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Influence of fall armyworm *Spodoptera frugiperda* egg mass scales and layers on the performance of three species of egg parasitoid *Trichogramma* with different ovipositor lengths

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Abstract

Background The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a highly polyphagous and destructive pest of maize and other cereal crops. Biological control is a potential alternative to chemical insecticides used for the management of FAW in maize. Egg parasitoids are promising biocontrol agents as they kill the insect pest at their egg stage before it hatches, thus preventing the damaging larval stage. *Trichogramma* is widely used in augmentative biological control of FAW in native and invaded regions. However, FAW lay egg masses in layer by layer and eggs are covered with egg scales, this may affect the performance of *Trichogramma* parasitoids. Therefore, the parasitism potential of three *Trichogramma* species was studied on eggs with or without scales and layered eggs of FAW, further the impact of parasitoids ovipositor length on parasitism was also determined. This helps to understand the parasitism potential of parasitoids on different egg type for better implementation of biological control programs against FAW.

Results The effect of FAW egg mass with or without scales and layered eggs on the performance of *Trichogramma chilonis*, *T. pretiosum* and *T. mwanzai* was studied and results indicated that egg mass scales and the layered eggs were significantly affected the parasitism potential of *Trichogramma* species, but did not affect the parasitoid emergence. In general, *T. chilonis* parasitized a higher percentage of eggs with or without scales and layered eggs of FAW than the other two species. *T. chilonis* and *T. mwanzai* had a greater ovipositor length than *T. pretiosum*.

Conclusion The performance of evaluated *Trichogramma* species on FAW eggs with or without scales and layered eggs affected the parasitism success. The parasitism success of *T. chilonis* was comparably higher than other tested species. Hence, the scales on egg masses and layered eggs of FAW should be taken into account while selecting the *Trichogramma* species in the biological control of FAW.

Keywords Egg parasitoids, Invasive, Biological control, *Spodoptera frugiperda*, Maize

Background

Eggs of insects are highly vulnerable and prone to mortality, since they are directly exposed to the environment and at risk of predation by other arthropods (Fatouros et al. 2020). However, various defense mechanisms can protect the egg stage, such as parental egg care, small egg

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size, faster egg development, hidden egg laying and secretion of defensive materials, such as pro-toxins against natural enemies (Fatouros et al. 2020). In addition, many insects use their hairs or scales, fecal matter, and secretions from glands to cover the eggs, creating a physical barrier for predators and parasitoids (Hilker and Meiners 2002). Lepidopterans have evolved several defense mechanisms, the most common being the use of toxic hairs or scales to protect eggs (Luna et al. 2016). Females in several lepidopteran families protect their eggs by depositing deciduous scales over and/or around them during oviposition (Fukuda et al. 2007). These scales often originate from an anal tuft at the tip of the female abdomen (Hou et al. 2022). Such scales protect the eggs by acting as an effective physical shield, giving an aposematic warning to natural enemies and also preventing the eggs from being washed away by rain.

The thickness of scales deposited on eggs varies among lepidopteran species (Hou et al. 2022). Several eggs or egg masses are covered in scales, and many are also left uncovered by females during oviposition. Females of several species deposit compact egg masses in multiple layers covered with scales of varying thicknesses (Peterson 1961). The outermost layer is deposited with thicker scales, which enhance the egg's protection against parasitoids (Hou et al. 2022). This thicker scale cover increases the handling time and impacts the control efficacy of parasitoids (Beserra et al. 2005). For example, the egg parasitoid *Trichogramma embryophagum* (Hbg.) prefers to parasitize the eggs of the pine processionary moth, *Thaumetopoea pityocampa* (Den. & Schiff.) that are situated in the top layers, or those not covered with scales (Tsankov 1990). Therefore, it becomes more essential to assess the possible impact of scales and layered eggs on the efficacy of biocontrol agents, such as egg parasitoids, when developing biocontrol programs (Li et al. 2023).

Globally, several species of the genus *Spodoptera* (Lepidoptera: Noctuidae) are polyphagous and destructive crop pests (Sparks 1979). Among these, fall armyworm (FAW), *S. frugiperda* is a notorious pest of maize and other cereal crops (Kenis et al. 2022) in its native range of the Americas and invaded regions, such as Africa, Asia and Oceania (CABI 2023). Due to the high damage potential of FAW, chemical insecticides are often used for the management of this pest. However, the application of these toxic chemical insecticides poses risks to non-target organisms, humans and the environment (Nicolopoulou-Stamati et al. 2016). Thus, the use of biocontrol agents for FAW management is widely encouraged for the safe production of maize (Kenis 2023). The use of egg parasitoids is widely practiced and is a key strategy in the management programs of FAW in both native and invaded regions of the world (Navik et al. 2023). The eggs laid in superimposed layers and covered with scales alter the oviposition behavior, making it harder for parasitoids to act and thereby influencing the control efficacy (Dong et al. 2021). Therefore, the scale of FAW eggs and layers should be taken into account while understanding the interaction between parasitoids and their hosts for better implementation of egg parasitoids in FAW management (Hend et al. 2023). In the present study, the parasitism potential of three *Trichogramma* species, namely *T. chilonis, T. pretiosum* and *T. mwanzai* on FAW egg masses with or without scales and layered eggs was investigated to find suitable parasitoids species for mass production and augmentative releases for FAW management.

Methods

Parasitoids and host insects

A colony of *T. chilonis* was established from the parasitized egg mass of FAW collected from a maize field in Chikkaballapur, Karnataka, India, in 2018–19 (Navik et al. 2021). *Trichogramma pretiosum* Riley and *T. mwanzai* Schulten and Feijen were collected from the ICAR-National Bureau of Agricultural Insect Resources, Bengaluru, India. These egg parasitoids were maintained and reared on eggs of *Corcyra cephalonica* (Stainton) under laboratory conditions (27 ± 2 °C; 65 ± 5% RH; 14:10 h L:D photoperiod). Before experimentation, all *Trichogramma* species were rejuvenated by transferring them for at least one generation on FAW eggs. Fall armyworm larvae (L3–L6) were collected from a maize field in Chikkaballapur, Karnataka, India (13° 27′ 44″ N 77° 37′ 11″ E) in 2021–22. Laboratory colonies of FAW were established by rearing larvae on an artificial diet (Ballal et al. 1995) in individual vials under controlled conditions (27 ± 2 °C; 65 ± 5% RH; 14:10 L:D photoperiod). Following emergence, moths were collected and transferred into an insect-rearing cage (45 × 45 × 45 cm) with fresh maize leaves and the moths were fed using cotton balls dipped in a 50% honey solution. The maize leaves containing egg masses were collected daily and fresh leaves were provided to the adults for oviposition during the experiment. To synchronize parasitoid emergence, *Trichogramma* species were reared on UV-treated *C. cephalonica* eggs by exposing them at different times based on their developmental period on aforementioned factitious host under controlled laboratory conditions (27 ± 2 °C; 65 ± 5% RH; 14:10 L: D photoperiod).

Effect of egg scales and layered eggs on *Trichogramma*

During the study, two factors were considered; parasitoid species and host types. Three species of *Trichogramma* viz. *Trichogramma chilonis*, *T. mwanzai* and *T. pretiosum* were tested to determine the impact of host type on parasitism: (1) egg mass with or without scales and, (2)

number of layers in FAW egg mass under laboratory conditions (27 ± 2 °C, 65 ± 5% RH; 14:10 L:D photoperiod). Ten newly emerged mated females (< 12 h old) of each *Trichogramma* species were introduced in glass vials (15 cm length × 2.5 cm diameter) containing one fresh egg mass. For each species, the egg mass with or without scales and egg mass in different layers (single, double and triple layers) were individually exposed for parasitism. To select egg mass with scales or layers, newly laid FAW egg masses (less than 24 h old) having natural variations in scale thickness (with or without scales) or egg masses laid naturally in different layers viz. single, double and triple layers were used for experimentation. Such egg masses were obtained by pairing newly emerged female and male adults of FAW. There were 20 replicates for each parasitoid species and egg types. Each replicate contained one egg mass. The number of eggs within egg mass ranged 123 ± 6.51 to 151.15 ± 7.98 for eggs with or without scales and was 110 ± 2.16 to 170.05 ± 10.75 for layered FAW eggs. The females were allowed to parasitize FAW eggs for 24 h and afterward females were removed and discarded. The vials were incubated under controlled conditions and observed daily until parasitoid emergence. The neonate larvae that hatched from unparasitized eggs were removed using a brush. On the seventh day, the number of parasitized eggs was recorded under a stereozoom microscope. Further, the egg masses were checked daily to determine the emergence of parasitoids until no more wasps emerged. The parasitism and emergence rates were calculated using the following equations (Hou et al. 2018).

$$\text{Parasitism (\%)} = \left(\text{Number of parasitized host eggs (turned black) / total number of host eggs}\right) \times 100.$$

$$\text{Percentage of emergence (\%)} = \left(\text{Number of parasitized eggs with emergence hole/ number of parasitized eggs}\right) \times 100$$

Ovipositor measurement

The females of each *Trichogramma* species reared on FAW eggs were processed and mounted on glass slides as described by Noyes (1982). The length of the female ovipositor of each parasitoid species was measured, following the procedures described by Grenier et al. (2001) under a compound microscope (Olympus BX43; Camera: Olympus SC50). In total, twenty female wasps, mounted on glass slides (Make: HiMedia) and their length of ovipositors were measured.

Statistical analysis

Percent parasitism, percent emergence, percentage of female progeny, developmental time and numbers of progeny that emerged from each parasitized FAW eggs were analyzed using two-way ANOVA. The means were separated by using Tukey's post hoc significance test at a significance level of 5%. The data on percent parasitism, percent emergence and percent female progeny were arcsine transformed to stabilize variances and untransformed means ± SE were presented. The ovipositor length of *Trichogramma* species was subjected to one-way ANOVA and means were separated by using Tukey's post hoc test ($P = 0.05$). Before conducting ANOVA, the data were tested for normality using the Shapiro–Wilk test. All analyses were performed using SAS Analytics software (SAS version 9.3; SAS Institute 2011).

Results

Effect of FAW egg scales on performance of *Trichogramma*

The performance of the three *Trichogramma* species viz. *T. chilonis, T. pretiosum* and *T. mwanzai* was evaluated on FAW eggs with or without scales. The egg parasitism was significantly different between the egg mass with or without scales ($F = 74.13$; $df = 1, 114$; $P < 0.0001$) and the parasitoids species ($F = 9.99$; $df = 2, 114$; $P = 0.0001$). The interaction between the FAW egg types and parasitoid species was non-significant ($F = 0.32$; $df = 2, 114$; $P = 0.723$). The parasitism of *T. chilonis, T. pretiosum* and *T. mwanzai* was significantly different for egg mass with scales ($F = 8.04$; $df = 2, 57$; $P = 0.0008$) or without scales ($F = 4.39$; $df = 2, 57$; $P = 0.0169$) (Fig. 1A). The higher egg parasitism was recorded by *T. chilonis* on FAW egg masses with (30.32 ± 1.23%) or without scales (52.64 ± 3.63%). There was non-significant difference in between the emergence rate of parasitoids from FAW egg mass with or without scales ($F = 0.30$; $df = 1, 114$; $P = 0.585$), however, it was significantly differed between the species ($F = 9.15$; $df = 2, 114$; $P = 0.0002$). The interaction between the FAW egg types and parasitoid species was non-significant ($F = 0.55$; $df = 2, 114$; $P = 0.578$). A higher percentage of adult emergence was recorded for *T. chilonis* and *T. mwanzai* (Fig. 1B).

Effect of FAW layered eggs on performance of *Trichogramma*

The performance of the *Trichogramma* species viz. *T. chilonis, T. pretiosum* and *T. mwanzai* was evaluated on different layers of FAW eggs. The parasitism level significantly varied with the number of layers in FAW egg mass ($F = 264.54$; $df = 2, 171$; $P < 0.0001$) and the

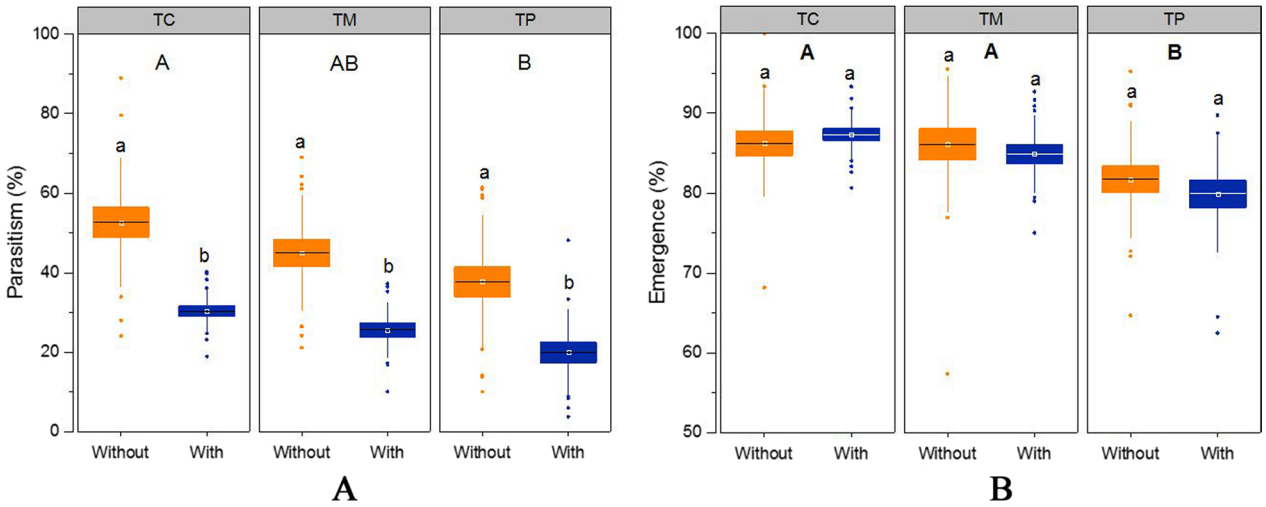

Fig. 1 Parasitism and emergence rate of *Trichogramma* species on FAW eggs with or without egg scales (**A** parasitism rate; **B** emergence rate). *TC Trichogramma chilonis*, *TM T. mwanzai*, *TP T. pretiosum*. Bars with different uppercase letters on the top of error bars indicate significant differences among parasitoid species and with different lowercase letters indicate significant differences between egg types ($P < 0.05$, Tukey's test)

parasitoid species ($F = 18.55$; $df = 2, 171$; $P < 0.0001$). The interaction of parasitoid species and the number of layers in FAW egg masses was non-significant ($F = 1.97$; $df = 4, 171$; $P = 0.1006$). The percentage of egg parasitized by *T. chilonis* ($F = 85.35$; $df = 2, 57$; $P < 0.0001$), *T. pretiosum* ($F = 142.06$; $df = 2, 57$; $P < 0.0001$) and *T. mwanzai* ($F = 59.10$; $df = 2, 57$; $P < 0.0001$) was significantly different for one-, two- and three-layered FAW egg mass. Parasitism of *T. chilonis* was higher for single (74.09 ± 1.97%), double (38.01 ± 2.74%) and three (33.37 ± 2.46%) layered FAW eggs than other species (Fig. 2A). The emergence rate of parasitoid from different layers of FAW eggs mass was not significantly differed ($F = 1.19$; $df = 2, 171$; $P = 0.307$), however, it was significantly different for parasitoid species ($F = 3.70$; $df = 2, 171$; $P = 0.026$). The interaction between the number of egg layers in egg masses and parasitoid species was non-significant ($F = 0.11$; $df = 4, 171$; $P = 0.980$) (Fig. 2B).

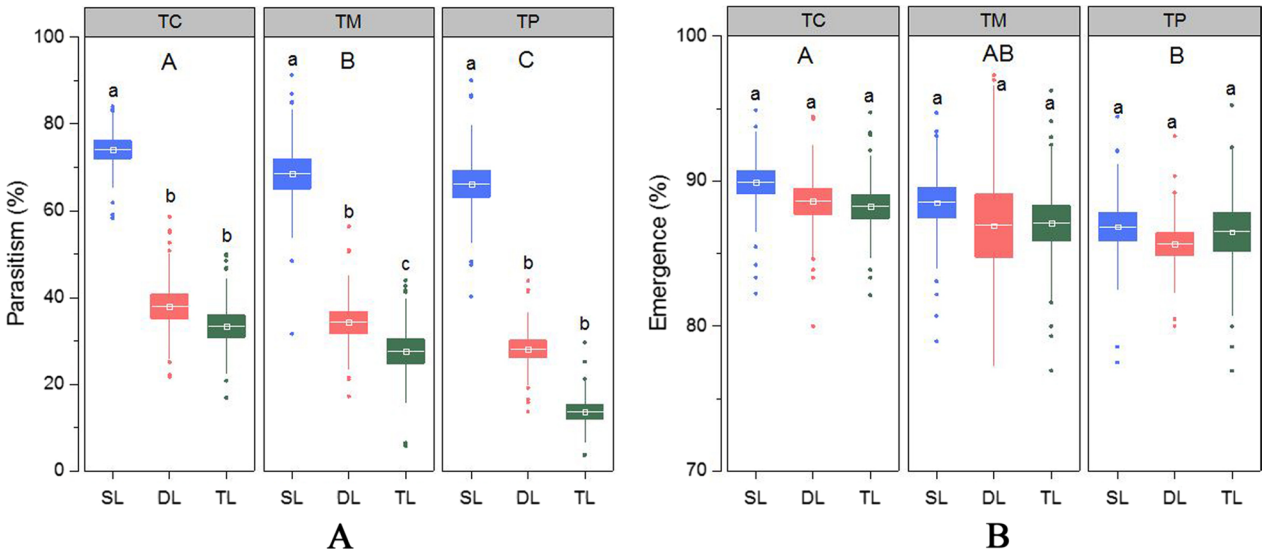

Fig. 2 Parasitism and emergence rate of *Trichogramma* species on layered FAW eggs. (**A** parasitism rate; **B** emergence rate). *TC Trichogramma chilonis*, *TM T. mwanzai*, TP *T. pretiosum*, *SL* single layer, *DL* double layers, *TL* three layers. Bars with different uppercase letters on the top of error bars indicate significant differences among parasitoid species and with different lowercase letters indicate significant differences between egg types ($P < 0.05$, Tukey's test)

Effect of ovipositor length on parasitoids' performance

The ovipositor length varied significantly among the *Trichogramma* species ($F=9.92$; $df=2, 57$; $P=0.0002$) (Fig. 3). *T. chilonis* and *T. mwanzai* that emerged from parasitized FAW egg mass had a similar ovipositor length and was longer than *T. pretiosum* (Fig. 4). The ovipositor length of *T. chilonis* and *T. mwanzai* were 190.27 ± 3.68 µm and 188.58 ± 3.71 µm, respectively.

Discussion

In the present study, the parasitizing efficiency of *T. chilonis*, *T. pretiosum*, and *T. mwanzai* on FAW eggs with or without scales and layered egg mass was investigated. Presence of scales on egg mass significantly affected the parasitism success of each *Trichogramma* species tested in this study. This implies that the females of *Trichogramma* species could not cope with the thickness of scales found on FAW egg masses. Several previous studies have also shown that FAW scales on egg mass modulated the performance of *Trichogramma* parasitoids (Hou et al. 2022). In the present study, among the three species, *T. chilonis* achieved a relatively higher parasitism success on FAW egg mass with or without scales than *T. pretiosum and T. mwanzai.* Correspondingly, Jin et al. (2021) also reported a greater parasitizing capacity of *T. chilonis* on FAW eggs than *T. pretiosum*. In the present study, the presence of a thick scales on FAW egg mass has effectively hindered the success of parasitism by *T. chilonis*, *T. pretiosum* and *T. mwanzai* than those without scales. Moreover, Li et al. (2023) reported that *Trichogramma* species can parasitize a higher percentage of FAW eggs when the scales cover is thinner (< 20 µm). The egg parasitism of 19.94 and 37.80% by *T. pretiosum* in eggs with or without scales, respectively, were recorded. The results corroborate earlier findings where *T. pretiosum* parasitized only 20% of FAW eggs with scales and 46% without scales (Dong et al. 2021). Further, the emergence rate of *Trichogramma* species did not influence by scales on FAW egg mass, and a similar result was reported by Li et al. (2023).

In the present study, *T. chilonis* recorded a greater (74.09%) parasitism rate in single-layered egg mass and (33.37%) in three-layered egg mass. A similar trend was also observed for the other two species of parasitoids tested in this study. Further, parasitism success of *Trichogramma* species was influenced by the number of egg layers in the FAW egg mass and parasitoids tested. Similarly,

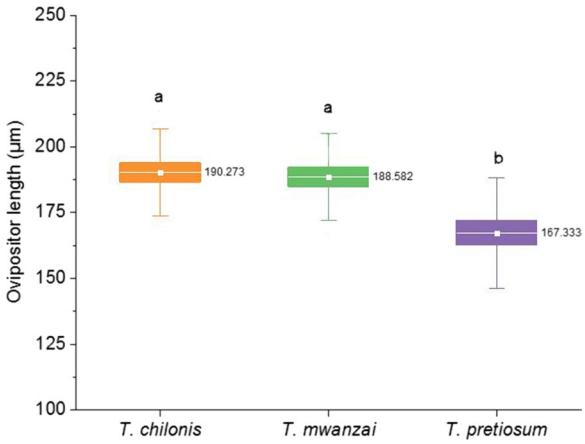

Fig. 3 Ovipositor length of *Trichogramma* species emerged from parasitized FAW eggs. Different letters on the top of error bars indicate statistically different values using Tukey's test ($P < 0.05$)

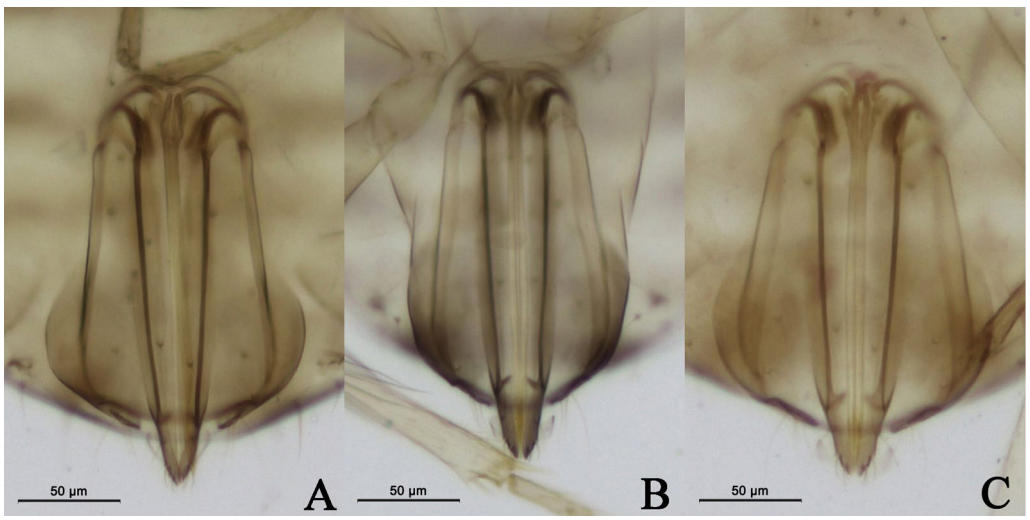

Fig. 4 Ovipositor morphology of *Trichogramma* species reared on FAW; **A** *T. chilonis*, **B** *T. mwanzai* and **C** *T. pretiosum*

Beserra and Parra (2005) found that the parasitism success of *Trichogramma atopovirilia* Oatman & Platner was influenced by the number of egg layers in the egg mass. This is due to females of *Trichogramma* species finding it hard to reach and parasitize the eggs in the interior layers. In this study, the parasitoid emergence was not affected by the layered egg mass, while the emergence rate varied with species.

Along with the inherent reproductive potential of the parasitoids, the female size of *Trichogramma*, particularly ovipositor length, was an important quality parameter that was directly linked with the successful parasitism of target hosts (Tang et al. 2017). In this study, the ovipositor length of three *Trichogramma* species that emerged from parasitized FAW eggs was measured and showed significant variations in the ovipositor length. The ovipositor length of *T. chilonis* and *T. mwanzai* was relatively longer than *T. pretiosum*. The difference in parasitism rates might be the result of variation in ovipositor length possessed by different *Trichogramma* species (Tang et al. 2017). Moreover, in the present study, *T. chilonis* parasitized a higher percentage of FAW eggs than *T. mwanzai* even though both had similar ovipositor length, therefore we speculated that along with ovipositor length, the inherent reproductive potential, adaptability of the parasitoids to the hosts and the environment influences the parasitism rate. In addition, continuous rearing on the factitious hosts also reduces the body size of *Trichogramma,* parasitism potential and the ovipositor length compared to the wild population inhabiting in the fields (Tang et al. 2017). Therefore, it was suggested that one or two generations of *Trichogramma* species should be reared on target host eggs before releasing them in the field and the selection of *Trichogramma* species with longer ovipositor may improve the parasitism success in eggs with or without scales and layered egg masses of FAW.

Conclusion

The present study provides baseline information on the performance among the *Trichogramma* species on different eggs types such as egg mass with or without scale and layered egg mass of FAW, which are a morphological barrier for parasitoids to parasitize the FAW eggs effectively. *Trichogramma chilonis* showed comparatively higher parasitism success against these morphological barriers than the other two species tested in this study. Therefore, egg mass scales and the number of egg layers in FAW egg masses should be considered when selecting the *Trichogramma* species for biological control or including them in integrated pest management programs of FAW.

Abbreviations

FAW	Fall armyworm
CABI	Centre for Agriculture and Bioscience International
RH	Relative humidity
L:D	Light: dark
h	Hour
P	Probability

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Author contributions

ON conceived, designed and executed the experiments, writing-original draft, and writing-review and editing. ON and LSD contributed to research work and data collection. JP analyzed the experimental data, writing-review and editing. SNS contributed to supervision, visualization and project administration. All authors read and approved the final manuscript.

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Availability of data and materials

The data sets supporting the conclusions of this article are included within the article.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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