (Lepidoptera: Noctuidae)

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Abstract- *Recently invaded fall armyworm in Sri Lanka has been regarded as a major maize pest and became a crucial pest with substantial yield losses. Management of the pest via sustainable environmentally friendly measures is essential and encourages rather than the usage of synthetic chemicals. The latent resistivity of traditional maize landraces, which are favoured by the Sri Lankan farmers has not yet been investigated. Thus, a laboratory experiment was designed to investigate the leaf-feeding and oviposition resistance of FAW in Sri Lankan maize landraces. Eight local (OP) maize landraces (SEU02, SEU06, SEU09, SEU14, SEU15, SEU16, and SEU17) with comercial varieties (Bhadra and GT722) were used. The feeding and oviposition preference assays were conducted and revealed that none of the accession showed complete resistance to FAW feeding, but detected differences in acceptance and preference with varying degrees. Nevertheless, a significant difference was observed in morphological traits viz. leaf trichomes density and leaf thickness. The Oviposition preference bioassay found that Bhadra ($\chi 2=5.4$, $df=1$, $p=0.02$,12/3) reported highly preferred by females as oviposition with the high mean number of eggs (638.40 ± 4.20), while SEU02, SUE06, SEU09, SEU10 and SEU17 ($\chi 2=5.4$, $df=1$, $p=0.02$, 3/12) reported with low preference. Our study provides insight into the density of trichomes on leaves does not seem to be linked to larvae feeding preferences at later stages of the larval phase.*

Keywords: Fall armyworm, landraces, oviposition preference, resistance

I. INTRODUCTION

Maize (*Zea mays* L.) is a cereal plant that belongs to the Poaceae family and second most important crop in Sri Lanka (Anon,2012) due to its importance as a food and feeds ingredient. As a feed, it is primarily used in the livestock industry, accounting for roughly a quarter of all poultry produced in the nation (Anon,1998). Fall armyworm (FAW) *Spodoptera frugiperda* Smith (Lepidoptera, Noctuidae) invasion has become the biggest threat to maize production and its rapid spread to almost all countries in the region and associated crop damage. Almost 50 per cent of maize cultivations were infested by FAW during the 2018/19 Maha season in Sri Lanka (Wijerathna *et al*.,2020). Buadron *et al*., (2019) reported that when there is 26.4 per cent to 55.9 per cent of pest incidence in maize then there is yield reduction under FAW damage.

The fall armyworm, *S. frugiperda* was first discovered in Sri Lanka in October 2018 as an invasive pest. FAW is a highly polyphagous insect pest that feeds on a variety of plants, including maize, sorghum, millet, sugarcane, and vegetable crops (Sisay *et al*.,2019). In addition, a higher reproductive rate and multiple generations of the pest would reason for significant crop damage in a single year. This large maize pest is difficult to control and can damage crops severely (Oliveria *et al*., 2018).

In Sri Lanka, FAW has been regulated through a variety of methods, including cultural practices, biological control, chemical control, and botanical pest control. The chemical insecticides have been become dominant mostly adopted by the farmers, which harm the environment, human health and can encourage the development of resistant populations (Paiva *et al*.,2016). Thus, management of the pest via sustainable environmentally friendly measures are essential and encourage.

Host plant resistance is a crucial part of integrated pest control (Mihm,1997). Landraces naturally possess morphological and genetic traits which are resistant to certain pests. The host plant resistance (HPR) has been investigated as a potential strategy for controlling FAW in maize crops in recent years (Paiva *et al*., 2016). It is primarily due to the host plant's antibiosis and antixenosis characteristics, which alter the insects' feeding and behaviour. Finding FAW-resistance maize landraces may be a key component of developing long-term strategies to combat this voracious insect and reduce yield losses in low-input agriculture in developing countries (Mihm *et al*,1988). Since the 1950s, extensive screening for FAW-resistant maize germplasm has been carried out in the Americas (Wiseman *et al*.,1979). However, the most common maize landraces, which are grown by smallholder farmers in Sri Lanka, have not been tested for resistance to FAW yet. Smallholder farmers have grown these open-pollinated varieties (OPVs) for generations because they are drought and pest resistant, have low seed costs and produce fair yields under marginal environmental conditions without the use of fertilizers or pesticides (Odendo *et al*., 2001).

However, the latent capacity for resistance of traditional maize landraces, which are favoured by Sri Lankan farmers, has not yet been investigated. Thus, an experiment was designed to evaluate the leaf-feeding and oviposition preference of FAW against Sri Lankan maize landraces in the laboratory. It was hypothesized that FAW larval arrestment (*i.e*., behaviour that restricts the insect's movement to a limited area), feeding, development, and plant damage differ depending on maize landraces and that these variables could be used as a proxy for FAW resistance.

II. METHODOLOGY

A. *Study Area*

The experiments were conducted in the Crop science laboratory, Faculty of Technology, South Eastern University of Sri Lanka (7 ̊18̓ 00.3" N and 81º 51̓ 41.8" E), located in Ampara district which belongs to the low country dry zone (WL2b) during December 2020 to April 2021.

B. *Planting materials*

A total of eight local maize landraces viz. SEU02, SEU06, SEU09, SEU10, SEU14, SEU15, SEU16, SEU17 which were collected major maize growing areas in Ampara, Moneragala, and Badulla districts were used for the study (Mufeeth *et al*., 2020). Seeds of selected landraces with commercial varieties, GT 722 and Bhadra were sawn in polythene pots (8L) and small disposal cups (150 ml). The media consisted of sand: topsoil: compost 1:1:1 ratio. Crops were managed without applying any synthetic chemicals and plants were at V3-V4 stages were used for the bioassay.

C. *FAW Culture*

The rearing of FAW was conducted at particular conditions as temperature (27 ± 2 ºC), 70-75 % RH, and a photoperiod of 14:10 (L: D) (Murua *et al*.,2008). The Egg masses were collected from infected maize plants at Agro Tech Park, Malwatta, and kept inside plastic bottles (2.5 L) with proper ventilation. To keep fresh, a wet tissue paper was kept inside the plastic bottle before introduction eggs. The 3rd instar larvae were transferred to individual cups (150 ml) and maintained separately to avoid cannibalism. Leaf was renewed daily and the amount of leaf provided was altered during the development of the caterpillars, to avoid any insufficiency of foods and a clean culture environment to avoid contaminations. After 50% of the pupation, they were sex separated (Sharanabasappa *et al*., 2018) and adults were kept in plastic bottles (2.5L) by feeding 10% sucrose solution, and muslin cloths were provided as the oviposition substrate.

D. *Leaf morphological traits*

The experiment was laid out on a completely randomized design (CRD) with 3 replications and plant morphological characteristics of selected ten accessions were recorded at the V7 stage. Leaf thickness (LT) was measured from the 15 leaves using the vainer calliper average was calculated. Similarly, Leaf trichomes density (LTD) was measured using size (1 cm x 1 cm) leaf samples from each accession were counted under a stereo zoom microscope. measurements were replicated five times.

E. *Larval feeding bioassay*

The study was designed to evaluate the feeding preference of the FAW larvae under laboratory conditions. The third instar larvae were introduced individually into the small plastic bottles. Each larva was provided with an adequate amount of leaf dishes (2 cm x 2 cm) from the V3 stage of selected eight landraces separately. Leaf dishes were renewed daily and to keep the freshness, wetted tissue papers were laid on the bottom of plastic bottles. The experiment was replicated six times and the following data were recorded. Leaf area consumption (LAC) was evaluated daily throughout the larval phase, determination of LAC was determined as the difference between leaf area offered and leaf area consumption after 24 hours. The larval weight (LW) (g) at 3-day intervals and pupal weight (PW) (g) were measured using an electric balance. Moreover, larval duration (LD) and pupal duration (PD) (days) were recorded. The dry weight of faeces (DWF) was measured in weekly intervals.

F. *Four choice oviposition preference study*

Oviposition preference for the gravid females to oviposition was assessed using four-choice oviposition chambers prepared by OHP transparent sheets (Fig 01). The rectangular shape boxes and cylinders were connected to each side. Four plants (V3-V5) from each landrace were kept on each side and ten gravid females were released into the middle of the oviposition chamber. Plants were replaced 24 hours after the moths introduction and the number of eggs/egg masses was counted using a Seteriozoom microscope. The end of each bioassay oviposition chamber was turned 180° from the position to prevent the effect of position. The study was replicated fifteen times for each landrace.

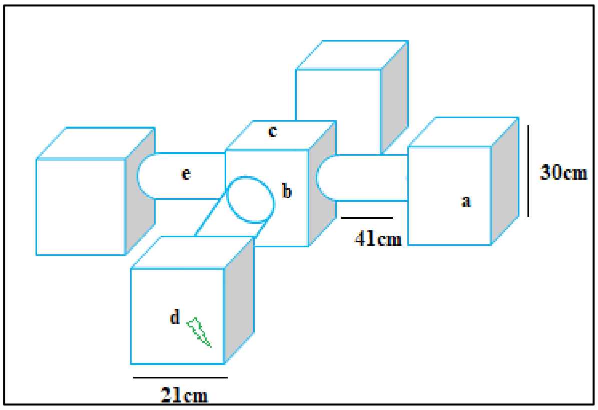

Figure 1: Four choice oviposition chamber

a. Rectangular shape box, b. Middlebox ,c. The honey solution,b. Maize plants, and e. Cylinder

G. *Statistical analysis*

Data were subjected to analysis of variance (ANOVA) procedure and the means were separated by Tukey post hoc test at p-value equal to 0.05, using IBM SPSS (version 25) statistical package. The varietal preference for oviposition was determined by the Chi-square test.

III. RESULTS

A. *Leaf morphological traits*

The results showed that significant differences ($p < 0.05$) in leaf thickness (LT) and leaf trichomes density (LTD) among the tested landraces. LT was significantly higher in the commercial variety GT 722 (4.14 ± 0.35 cm) compared to the SEU 10 which showed the least (2.78 ± 0.26 cm) (Fig.2). Whereas LTD was significantly higher in the SEU02 (124.20 ± 8.45) compared to the GT722 (59.00 ± 3.98) and SEU10 (59.20 ± 2.22) and which were the lowest than rest of the local landraces (Fig.3).

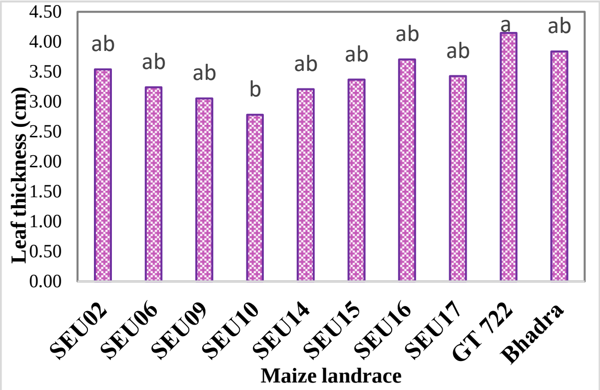

Figure 2: Leaf thickness of selected maize landraces.

Each column represents the mean leaf thickness (cm), followed by the same letter in the columns are not significantly different by the Tukey post hoc test at 0.05 significant level (n =06).

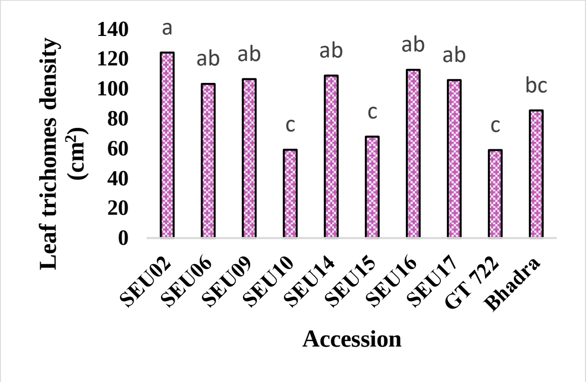

Figure 3: Leaf trichomes density of selected maize landraces.

Each column represents the mean number of trichomes present in the one square cm of the leaf blade. The same letter followed by the columns is not significantly different by the Tukey post hoc test at 0.05 significant level (n = 6).

B. Four choice oviposition preference study

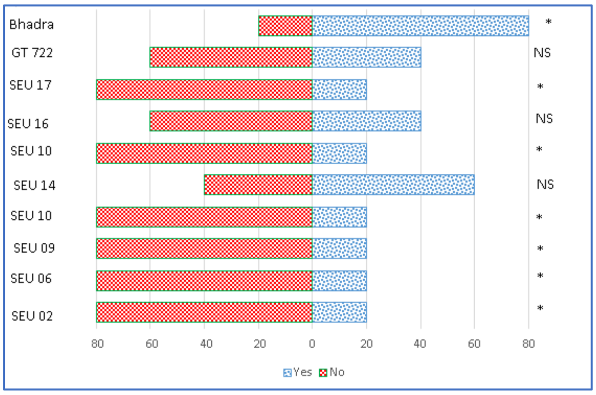

Figure 4: The oviposition preference among maize accessions in four-choice oviposition experiment after 24 hours.

Asterisks represent significant differences (* $p \leq 0.05$) and (ns) represent no significant difference between landraces (n = 15), based on the Chi-square test.

The results of gravid female's preference for oviposition among the selected accessions indicated that three out of ten which GT722, SEU16 and SEU14 having a neutral preference for egg-laying. However, remaining accessions SEU02, SUE06, SEU09, SEU10 and SEU17 ($\chi2$=5.4, df= 1, p=0.02, 3/12) were significantly lower preference. Eighty per cent females were repelled by these accessions compare to the other three accessions in the arms. Nevertheless, Bhadra ($\chi2$=5.4, df =1, p=0.02,12/3) reported an inverse relationship where 80% of the females were more willing to select those plants as their egg-laying substrate (Fig.3).

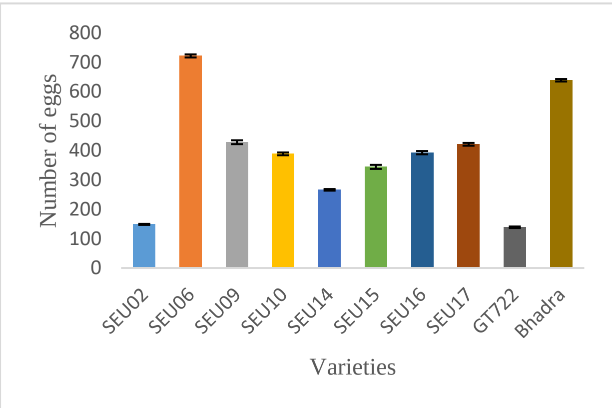

Figure 5: The number of FAW eggs were not statistically different between maize varieties.

The mean number of eggs of a 24-hour duration period among accessions showed SEU06 (721.20 ± 5.23) and Bhadra (638.40 ± 4.20) were higher whereas GT722 (138.60 ± 2.63) and SEU02 (148.20 ± 1.75) were lower.

C. Larval feeding bioassay

None of the landraces was reported significant differences (p<0.05) for the evaluated larval parameters. The mean larval weight (LW) was varying 0.22-0.36g among the accessions and which showed highest at SEU06 (0.36±0.00 g) and the lowest weight were at SEU17(0.22 ± 0.03 g) (Table 01). The mean Fecal weight (FW) of accession showed that SEU16 (0.72 ± 0.05g) was weightiest as well SEU09 (0.28 ± 0.02g) was the lowest (Table 01). There was no apparent significant difference among the leaf area consumption (LAC) by the larvae on each accession. The mean LAC of the lifetime of the larvae were varied from 101.8 -137.05 mm^2. The commercial elite variety GT722 (101.68±14.10mm^2) was highly resistant to leaf-feeding compared to other tested accessions. (Table 01). As same as per the other measured larval traits the mean PW of varieties showed a lack of significant difference among the accessions however apparent differences were observed among SEU14 (0.178±0.007g) and the SEU10 (0.150±0.017g) (Table 01). The Larval duration (LD) are almost similar among the accessions and it was between 7.6-8.6 days (Table 01).

Table 01: Different parameter under larval feeding bioassay on selected maize landraces

Varieties	Larval weight(g)	Fecal weight(g)	Leaf area consumption (cm^2)	Larval duration (days)	Pupal weight (g)
SEU02	0.30±0.03	0.45±0.16	123.94±9.15	8.33±0.66	0.17±0.01
SEU06	0.36±0.00	0.31±0.09	121.97±4.77	7.66±0.33	0.16±0.00
SEU09	0.30±0.02	0.28±0.02	102.97±10.76	8.33±0.33	0.17±0.00
SEU10	0.24±0.02	0.38±0.04	137.05±14.82	8.66±0.33	0.15±0.00
SEU14	0.27±0.05	0.41±0.10	131.42±16.08	8.66±0.33	0.17±0.00
SEU15	0.28±0.02	0.44±0.13	133.16±8.88	8.33±0.33	0.16±0.01
SEU16	0.25±0.05	0.72±0.05	117.01±7.54	8.00±0.00	0.17±0.00
SEU17	0.22±0.03	0.52±0.05	109.40±12.82	8.66±0.33	0.16±0.00
GT722	0.29±0.05	0.56±0.04	101.68±14.10	8.00±0.00	0.17±0.00
Bhadra	0.26±0.02	0.61±0.13	116.90±15.33	8.66±0.33	0.16±0.00

The values of respective colums indicated the mean ± SE, (n = 15)

IV. DISCUSSION

The ten maize landraces with two commercial varieties (GT 722 and Bhadra) were assessed in the experiments in laboratory and field studies. Landraces were rigorously evaluated for several aspects of resistance to FAW feeding. However, none of the landraces was found to be fully resistant to FAW larvae feeding but some differences in acceptance and preference were observed under experiments. In Larval feeding bioassay, larval weight, pupal weight, leaf area consumption, larval duration and faecal weight were also measured. According to findings feeding pattern on maize landraces by third instar larvae were not statistically different. However, there was a trend with larvae consuming relatively more leaf area of SEU 10 variety compared to GT722. Furthermore, many factors unrelated to choice affect how much an insect eats; for example, larvae will consume more of a low-protein or high-protein inhibitor-rich plant to compensate for its lower nutritional value (Knolhoff and Heckel.,2014).

Through experiments investigating insect weight gain, we show that FAW larvae gained more weight on the SEU06 variety compared to the same instars developed on the rest of the accession. Indeed, several studies have shown that certain maize cultivars have an impact on larvae weight (Wiseman *et al*.,1996), development period (Wiseman *et al*.,1986), and mortality of FAW larvae (Wiseman *et al*.,1986) when used as food. Some forms of Flavones-C-glycosides and chlorogenic acid, for example, have been shown to have antibiosis activity in maize plants. (Mihm.,1997). FAW feeding activates other defence mechanisms, such as maize defence genes (Chuang *et al*.,2014) or toxic proteins (Chuang *et al*.,2014). Characteristics of plant cultivars that impart partial insect resistance often affect their biology and subsequent performance (Gatehouse.,2002). The same pattern was also observed for the pupal weight. The mean PW on varieties showed that SEU14 was higher among the SEU10 was the lower. The selection and acceptance of a host plant by an insect is the product of the integration of the insect's internal physiological state parameters and involves several behavioural steps (Knolhoff *et al*., 2014). Initially, when an insect touches a plant, it evaluates physical and chemical plant traits which are often used to make an initial behavioural decision on whether to accept or reject a plant. During the evaluation process, insects restrict their movement to a smaller location, a behaviour known as arrestment. The insect will then test-bite the plant, and if its nervous system considers the sensory information to be positive, the final decision will be taken, the host plant will be accepted, and food intake will begin (Schoonhoven *et al*.,2017). Plant organs and tissues, as well as secondary toxic metabolites including trichomes, wax crystal structures, leaf thickness and longevity, and silica material, may influence host-plant selection actions and are part of the plant's array of direct defences

(Gatenhouse.,2002). Several characteristics of maize cultivars have been reported to confer resistance to FAW damage. Cuticular lipids in maize leaves, for example, have been found to influence FAW larvae performance. FAW larvae that were fed leaves without cuticular lipids weighed more and grew faster than those that were fed leaves with cuticular lipids. (Yang *et al*.,1993). FAW neonate larvae migrated longer distances and crawled faster on upper leaves with a smooth appearance than on lower leaves with a thick array of wax crystals, according to another report. (Yang *et al*.,1993). The Leaf trichomes density and leaf thickness were all calculated as part of the morphological character measurement experiment. The results showed that significant differences ($p < 0.05$) in leaf thickness (LT) and leaf trichomes density (LTD) among maize tested plants. LT was significantly higher in the commercial variety GT 722 compared to the SEU 10. LTD was significantly higher in SEU02 compared to the GT722 and SEU10. Lipophilic constituents of leaf surfaces (alkenes, esters, and fatty acids) and secondary plant metabolites, on the other hand, have been shown to encourage test-biting and subsequent feeding in a variety of insects. (Schoonhoven *et al*.,2007). Four choices oviposition preference experiment number of eggs/egg masses were counted. The mean percentage of female moths were significantly different such as SEU02, SEU06, SEU09, SEU10, SEU15, SEU17 and Bhadra landraces. Thus this could be more favourable volatiles include in the Bhadra variety compare to others. Finally, we could not have identified distinct high levels of resistance accessions to larvae feeding in our analysis of FAW larval preferences on Sri Lankan maize landraces. Thus to trap latent genetic diversity trials should be extended to landraces of remaining maize growing areas in Sri Lanka. Moreover, field trials will be conducted under natural infestation.

V. CONCLUSION

These results indicate that the tested maize landraces do not have full resistance to FAW larval feeding. Certain maize cultivars, however, have different levels of acceptance and preference. The density of trichomes on maize leaves does not seem to be linked to larvae feeding preferences after the later stages of the larval phase. It could be the Bhadra variety contains more desirable volatiles for the gravid female attractant compounds.

REFERENCES

Anonymous., (2012). AgStat. The pocket book of agriculture statistics. Socio Economic and Planning Centre, Department of Agriculture, Peradeniya, Sri Lanka, 21p.

Anonymous.,1998).Saubhagyamath Sri Lankawak Sandaha. Crop recommendations. (In Sinhala medium) Department of Agriculture, Sri Lanka, pp. 7-9.

Baudron, F. Zaman-Allah, M.A. Chaipa, I.; Chari, N.; Chinwada, P. (2019). Understanding the factors influencing fall armyworm (Spodoptera frugiperda J. E. Smith) damage in African smallholder maize fields and quantifying its impact on yield. A case study in Eastern Zimbabwe. *Crop Prot*., 120, 141–150.

Chuang, W.P.; Herde, M.; Ray, S.; Castano-Duque, L.; Howe, G.A.; Luthe, D.S. (2014). Caterpillar attack triggers accumulation of the toxic maize protein RIP2. *New Phytol.*, *201*, 928–939.

Chuang, W.P.; Ray, S.; Acevedo, F.E.; Peiffer, M.; Felton, G.W.; Luthe, D.S. (2014) Herbivore cues from the fall armyworm (*Spodoptera frugiperda*) larvae trigger direct defences in maize. *Mol. Plant Microbe Interact*, *27*, 461–470.

Costa, E.N., Fenandes, M.G., Medeiros, P.H., Evangelista, B.M.D. (2020). Resistance of maize landraces from Brazil to fall armyworm (Lepidoptera:Noctuidae) in the winter and summer seasons. *Bragantia*, 79(3), 377-386.

Gatehouse, J.A. (2002). Plant resistance towards insect herbivores: A dynamic interaction. *New Phytol*., *156*, 145–169.

Knolhoff, L.M., Heckel, D.G. (2014). Behavioral assays for studies of host plant choice and adaptation in herbivorous insects. *Annu. Rev. Entomol.*, *59*, 263–278.

Malaviarachchi, M.A.P.W.K., Costa, W.A.J.M., Fonseka, R.M., Kumara, J.B.D.A.P., Abhayapala, K.M.R.D., Suriyagoda, L.D.B. (2014). Response of maize (*Zea mays* L.) to a temperature gradient representing long-term climate change under different soil management systems. *Agricultural Research*., 25 (3): 327 – 344.

Murua, M.G., Vera ,M.T., Abraham, S., Juarcz, M.L., Prieto, S., Head, G.P., Willink, E. (2008). Fitness and mating compability of Spodoptera fruigiferda (Lepidoptera:Noctudia) Populations from different host plant species and rigons in Argentina. *Annals of the Entomological Society of America*., 3:639-649.

Mihm, J.A. (1997). Insect Resistant Maize-Recent Advances and Utilization; Mihm, J.A., (Ed.) *CIMMYT: El Batan*, Mexico, p. 304.

Muffeth, M., Mubarak, A.N., Ranaweera, G.K.M.M.A., Nusrathali, N., Roshana, M.R., RifnaBanu, A.R.F., Kumara, A.D.N.T. (2020). Characterization of morphometric,physiological and biomass production in local maize(Zea mays L.)

landraces of Sri Lanka. *Sri Lankan Journal of technology,* 1(1): 21-29.

Midega, C.A.O., Pickett, J.A., Hooper, A., Pittchar, J.O., Khan, Z.R. (2016). Maize landaraces are less affected by Striga hermonthica relative to hybrids in Western Kenya. *Weed Technol*. 30, 21–28.

Odendo, M., de Groote, H., Odongo, O.M. (2001). Assesment of farmers' preferences and constraints to maize production in the moist mid-altitute zone of Western Kenya. *Afr. Crop Sci. Conf. Proc*. 5, 769–775.

Prasanna, B.M., Bruce, A., Winter, S., Otim, M., Asea, G., Sevga, S., Ba, M. (2018). Host plant resistance to fall armyworm. Fall Armyworm in *Africa.A guide for Integrated Pest Management*, 45-62.

Paiva, L.A., Correa, F., Silva, F.C., da Silva Araujo, M., de Jesus, F.G. (2016). Resistance of corn genotypes to fall armyworm Spodoptera frugipereda (Lepidoptera:Noctuidae).*African Journal of Biotechnology*,15(35),1877-1882.

Ranaweera, N.F.C., de Silva, G.A.C., Fernando, M.H.J.P., Hidagala, H.B.(1984). Maize production in Sri Lanka. *CGPRT*., pp86-90

Sisay, B., Tefera, T., Wakgari, M., Ayalew, G., Mendesil, E.(2019). The efficacy of selected synthetic insecticides and botanicals agaist fall armyworm, *Spodoptera frugiperda,* in maize .*Insects*,10(2),45.

Schoonhoven, L.M., van Loon, J.J.A., Dicke, M. (2007). *Insect-Plant Biology*, 2nd ed.; Oxford University Press: New York, NY, USA, p. 421.

Tamiru, A., Bruce, T.J.A., Midega, C.A.O., Woodcock, C.M., Birkett, M.A., Pickett, J.A., Khan, Z.R. (2012). Oviposition Induced Volatile Emissions from African Smallholder Farmers' Maize Varieties. *J. Chem. Ecol*., 38, 231–234.

Wijerathna, D.M.I.J., Ranaweera, P.H., Perera, R.N.N., Dissanayake, M.L.M.C., Kumara, J.B.D.A.P. (2020). Biology and feeding preferences of Spodoptera frugiperda (Lepidoptera: Noctuidae) On maize and selected vegetable crops. The Journal of Agricultural Sciences - Sri Lanka. Pp 126-134.

Wiseman, B.R., Davis, F.M., Williams, W.P., Widstrom, N.W. (1996). Resistance of a maize population, FAWCC(C5), to fall armyworm larvae (Lepidoptera: Noctuidae). Fla. Entomol. 79, 329–336.

Wiseman, B.R., Widstrom, N.W. (1986). Mechanisms of Resistance in 'Zapalote Chico' Corn Silks to Fall Armyworm (Lepidoptera: Noctuidae) Larvae. *J. Econ. Entomol. 79*, 1390–1393.

Wiseman, B.R., Davis, F.M. (1979). Plant Resistance to Insects Attacking Corn and Grain Sorghum. *Fla. Entomol*. 62, 123–130.

Yang, G., Wiseman, B.R., Isenhour, D.J., Espelie, K.E. (1993). Chemical and ultrastructural analysis of corn cuticular lipids and their effect on feeding by fall armyworm larvae. *J. Chem. Ecol*. 19, 2055–2074.