Navik *et al.*
Egyptian Journal of Biological Pest Control (2023) 33:118
https://doi.org/10.1186/s41938-023-00759-z

Egyptian Journal of
Biological Pest Control

REVIEW ARTICLE

Open Access

Biological control of fall armyworm *Spodoptera frugiperda* (JE Smith) using egg parasitoids, *Trichogramma* species (Hymenoptera: Trichogrammatidae): a review

Omprakash Navik[1*], Yogesh Yele[2], Santosh C. Kedar[3] and S. N. Sushil[1]

Abstract

Background Fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is an invasive pest that can cause serious crop loss to various important food crops and risk to global food security. FAW can cause damage to over 350 plant species by feeding on vegetative and reproductive stages of crops. Currently, chemical pesticides and transgenic maize are widely used to safeguard crops from this serious pest. However, biological control is a safer and more sustainable alternative in the long term for FAW management. Of the various natural enemies of FAW, egg parasitoids of genus *Trichogramma* have been used in augmentative biological control of FAW in the Americas and invaded regions such as Africa and Asia.

Main body Several species of *Trichogramma* have been reported naturally parasitizing FAW eggs and emerged as important biocontrol agents. This paper presents a comprehensive review of potential and challenges associated with *Trichogramma* in biological control of FAW. A total of 11 species of trichogrammatids occurred naturally on FAW eggs. This review includes the occurrence of *Trichogramma* species on FAW, biological attributes, mass rearing, release techniques, field efficacy and interaction and integration with other parasitoids. Integration of *Trichogramma* with other parasitoids can resolve the problem related to its penetrative ability against scaled and multi-layered FAW eggs which were discussed.

Conclusion Invasion of FAW in Africa and Asia has provided a prospect for augmentative biological control of FAW using *Trichogramma* for sustainable production, especially in maize which is used as food and fodder. Integrating *Trichogramma* with safer and selective green pesticides and their conservation with other natural enemies could help in sustainable and environment-friendly FAW control.

Keywords Biological control, Egg parasitoids, *Spodoptera frugiperda*, *Trichogramma*, Parasitism, Field efficacy

*Correspondence:
Omprakash Navik
omnavikm@gmail.com
Full list of author information is available at the end of the article

Background

Fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a highly polyphagous pest of maize and other cereals in tropical and subtropical regions of the world (Sparks 1979). FAW is native to the Americas and its recent invasion in Africa, Asia and Oceania (FAO 2023; Fig. 1) has severely impacted yields of several food crops (Overton et al. 2021). This noctuid pest is highly destructive and the caterpillars can feed on over 350 plant species grown commercially or non-commercially across 76 plant families, with a preference for maize (*Zea mays* L., Poaceae) (Montezano et al. 2018). These caterpillars can feed on different phenological stages of maize and could result in maize yield loss of up to 70% if attacked early growth stage of maize (Hruska 2019). Owing to the increase in international trade and long-distance migration ability, the FAW has rapidly spread in new geographical regions and threatened global maize production (Early et al. 2018). The high adaptability, fecundity and polyphagous nature made them a key pest of maize in the invaded region under suitable environmental conditions (Jing et al. 2021).

Outside its native range, FAW is now recognized as an important pest of maize and several other crops (Rane et al. 2023). Within 5 years of invasion in West and Central Africa, and almost 3 years in India, Asia, this pest has changed the pest status of maize and the existing control strategies become less effective (Prasanna et al. 2022). Nevertheless, several control strategies have been deployed against FAW including chemical methods, biological control agents, and physical methods to reduce the crop yield loss (Kenis et al. 2022). The invasiveness and the destructive nature of FAW have attracted the attention of applied pest management for sustainable crop production (Kumar et al. 2022). In the invaded regions, especially in Africa and Asia, the chemical methods remain a mainstay for FAW control on an emergency basis to reduce crop damage and further spread (Deshmukh et al. 2020). However, several issues remain with chemical control methods due to the heavy application of conventional chemical insecticides such as cypermethrin, lambda-cyhalothrin and chlorpyrifos (Tambo et al. 2019) that cause the development of resistance in FAW populations and redundant use of insecticides kill the non-targets including natural enemies, cause environmental pollution and pose risk to human health (Kebede and Shimalis 2018). The long-term use of chemical measures may be ineffective and non-sustainable (Day et al. 2017). Therefore, the development of efficient control measures is the greatest challenge in the invaded region (Guo et al. 2020). However, in the Americas, the use of transgenic *Bt* maize is the leading control approach against FAW, besides the use of insecticides and biological control also used by farmers (Burtet et al. 2017). Consequently, there is a need to develop and introduce safer alternatives, such as biological control against FAW in invaded regions.

Egg parasitoids (Hymenoptera: Trichogrammatidae) are considered excellent candidates for the biological control of FAW and are also crucial components during designing the integrated pest management (IPM) of FAW (Navik et al. 2023). In the Americas, several egg parasitoids have been collected, mass-produced and

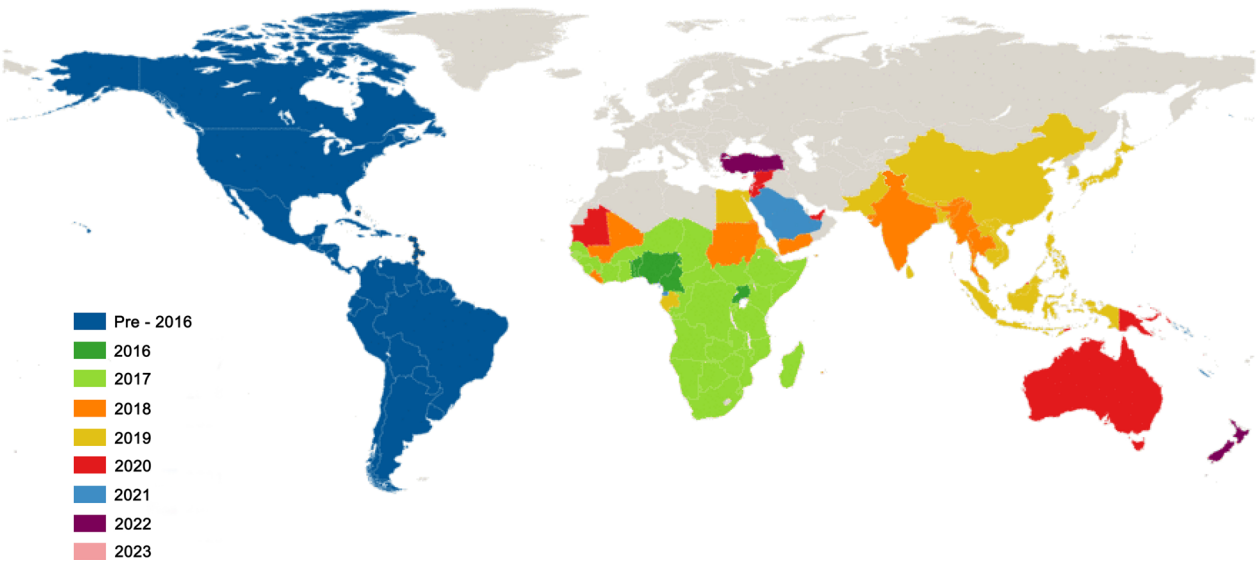

Fig. 1 Global spread of fall armyworm, *Spodoptera frugiperda* (Source: FAO 2023). Note: Canada (northern provinces) and Alaska with restricted distribution and distribution in all grey countries uncertain or absence (Source: https://gd.eppo.int/taxon/LAPHFR/distribution)

augmented for FAW management (Bueno et al. 2023). Similarly, efforts were made to collect native egg parasitoids of FAW in the invaded region, so that they could be recruited for biological control or deployed through IPM in sustainable crop production (Sun et al. 2021). It is fascinating that several native egg parasitoids have been found parasitizing the FAW eggs naturally and controlling them at their egg stage before they inflict any damage (Parra and Coelho 2022). This provides an opportunity for the development of augmentative biological control using egg parasitoids against FAW. This manuscript presents a review of the natural occurrence of *Trichogramma* on FAW, biological attributes, laboratory evaluation, mass-rearing and field application against FAW.

Trichogramma parasitoids of fall armyworm

The egg parasitoids mainly belong to the genus *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) considered for FAW control in the Americas and invaded regions such as Africa and Asia. Eight species of *Trichogramma* have been found naturally parasitizing the FAW egg masses in the maize and other crop environments in its native range as well as in three species in the invaded regions (Table 1). Of these egg parasitoids, various species of trichogrammatids have been mass-reared on suitable factitious hosts such as *Sitotroga cerealella* (Oliver), *Anagasta kuehniella* Zeller and *Corcyra cephalonica* (Stainton) (Table 4) and demonstrated for FAW control at field conditions. Based on reports in the literature, 11 species of trichogrammatid egg parasitoids were found associated with FAW and parasitized egg masses with different rates in various crops (Table 2). In addition, a recent study reported the occurrence of *Trichogrammatoidea lutea* Girault (Hymenoptera: Trichogrammatidae) from parasitized FAW egg masses based on morphology and molecular analysis (Sun et al. 2021).

Based on the literature survey, 10 species of *Trichogramma* have been known to parasitize FAW eggs in various crop habitats (Table 1). Of these, 8 species are known to parasitize the eggs of FAW attacking different crops (e.g. Malachra, Sorghum) in the native range, especially in Latin American and Caribbean countries. Amongst the species, *Trichogramma pretiosum* Riley (Fig. 2A) and *T. atopovirilia* Oatman and Platner were potential egg parasitoids of FAW and have been used for augmentative biological control. In Africa, *Trichogramma chilonis* Ishii (Fig. 2B), *T. mwanzai* Schulten and Feijen (Fig. 2C) and *Trichogrammatoidea lutea* were found parasitizing the FAW eggs in maize (Sun et al. 2021). In Asia, the natural occurrence of *T. chilonis* on FAW has been in maize from

Table 1 Occurrence of *Trichogramma* species on the eggs of fall armyworm *Spodoptera frugiperda* in the different crops

Species	Country	Host plants	References
Trichogramma pretiosum	Brazil	Maize	De Sa and Parra (1994), Beserra et al. (2002), Zucchi et al. (2010), Ribeiro et al. (2014), Dequech et al. (2013), Dasilva et al. (2015) and Querino et al. (2016)
Trichogramma atopovirilia	Brazil	Maize	Beserra et al. (2002), Zucchi et al. (2010), Ribeiro et al. (2014), Dequech et al. (2013) and Dasilva et al. (2015)
	Venezuela	*Malachra* sp. Maize	Rios and Teran (2003) and Morales et al. (2007)
	Mexico	Maize, Sorghum	Jaraleno-Teniente et al. (2020) and Hoballah et al. (2004)
Trichogramma exigum	Latin American and Caribbean countries	Maize	Andrews (1988)
	Venezuela	Maize	Morales et al. (2007) and Zucchi et al. (2010)
Trichogramma colombiensis	South America	Maize	Zucchi et al. (2010)
Trichogramma rojasi	Brazil	Maize	Camera et al. (2010) and Ribeiro et al. (2014)
Trichogramma demoraesi	Latin American and Caribbean countries	Maize	Molina-Ochoa et al. (2003)
Trichogramma fasciatum	Latin American and Caribbean countries	Maize	Molina-Ochoa et al. (2003)
Trichogramma minutum	Latin American and Caribbean countries	Maize	Molina-Ochoa et al. (2003)
Trichogramma chilonis	Kenya, Tanzania and Ethiopia	Maize	Sisay et al. (2019)
	Hong Kong, China	Maize	Li et al. (2019)
	China	Maize	Tang et al. (2020)
	Kenya, Tanzania and Nepal	Maize	Elibariki et al. (2020)
	India	Maize, Sugarcane	Navik et al. (2021) and Mahanthi et al. (2019)
	Cameroon	Maize	Abang et al. (2021)
Trichogramma mwanzai	Kenya, Tanzania and Nepal	Maize	Elibariki et al. (2020)
	Zambia	Maize	Sun et al. (2021)
Trichogrammatoidea lutea	Zambia	Maize	Sun et al. (2021)

Table 2 Natural parasitism of *Trichogramma* species on fall armyworm eggs

Species	Parasitism (%)	Country	Host plants	References
Trichogramma pretiosum	≤ 20%	Brazil	Maize	De Sa and Parra (1994)
T. pretiosum and *Trichogramma atopovirilia*	2.21%	Brazil	Maize	Beserra et al. (2002)
T. pretiosum and *T. atopovirilia*	0.72–2.36%	Brazil	Maize	Dequech et al. (2013)
Trichogramma chilonis	20.9%	Kenya, Tanzania and Ethiopia	Maize	Sisay et al. (2019)
T. atopovirilia	2.8–3.75%	Mexico	Maize	Jaraleno-Teniente et al. (2020)
T. atopovirilia	2.47%	Mexico	Sorghum	Jaraleno-Teniente et al. (2020)
T. chilonis	15.81–23.87%	India	Maize	Navik et al. (2021)
T. chilonis	7.7%	Cameroon	Maize	Abang et al. (2021)
T. atopovirilia	0.1%	Mexico	Maize	Hoballah et al. (2004)
Trichogramma spp.	1.4%	Florida, USA	Maize and Sorghum	Waddill and Whitcomb (1982)
Trichogramma spp.	52.5%	Brazil	Maize	Figueiredo et al. (2002)
Trichogramma sp.	3.33%	India	Maize	Shylesha et al. (2018); Udayakumar et al. (2021)

India (Navik et al. 2021) and China (Jin et al. 2021). However, the natural occurrence and parasitism by *Trichogramma* spp. parasitizing FAW eggs is largely influenced by egg types, crop growth stages and environmental conditions.

Natural parasitism by *Trichogramma*

Several species of *Trichogramma* have been found naturally associated with FAW eggs in the native ranges as well as in invaded regions (Table 2). Parasitism of these species varied between 1 and 52.5% in different crops' ecosystems. In the native range, the parasitism by *T. pretiosum* and *T. atopovirilia* was low (2.21%) in maize fields, and *T. pretiosum* was recorded as the most frequent parasitoid found in 93.7% of parasitized eggs (with an average < 20% parasitism in Brazil maize), followed by *T. atopovirilia* with 2.07% parasitism (Beserra et al. 2002). Further, Dequech et al. (2013) also recorded *T. pretiosum* as a dominating species that parasitized 82.73% of FAW eggs compared to *T. atopovirilia* (17.27%) and both the species concurrently parasitized 13.33% of FAW eggs in maize fields. Nevertheless, the natural occurrence of *T. atopovirilia* on FAW was low in maize (2.47%) and sorghum (3.75%) fields in Mexico (Jaraleno-Teniente et al. 2020). In Africa, the natural occurrence of *T. chilonis* was recorded at the rate of 20.9% in the maize field of Kenya (Sisay et al. 2019). Similarly, in Asia, the parasitism of *T. chilonis* to FAW eggs ranged from 15.81 to 23.87% in the maize fields of India (Navik et al. 2021). The lower parasitism by *Trichogramma* species in natural conditions might be due to the distribution of FAW egg masses on plants, eggs in layers and the presence of scales, phenological stages and plant age (Durocher-Granger et al. 2021). In addition, the plant region with the greatest leaf mass preferred for oviposition by the FAW females, which provides protection (Beserra et al. 2002) and the increased scale thickness (Hou et al. 2022) on egg masses reduced the parasitism success of *Trichogramma* under natural conditions.

Biological characteristics of *Trichogramma* reared on fall armyworm

For successful biological control programmes, the suitability of *Trichogramma* species is usually assessed based on biological attributes such as parasitism and emergence rate, adult emergence per egg, female progeny and developmental time on the target pest (Hou et al. 2018). Many species of *Trichogramma* are specific to host species and some are generalists attack native Lepidoptera and beneficial lepidopteran eggs used for biocontrol projects (e.g. *T. chilonis*) and their response to the hosts and host age is independent of the egg parasitoid species (Monje et al. 1999). Thus, host age influences the performance of some *Trichogramma* species by affecting their biological attributes (Hou et al. 2018). In general, the host egg age is known to affect the parasitism potential of *Trichogramma* parasitoids (Pizzol et al. 2012). Likewise, the different ages of FAW eggs also affected the parasitism rate of *Trichogramma* species and research indicated that older FAW eggs were less parasitized by parasitoids (Sun et al. 2021). In Zambia, five species of trichogrammatids, viz. *T. mwanzai*, *T. japonicum* Ashmead, *T. ostriniae* (Peng and Chen), *T. leucaniae* Pang and Chen and *T. lutea* were exposed to various egg ages of FAW and found that the egg age of FAW had influenced the parasitism rate of the four tested species except *T. japonicum* preferred to parasitize 1-day-old eggs over 0- and 2-day-old eggs. In addition, *T. mwanzai* and *T. lutea* parasitized a

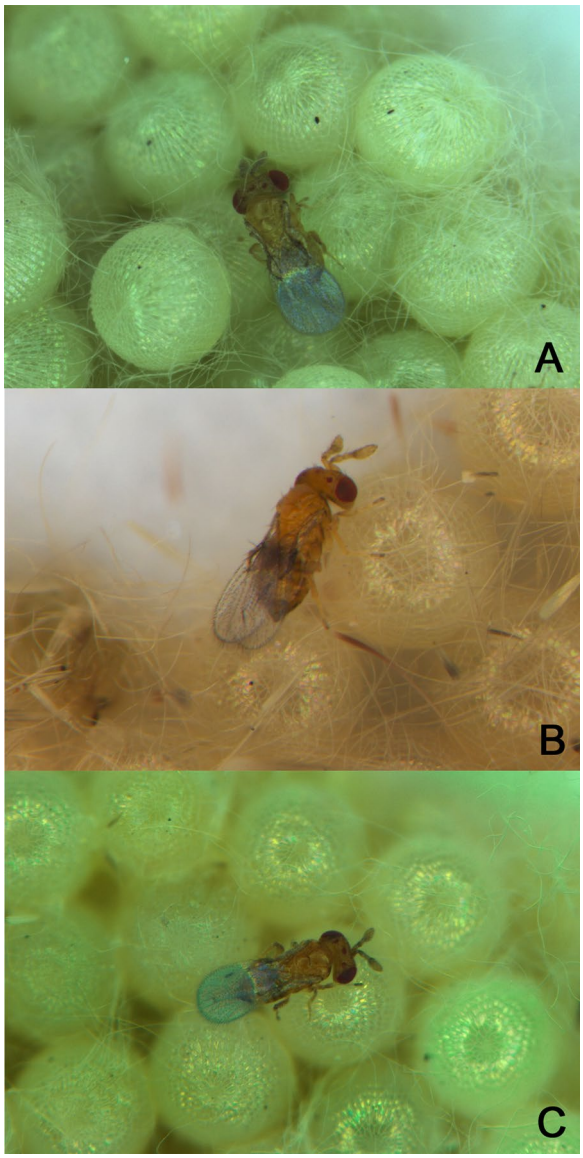

Fig. 2 *Trichogramma* species parasitizing the egg mass of *Spodoptera frugiperda*. **A**. *Trichogramma pretiosum*, **B**. *Trichogramma chilonis* and **C**. *Trichogramma mwanzai*

higher percentage of 0-day-old FAW eggs as compared to other species (Sun et al. 2021). In Hainan Island, China, Jin et al. (2021) compared the host selection, fitness and parasitization capacity of *Trichogramma* species on FAW eggs. The parasitism rate for *T. chilonis*, *T. ostriniae*, *T. confusum*, and *T. pretiosum* on FAW egg masses ranged from 61.5 to 87.5%. The highest parasitism rate was observed for *T. ostriniae* to the tune of 87.5%. This study reported that the females of *T. chilonis*, *T. ostriniae*, and *T. confusum* prefer to parasitize the FAW eggs within 0–24 h-old, while females of *T. chilonis*, *T. ostriniae*, and *T. confusum* prefer 0–72 h-old FAW eggs. Furthermore, Yang et al. (2022) observed that *T. chilonis*, *T. dendrolimi* Matsumura and *T. pretiosum* parasitized the FAW eggs with a 15.87, 29.98 and 25.73% parasitism rate, respectively, in Hainan Island, China. Parasitism by *T. dendrolimi* was 33.4% on FAW eggs on 8 day of the oviposition by females (Li et al. 2023).

Besides, the FAW egg age has not affected the adult emergence of *Trichogramma* (Sun et al. 2021). The emergence rate of *T. mwanzai* was 98.3, 94.8 and 93.2% on 0-, 1-and 2-days old FAW eggs, respectively. In the case of *T. ostriniae*, adult emergence ranged from 93.3 to 97.5% for all egg ages. Similarly, *T. leucaniae* also produced 96.3–97.1% adult emergence from 0-, 1-and 2-day-old FAW eggs. The emergence rate for *T. japonicum* and *T. lutea* varied between 85.7 to 99.1% and 98.2 to 99.4%, respectively, when exposed to various egg ages of FAW (Sun et al. 2021). Further, the emergence rate of *T. dendrolimi* and *T. chilonis* was similar on FAW eggs collected on different oviposition days and ranged between 95.4 to 98.7% and 98.3 to 99.5%, respectively (Li et al. 2023).

The developmental time of *Trichogramma* species is influenced by the various egg ages of lepidopteran eggs (Atashi et al. 2021). In the case of FAW, the age of eggs had a significant effect on the development time of *Trichogramma* parasitoids. Significant differences were observed in the developmental time of five species of *Trichogramma* when exposed to various egg ages of FAW (0-, 1- and 2-days old eggs). The developmental time of *T. japonicum* (10.6–11.7 days) and *T. leucaniae* (10.3–11.6 days) was increased with the age of the host eggs, while it was similar for *T. ostriniae* (10.2–10.5 days). In contrast, the developmental time of *T. mwanzai* (9.5–10.5 days) and *T. lutea* (10.2–11.4 days) was decreased as the age of the host eggs increased (Sun et al. 2021). On FAW, the development period of *T. chilonis* varied between 8.40 and 10.9 days under different experimental conditions (Yang et al. 2022). Development for *T. dendrolimi* also varied between 8.17 and 9.5 days on FAW eggs (Li et al. 2023). Although, there was no remarkable difference in the developmental period for *T. chilonis*, *T. dendrolimi* and *T. pretiosum* when exposed to same age of FAW egg masses (24 h) (Yang et al. 2022). However, Li et al. (2023) recorded the shortest development time for *T. dendrolimi* than that of *T. chilonis* on FAW eggs. The developmental time for the thelytokous strain of *T. pretiosum* was 8.93 days (Yang et al. 2022).

Females of *Trichogramma* can control the sex ratio and allocate the progeny based on their wide range of host sizes (Varshney et al. 2022). During oviposition, female adults control the sex ratio and lay a female-biased sex ratio which identifies the success of *Trichogramma* parasitoids in biological control (Zang et al. 2021). The FAW egg age influences the per cent female

progeny of *Trichogramma* species that emerged from parasitized eggs batches. The variable impact of host egg age on the production of female progeny has been reported for *Trichogramma* species (Atashi et al. 2021). In the case of FAW, the egg age had a significant effect on the *Trichogramma* spp. sex ratio, although it was female-biased for all species (Sun et al. 2021). The per cent female progeny for *T. mwanzai* was higher in younger FAW eggs (85.1%) and declined significantly with the age of FAW egg masses (for 3-day-old eggs; 60.1%). Similarly, for *T. lutea*, the percentage of female progeny was 82.2% on 0-day-old eggs and reduced to 50.8% when offered 2-day-old eggs. The female progeny for *T. ostriniae* and *T. leucaniae* varied with the host egg age and ranged between 69.9 to 82.5% and 70.8 to 82.7%, respectively. Conversely, the per cent female progeny for *T. japonicum* was similar for 0- and 2-days old eggs (63.6 and 64.45%, respectively) and was lowest on 1-day-old eggs (49.6%) (Sun et al. 2021). The percentage of females' proportion declined with generations for *T. dendrolimi* and was 85.13% in *F*1 and 76.44% in the *F*2 generations (Yang et al. 2022). However, the per cent female progeny was consistent in *F*1 and *F*2 generations for *T. chilonis* (55.47 and 60.49%) and *T. pretiosum* (100% in both generations) (Yang et al. 2022). Further, Li et al. (2023) did not find a significant difference in the percentage of female progeny that emerged from FAW egg masses for *T. chilonis* (81.4–82.1%) and *T. dendrolimi* (81.6–83.7%) and was comparably higher than other experimental conditions.

Host egg-size influences the oviposition and production of offspring by *Trichogramma* females (Jin et al. 2021). The optimum number of offspring that emerged from individual hosts adds benefits to applied biological control by avoiding super parasitism (Iqbal et al. 2020). Jin et al. (2021) reported that 0.6 to 1.6 parasitoid progeny emerged per egg from 0 to 24 h-old FAW eggs for seven species of *Trichogramma*. The number of emerged offspring from an individual parasitized FAW egg was similar for *T. chilonis* (1.0), *T. ostriniae* (1.2), *T. confusum* (1.6), *T. embryophagum* (1.4) and *T. dendrolimi* (1.5). However, the number of emerged offspring per eggs by *T. pretiosum* and *T. japonicum* at 24–48 h old FAW eggs was 1.0 and 1.1, which was higher than 0–24, 48–72 or 72–96 h of time duration. Further, Jin et al. (2021) also measured the FAW eggs approximately 0.4–0.5 mm in diameter and 0.3–0.4 mm in height and the results showed that all seven *Trichogramma* species produced more than one offspring per FAW egg. This result suggested that an individual FAW egg accepted at least two eggs of *Trichogramma* and supported the emergence of both adult parasitoids.

Effect of climatic factors on *Trichogramma* species

Climatic variables influence the performance of parasitoids and therefore must be considered while selecting the potential strain/species for biological control (Grande et al. 2021). Temperature and humidity are the climatic variables that affect the biology and performance of *Trichogramma* and thereby the overall success of biological control in the fields (Tabebordbar et al. 2022). Developmental time and emergence of *Trichogramma* parasitoids are greatly affected by temperature. The emergence of *T. pretiosum* on FAW eggs was lowest at 32 °C (88.9%) and highest at temperatures 18 °C (100%) and 20 °C (99.5%) (Bueno et al. 2010). Temperature is the most critical climatic variable that affects the parasitism rate of *Trichogramma* (Tang et al. 2023). The parasitism rate by *T. dendrolimi* and *T. lutea* was gradually increased with temperature and then decreased with higher temperature. The parasitism rate was higher at the middle temperature at 25 and 29 °C and was lower at 21 and 33 °C at all relative humidity levels for both parasitoids (Tang et al. 2023). Among the two parasitoids, the parasitism rate by *T. dendrolimi* was significantly higher than that of *T. lutea* under different combinations of temperature and humidity. This showed that along with temperature, relative humidity was also responsible for changes in parasitism rate by parasitoids. *Trichogramma dendrolimi* had a better temperature and humidity adaptation than that of *T. lutea*. Besides, temperature and relative humidity also affected the emergence of *T. dendrolimi* and *T. lutea* (Tang et al. 2023). The developmental time of *T. dendrolimi* and *T. lutea* was decreased on FAW eggs with increasing temperature (Tang et al. 2023). The higher temperature probably increases the metabolic activity of parasitoids (Bueno et al. 2009). The shorter developmental time for *T. dendrolimi* was the consequence of higher temperature. Temperature and humidity also influence the sex ratio of *Trichogramma* species (Tabebordbar et al. 2022). The highest female ratio (94.6%) for *T. dendrolimi* was recorded at 33 °C and 60% humidity, while the lowest (79.5%) was recorded at 25 °C and 60% humidity. However, there was a non-significant effect of temperature and humidity regimes on the sex ratio of *T. lutea* (Tang et al. 2023). Further, other climatic variables such as photoperiod and precipitation can also have an impact on the biological characteristics of *Trichogramma* (Pratissoli & Parra 2000).

Parasitism of *Trichogramma* in laboratory and field cages

The parasitizing capacity of various *Trichogramma* spp. has been evaluated in the laboratory before testing in open field conditions (Table 3). Beserra and Parra

Table 3 Parasitism of *Trichogramma* species under laboratory, cage/greenhouse or field conditions used for fall armyworm control

Species	Experimental set up	Rearing host	Parasitism (%)	Country	References
Trichogramma pretiosum	Laboratory	*Anagasta kuehniella*	27.5–89.3%	Brazil	Beserra et al. (2003)
T. pretiosum	Laboratory	–	29.7%	Brazil	Beserra and Parra (2004)
T. atopovirilia	Laboratory	–	48.3%	Brazil	Beserra and Parra (2004)
T. atopovirilia	Field cage	–	40.10–66.24%	Brazil	Beserra and Parra (2005)
T. pretiosum	Microcosms	*Sitotroga cerealella*	34.0%	Colombia	Diaz et al. (2012)
T. atopovirilia	Microcosms	*S. cerealella*	28.81%	Colombia	Diaz et al. (2012)
T. exigum	Microcosms	*S. cerealella*	12.8%	Colombia	Diaz et al. (2012)
T. pretiosum	Field	*A. kuehniella*	68.75–79.2%	Brazil	Figueiredo et al. (2015)
T. atopovirilia	Laboratory	*Spodoptera frugiperda*	70.14%	Mexico	Jaraleno-Teniente et al. (2021)
T. pretiosum	Laboratory	*S. frugiperda*	29.23%	Mexico	Jaraleno-Teniente et al. (2021)
T. atopovirilia	Field cage	*S. frugiperda*	8%	Mexico	Jaraleno-Teniente et al. (2021)
Trichogramma dendrolimi	Laboratory	*Corcyra cephalonica*	20 eggs/female	China	Junce et al. (2020)
Trichogramma bilingense	Laboratory	*C. cephalonica*	9.6–13.4 eggs/female	China	Junce et al. (2020)
Trichogramma ostriniae	Laboratory	*C. cephalonica*	1.0 eggs/female	China	Junce et al. (2020)
T. chilonis	Laboratory	*C. cephalonica*	–	China	Junce et al. (2020)
Trichogramma japonicum	Laboratory	*C. cephalonica*	–	China	Junce et al. (2020)
T. pretiosum	Field	*C. cephalonica*	–	India	Varshney et al. (2021)
T. chilonis	Field	*C. cephalonica*	75%	China	Jin et al. (2021)
T. ostriniae	Field	*C. cephalonica*	87.5%	China	Jin et al. (2021)
T. confusum	Field	*C. cephalonica*	61.5%	China	Jin et al. (2021)
T. pretiosum	Field	*C. cephalonica*	76.9%	China	Jin et al. (2021)
T. mwanzai	Laboratory	*C. cephalonica*	< 15 eggs/5 female	Zambia	Sun et al. (2021)
Trichogrammatoidea lutea	Laboratory	*C. cephalonica*	< 20 eggs/5 female	Zambia	Sun et al. (2021)
T. ostriniae	Laboratory	*C. cephalonica*	–	Zambia	Sun et al. (2021)
T. leucaniae	Laboratory	*C. cephalonica*	–	Zambia	Sun et al. (2021)
T. japonicum	Laboratory	*C. cephalonica*	–	Zambia	Sun et al. (2021)
T. chilonis	Field	*C. cephalonica*	–	India	Patil et al. (2022)
T. chilonis	Laboratory	*S. frugiperda*	15.87%	China	Yang et al. (2022)
T. dendrolimi	Laboratory	*S. frugiperda*	29.98%	China	Yang et al. (2022)
T. pretiosum	Laboratory	*S. frugiperda*	25.73%	China	Yang et al. (2022)
T. dendrolimi	Laboratory	*C. cephalonica*	33.4%	China	Li et al. (2023)
Trichogrammatoidea bactrae	Laboratory	*S. cerealella*	36.05–88.98%	Egypt	Mohamed et al. (2023)

(2004) evaluated the parasitism potential of *T. atopovirilia* and *T. pretiosum* on FAW eggs to select the most suitable species for FAW control in Brazil and found that the females of *T. atopovirilia* were more aggressive and showed higher affinity towards the FAW eggs with higher parasitism (48.3%) than *T. pretiosum* (29.7%). Further, Beserra et al. (2005) showed that *T. atopovirilia* parasitized 100% FAW eggs as compared to *T. pretiosum* (60%) under laboratory conditions. Three species of *Trichogramma* namely, *T. atopovirilia*, *T. exigum* and *T. pretiosum* were tested against the FAW and *T. pretiosum* (34.0%) parasitized a higher percentage of host eggs than the *T. atopovirilia* (28.81%) and *T. exigum* (12.8%) (Diaz et al. 2012). In addition, the parasitizing efficacy of field-collected *T. atopovirilia* and *T. pretiosum* was tested on FAW eggs in the laboratory and found that *T. atopovirilia* parasitized 70.14% of FAW eggs as compared to *T. pretiosum* which could only parasitize 29.23% host eggs under laboratory conditions in Mexico (Jaraleno-Teniente et al. 2020). In China, Junce et al. (2020) evaluated the parasitism potential of five native *Trichogramma* species on FAW eggs and the results revealed that *Trichogramma dendrolimi* Matsumura, *T. bilingense* He and Pang, *T. ostriniae* Peng and Chen could parasitize 20, 9.6, 1.0 FAW eggs per female wasp, respectively, and *T. dendrolimi* reported as superior species for FAW control. In another study, Beserra et al. (2003) compared parasitizing efficacy of 20 strains of *T. pretiosum* on FAW eggs and found that there was the difference in

parasitizing capacity between the strains of *T. pretiosum* and parasitism rate varied between 80.9 and 89.3%.

Generally, the parasitism potential of *Trichogramma* species is assessed in cages/ field cages on a larger to find out potential and suitable species/strain field releases (Chailleux et al. 2012). Beserra and Parra (2005) assessed the parasitism potential of *T. atopovirilia* in the field cages (1.5 × 1.1 × 1.5 m) and found that *T. atopovirilia* parasitized 66.24, 45.20 and 40.10% of egg masses with one, two, and three layers, respectively, without taking into account the presence or absence of scales on the egg masses. While, Diaz et al. (2012) tested the efficacy of *T. atopovirilia*, *T. exigum*, and *T. pretiosum* for the control of FAW in *Physalis peruviana* L. (Solanaceae) in microcosm and results revealed that *T. atopovirilia* parasitized a higher percentage of FAW eggs with lowest plant damage than other species of *Trichogramma*. In the field cages, Jaraleno-Teniente et al. (2020) found that the parasitism of *T. atopovirilia* and *T. pretiosum* did not surpass 8%. *T. atopovirilia* parasitized a greater number of hosts than *T. pretiosum* when released using one, two and three parasitoids per pest egg. The parasitism of *T. atopovirilia* was similar at the dose of two and three *T. atopovirilia* parasitoids per egg. In another field cage study in Mexico, Jaraleno-Teniente et al. (2021) reported that *T. pretiosum* could parasitize about 7.5% of the FAW egg masses.

Interaction of *Trichogramma* and *Telenomus*

Understanding the role of intraguild interactions may contribute to an effective pest management strategy when multiple natural enemies may be essential to control a target pest (Zang and Liu 2007). Before an introduction or release of natural enemies, the intraguild interaction should be well characterized, since several aspects may interfere with the results of pest control as different pest species have different arrays of natural enemies (Ksentini and Herz 2019). FAW eggs are parasitized by several species of egg parasitoids; mainly the species of the genus *Trichogramma* and *Telenomus* (Hymenoptera: Platygastridae). The simultaneous occurrence of egg parasitoids of these two genera has been already recorded on FAW eggs from various crop ecosystems (Laminou et al. 2020). In the field conditions in Brazil, Dasilva et al. (2015) reported evidence of exploitative competition among egg parasitoids of FAW in maize. Egg parasitoids, viz. *T. pretiosum*, *T. atopovirilia* and *T. remus,* were engaged in exploitative competition and involved in interference competition towards eggs of FAW. *Telenomus remus* emerged from every egg mass exposed in the field and reported that it had competitive dominance over both species of *Trichogramma*. Under laboratory conditions, the intraguild interaction of *T. pretiosum* and *T. remus* on FAW eggs when evaluated at different ratios displayed that only two *T. remus* for each eight *T. pretiosum* were enough to significantly increase the parasitism rate as compared to other ratios of these two egg parasitoids. However, the higher proportion of *T. remus* resulted in the most effective parasitism, while the sole release of *T. pretiosum* was less efficient than when released associated with the parasitoid *T. remus* (Goulart et al. 2011a). Besides, the interspecific interaction between *T. pretiosum* and *T. remus* showed when FAW eggs were earlier exposed to either parasitoid, there was no emergence of the other parasitoid. Interestingly, *T. remus* showed a greater parasitism rate when both parasitoid females were exposed together with host eggs. Further, both egg parasitoids could recognize host eggs previously parasitized by the other (Carneiro and Fernandes 2012). The comparative parasitism capacity of *T. pretiosum* and *T. remus* when exposed together showed that females of *T. pretiosum* parasitized 121.3 eggs of FAW, while *T. remus* could parasitize 574 eggs during adulthood with maximum parasitism in the first 24 h of exposure (Pinto and Fernandes 2020). Furthermore, the interaction between *Trichogrammatoidea* sp. and *T. remus* resulted in lower parasitism when exposed together to FAW eggs in comparison with *T. remus* released alone which parasitized 78% FAW eggs under laboratory conditions in Niger, Africa (Laminou et al. 2020).

Effect of egg mass scales and layers on parasitism

Parasitism of *Trichogramma* is influenced by several factors such as the host egg size, shape, colour and morphological defences such as host scales, hairs and spines on egg batches are the important characteristics for their survival as these insects eggs cannot move and escape from natural enemies (Dong et al. 2021). FAW egg masses often covered with protected scales constitute a physical barrier for egg parasitoids (Floater 1998). Adult female of FAW lays eggs in masses and protect them by depositing scales around and over the eggs at the time of oviposition (Fukuda et al. 2007). These scales often originate from an anal tuft at the tip of the female' abdomen (Hou et al. 2022). The thickness of scales on FAW egg masses varies with egg masses showing no scales (eggs are visible), partially covered and the egg masses being fully covered with scales (egg masses completely invisible) which maximizes the protection of eggs (Hou et al. 2022). These scales modify the oviposition behaviour of egg parasitoids and influence the control efficacy of biocontrol agents, particularly *Trichogramma* spp. (Hou et al. 2022). Further, the thickness of the scale layer on egg masses of FAW varied with the age of the female (Hou et al. 2022). Furthermore, the poor performance of *Trichogramma* females on FAW eggs is linked to their smaller

body size compared to other egg parasitoids (Dong et al. 2021).

The parasitism rate of FAW eggs by *T. dendrolimi* varied with the scales thickness and higher parasitism on eggs (31.6%) and egg masses (78.3%) was recorded at level I (71.6 μm thickness). The egg mass parasitism on levels II (169.3 μm) and III (281.6 μm) thickness of scales was 48.2% and 23.1%, respectively. Similarly, egg parasitism was also significantly lower with 12.6% and 1.9% of eggs parasitized by *T. dendrolimi* on levels II and III of the scale thickness (Hou et al. 2022). Similarly, *T. dendrolimi* struggled to parasitize the FAW egg masses covered with scales and the average egg parasitism on eggs without scales and with scales was 22.2% and 12.9%, respectively, while *T. pretiosum* parasitized comparably higher percentage of host eggs and parasitism on without and with scales was 46 and 19.90%, respectively (Dong et al. 2021). However, the parasitism rate by *T. pretiosum* and *T. dendrolimi* on egg masses with scales was significantly lower than that on egg masses without scales and parasitized the eggs located on the periphery of the egg mass (Dong et al. 2021). When parasitism of *T. pretiosum* compared with *T. atopovirilia*, only 60% of *T. pretiosum* females were able to parasitize the FAW eggs due to difficulty in parasitizing high-scale-density eggs, while 100% of *T. atopovirilia* females could parasitize the FAW eggs (Beserra et al. 2005). The egg masses laid first in the first 3 days by FAW females have numerous scales which protect from egg parasitoids like *Trichogramma* spp. Thereafter, the thickness of scales decreased daily and such eggs with thin layers of scales (< 20.0 μm) were actively parasitized by *Trichogramma* spp. (Li et al. 2023). Parasitism by *T. dendrolimi* was 33.4% on such FAW egg masses with decreased scale covers. Besides, the *Trichogramma* females also parasitize eggs that are half exposed or situated at the periphery of the egg masses (Dong et al. 2021).

The number of egg layers (one to > 3 layers; 89–300 eggs) also influences the biological control efficiency of FAW using *Trichogramma* (Mohamed et al. 2023). Several studies have reported that some *Trichogramma* can only reach and parasitize upper-layered eggs, while eggs at the internal layer were difficult to parasitize (Beserra et al. 2005). When *T. atopovirilia* was exposed to FAW egg masses with different layers, the parasitism on single-layered eggs was higher (66.24%) than those of two (45.2%) and three egg layers (40.1%). It showed that the number of egg layers affects the parasitizing efficiency of *T. atopovirilia* and the control efficacy may reduce when using this species in control of FAW (Beserra and Parra 2005). Further, the females of *T. pretiosum* were also found hard to parasitize lower layers of FAW eggs and could parasitize the eggs on the periphery of the egg masses from the side when two layered eggs were offered for parasitism. Further, the emergence rate of *T. pretiosum* from single and double-layered FAW egg masses ranged from 59.7–73.1% to 36.8–57.2%, respectively (Carneiro and Fernandes 2012). In contrast, *T. pretiosum* parasitized 98.3% of single-layered egg masses laid on maize in Brazil (De Sa et al. 1994).

The presence of scale layers on FAW egg masses affects the parasitism by *Trichogramma* species as the females found it difficult to move on the scales of the egg masses, therefore they prefer to parasitize the eggs on the periphery with fewer or with no scales (Carneiro and Fernandes 2012). Besides, several studies indicated that *Trichogramma* species have the potential to parasitize FAW eggs without scale layers and preferably those are laid in single-layered rather than laid in overlapping layers. The variation in the thickness of scales and layered eggs of FAW explains the obvious difference in parasitism rates by *Trichogramma* species in the field (Hou et al. 2022). Therefore, the scales on egg masses and layered eggs of FAW should be considered wisely while understanding the interaction between FAW and *Trichogramma* species and the implications in the biological control of FAW (Dong et al. 2021). Further, considering the mass-rearing cost of *Trichogramma* and control efficiency, a variety of parasitoids can be combined and released to control FAW to overcome the proportions of egg mass covered with scales and laid in overlapping layers at the field level.

Mass rearing of *Trichogramma* species for augmentative biocontrol

Mass rearing is a crucial step to achieve the success of biological control or/and to support IPM which involves the production of millions of insects to control the insect pests (Parra 2010). The success of biological control programmes depends on the scale of mass production and the cost efficiency of mass production. Several stages of mass rearing process such as the collection of host eggs, cleaning of egg, drying of host eggs, sterilization of eggs, collection of parasitized host eggs, parasitoid inoculation, preparation of egg cards etc. have been mechanized to reduce the cost of production (Wang et al. 1999). However, the cost efficiency of mass rearing majorly depends on the low-cost and quality factitious hosts for rearing the selected biocontrol agent. Historically, *Trichogramma* spp. have been mass-reared on several factitious hosts, with the earliest practical attempt for rearing of *Trichogramma* on Angoumois grain moth, *Sitotroga cerealella* (Oliver) (Lepidoptera: Gelechiidae) (Flanders 1927). Most successful *Trichogramma* mass rearing methods are developed using large-size host eggs as large-size eggs are considered suitable for mass rearing. However, small eggs are also used for *Trichogramma* mass rearing

and they are useful for rearing *Trichogramma* species having a weak ovipositor and mouthparts (Zang et al. 2021). For the control of FAW, *Trichogramma* spp. are mass-reared on different factitious hosts in the native range and invaded regions (Table 4). *Sitotroga cerealella, Ephestia kuehniella* (Lepidoptera: Pyralidae) and *Corcyra cephalonica* (Lepidoptera: Pyralidae) are among the most widely used factitious hosts for mass rearing of *Trichogramma* spp. across the world (Zang et al. 2021). In Brazil, the eggs of *S. cerealella* previously used in mass rearing are found nutritionally poorer as well as smaller than eggs of *A. kuehniella* (Parra et al. 2014). For this reason, eggs of *A. kuehniella* are the most suitable factitious host for *Trichogramma* rearing in Brazil, as several species had a lower acceptance and parasitism rate on eggs of *S. cerealella* (Gomes & Parra 1998). In China, the successful rearing method of *Trichogramma* was adopted using the host species showing large-size eggs such as *Antheraea pernyi* which enabled commercial production of *T. dendrolimi* and *T. chilonis* (Zang et al. 2021). Besides, the small eggs of *C. cephalonica* and *S. cerealella* are highly suitable for mass rearing of *T. japonicum* and *T. ostriniae*, respectively, in China (Zang et al. 2021). In Brazil, the rearing cost of 100,000 parasitoids on *A. kuehniella* eggs required for a one-hectare area is US$8–10, adding a cost of US$2–3 for application via drone in the fields (Parra and Coelho 2022). Further, the cost of *T. pretiosum* wasp and its commercial release was US$15.76 per hectare for a single release to control FAW in Brazil (Figueiredo et al. 2015). The rearing cost of 20,000 parasitoids of *T. chilonis* on *C. cephalonica* eggs is US$0.34, in India (Lalitha et al. 2023). In China, the production of 2 billion *Trichogramma* yearly using *C. cephalonica* as a factitious host costs about US$0.43 million and using *A. pernyi* as a host has enabled the production of 400 billion *T. dendrolimi* per year for a cost of US$11.4 million in production facilities at Jilin province (Zang et al. 2021). Furthermore, the cost of 100,000 *Trichogramma* adults reared on the Chinese artificial diet was approximately $0.06 (Greenberg et al. 1998). In addition, the mass rearing of factitious host *E. kuehniella* is costly and the market price is in the range of 600–800 EUR/kg in Europe (Vandekerkhove and De Clercq 2010). In the United States, the production cost of *S. cerealella* eggs was US$2.43 for 100,000 eggs (Greenberg et al. 1998). The rearing cost of *C. cephalonica* on a broken sorghum-based diet was US$0.27 for the production of 20,000 eggs in India (Lalitha et al. 2023). Currently, some commercial companies are producing 10–20 kg of *A. kuehniella* egg per day, with total quantities of up to 30–40 kg eggs per day with a labour cost representing 70–80% of total cost of production in Brazil (Parra and Coelho 2022). Thus, automation is necessary to produce adequate insects under well-controlled temperatures with knowledge of degree-day requirements to maximize the production of factitious hosts and parasitoids (Coelho et al. 2016).

Table 4 Rearing of *Trichogramma* species for control of fall armyworm in different regions

Species	Factitious host	Country	Target crop	References
Trichogramma pretiosum	*Sitotroga cerealella*	Brazil	Maize	Parra (2010)
T. pretiosum	*Anagasta kuehniella*	Brazil	Maize	Bueno et al. (2010) and Parra et al. (2021)
T. pretiosum	*A. kuehniella*	Brazil	–	Goulart et al. (2011b)
T. pretiosum	*A. kuehniella*	Brazil	–	Carneiro and Fernandes (2012)
Trichogrammatoidea armigera	*C. cephalonica*	Niger	–	Laminou et al. (2020)
T. chilonis	*C. cephalonica*	Kenya	Maize	Elibariki et al. (2020)
T. chilonis	*C. cephalonica*	Nepal	Maize	Elibariki et al. (2020)
T. pretiosum	*C. cephalonica*	India	Maize	Varshney et al. (2021)
T. pretiosum	*C. cephalonica*	China	Maize	Jin et al. (2021)
T. chilonis	*C. cephalonica*	India	Maize	Navik et al. (2021)
T. chilonis	*C. cephalonica*	China	Maize	Jin et al. (2021)
Trichogramma ostriniae	*C. cephalonica*	China	Maize	Jin et al. (2021)
Trichogramma confusum	*C. cephalonica*	China	Maize	Jin et al. (2021)
Trichogramma mwanzai	*C. cephalonica*	Zambia	–	Sun et al. (2021)
Trichogramma dendrolimi	*C. cephalonica*	China	Maize	Dong et al. (2021)
T. pretiosum	*C. cephalonica*	China	Maize	Dong et al. (2021)
T. dendrolimi	*C. cephalonica*	China	–	Hou et al. (2022)
T. chilonis	*C. cephalonica*	India	–	Dupatne et al. (2023)
T. dendrolimi	*C. cephalonica*	China	–	Hou et al. (2022) and Li et al. (2023)

Trichogramma release strategies

Several approaches have been adopted for *Trichogramma* release worldwide (Parra et al. 2015). Amongst, the inundative release method has been the most adopted method for *Trichogramma* release programmes (Zang et al. 2021). Besides, the mixed species releases have been also explored to increase the effectiveness of biological control using *Trichogramma* parasitoids (Zang et al. 2021). In the inundative release, a large number of parasitoids are released for pest control which basically act as a biopesticide (Zang et al. 2021). To release parasitoids in the field, several release techniques have been used in biological control programmes which include—the release of parasitized eggs glued on cardboard just before adult emergence, the release of adult or late pupal stages that are very close to adult emergence (Pinto et al. 2003), or parasitized eggs encased in cardboard capsules (Parra et al. 2015). In recent times, an inventive method of release has been deployed which uses capsules containing *Trichogramma* parasitized eggs (Zang et al. 2021). With the advent of new technologies, the use of unmanned aircraft systems (UAS) in the form of drones have been deployed to release the *Trichogramma* parasitized eggs of *E. kuehniella* with fine vermiculite for control of maize and forest pests (Martel et al. 2021).

For biological control of FAW, the inundative releases of *Trichogramma* spp. have been adopted for field release. In Brazil, Figueiredo et al. (2015) released *T. pretiosum* adults after 24 h of adult emergence using glass containers in the morning hours in maize fields against FAW. These parasitoids were released in the centre of each plot by opening the containers for adult dispersal. Furthermore, Varshney et al. (2021) used *T. pretiosum* parasitized *C. cephalonica* eggs glued-on paper cards that were cut into small pieces and stapled on the lower side of the upper part of the maize leaf. These small pieces were uniformly dispersed in the maize field when at least 5% adult emergence (pharate) was observed. In China, eggs of *C. cephalonica* glued on paper cardboard parasitized by *Trichogramma* spp. and anticipated to emerge within two days were placed on maize leaves to target egg masses of FAW (Jin et al. 2021). The release of *Trichogramma* through parasitized egg on cards/cardboard is the most commonly adopted technique at the field level. However, this method has some limitations, as these parasitized eggs prone to predators and exposed to extreme weather conditions that influence the field efficacy of parasitoids. Thus, the protection of these wasps is important to ensure maximum parasitization in the field. Over time field release method has been upgraded (e.g. encased in a capsule) to improve the efficacy of parasitoids and protection from extreme weather conditions.

Integration of *Trichogramma* with other egg parasitoids

Integration of *Trichogramma* species with other parasitoids, such as *Telenomus remus* Nixon could be effective in controlling the FAW. *T. remus* can penetrate the protective scale covering of FAW egg masses and parasitize the eggs (Fortes et al. 2023). This parasitoid also has the potential to parasitize multi-layered FAW eggs, indicating their ability and effectiveness by creating an efficient avenue for parasitism (Goulart et al. 2011b). Besides, the natural occurrence of multiple parasitoids on FAW is effective in controlling pests (Kenis et al. 2022). Notably, more than one species of *Trichogramma* can occur and parasitize the same FAW eggs mass in the same field (Jaraleno-teniente et al. 2020). In addition, the parasitism of multiple egg parasitoids, such as *T. pretiosum, T. atipovillia* and *T. remus* was also observed from a single FAW egg mass in a maize field (Dasilva et al. 2015). This co-occurrence indicated that *T. remus* emerge from all parasitized FAW egg masses, while *Trichogramma* species alone did not emerge from host egg masses. Although, Carneiro and Farnandes (2012) found no evidence of the emergence of *T. pretiosum* from FAW eggs previously parasitized by *T. remus*. This suggests that *T. remus* can recognize the host eggs previously parasitized by *Trichogramma* spp. Moreover, the larger size, robust body, and ability to penetrate the inner layers of FAW eggs explain its dominance over *Trichogramma* species (Lacerda et al. 2023). However, the parasitism to egg masses without physical scales and single layered and also partial parasitism to layered eggs (periphery of layered eggs) suggest the implication of *Trichogramma* species along with *T. remus* in the biological control of FAW. No doubt, *T. remus* is the most effective egg parasitoid of FAW, but it is a serious challenge to find a suitable laboratory host for economic mass-rearing (Li et al. 2023). On the contrary, rearing on FAW makes it difficult due to its highly cannibalistic nature and also large-scale rearing is not affordable in terms of time and resources (Li et al. 2023). Further, the rearing of *T. remus* using *C. cephalonica* as an alternate host is debatable (Chen et al. 2021), with few reports indicating its feasibility (Queiroz et al. 2017a, b). Thus, large-scale production of *T. remus*, even on its potential host, *Spodoptera litura* (Fabricius) is challenging as compared to *Trichogramma* production. In addition, rearing of *Trichogramma* on the factitious host is easy and less expensive which reduces the cost of biological control (Zang et al. 2021). Integration of *Trichogramma* species with *T. remus* could be effective, by releasing *T. remus* in the early stage of egg masses with thick scales and *Trichogramma* subsequently to achieve better control and reduction in overall cast (Li et al. 2023).

Field efficacy of *Trichogramma* spp. in biological control

Various species of *Trichogramma* have been released for biological control of FAW in the native as well as in the invaded region worldwide. The inundative release method was followed in most of the cases by releasing these egg parasitoids in large numbers in the various crops for FAW control. Loya (1978) conducted a field experiment in Mexico with mass releases of an unspecified *Trichogramma* sp. to control FAW and recoded low parasitism level (0.56%) in the parasitoid-released field as compared to the unreleased field (0.18%). In contrast, Montoya (1980) recorded parasitism 45–55% egg parasitism by the release of *Trichogramma* spp. in the maize fields during different years in Veracruz, Mexico. While, Peralta et al. (1981) reported the average parasitism by *Trichogramma* sp. on FAW eggs was less than 15% in Tamaulipas, Mexico. Besides, the field release of 30,000 individuals of *Trichogramma* sp. in maize fields resulted in only 4% egg parasitism. The lower parasitism by *Trichogramma* sp. owing to a higher number of brachypterous (deformed wings in adult) individuals was responsible for the decrease in the dispersal capacity of the parasitoid and also other factors such as predation by ants and impact of rainfall together affected parasitism (Toonders and Sanchez 1987). In Southern Brazil, two weekly releases of *T. pretiosum* at 200,000 adults per hectare from a week old plant onwards in maize fields recorded a 63% reduction in plant damage after the second week onwards as compared to non-released fields (Martinazzo et al. 2007). In addition, when *T. pretiosum* was applied one, two and three times at 100,000 per hectare resulted in 69.8, 79.2 and 68.7% egg mass parasitism, respectively, in Brazil. Three parasitoid releases recorded the lowest maize leaf damage (1.35 leaf damage score on 0–5 score) in the plot as compared to two (1.51 leaf damage) and one (1.53 leaf damage) release. Overall, the inundative field releases of *T. pretiosum* increased organic maize productivity by 19.4% (Figueiredo et al. 2015).

FAW invasion in Africa and subsequently in Asia also invited the need for biological control, as the pest settled in maize, sugarcane and other crop ecosystems. Field efficacy of four species of *Trichogramma*, viz. *T. chilonis, T. ostriniae, T. confusum* and *T. pretiosum,* were investigated and found that all the species were effectively parasitized FAW egg masses in the field trails and the parasitism rate on the egg masses ranged from 61.5 to 87.5% in China. The field release of *T. ostriniae. T. pretiosum, T. confusum* and *T. chilonis* recorded plant damage rates were 36.1, 38.8, 51.9, and 59.7%, respectively, as compared to the non-released field (95.6% plant damage). In addition, parasitoid releases reduced the FAW larval density from 0.83 to 0.43 larvae/plant as compared to the non-released field (1.37 larvae/plant) suggesting these four species are viable biocontrol candidates for FAW in Hainan, China (Jin et al. 2021). In India, four field releases of *T. pretiosum* at 50,000 per hectare at weekly intervals during the early stage to 60 days old maize crop recorded reduction in FAW egg masses up to 76.25 and 71.64% in winter and rainy seasons, respectively. The reduction in egg masses was evident after the second release of the *T. pretiosum* in the maize (Varshney et al. 2021). The presence of scales/hairs over the egg masses act as a barrier against parasitism by *Trichogramma* spp. This difficulty can be overcome by using a more aggressive parasitoid, capable of breaking the physical barrier imposed by scales on the eggs. *T. remus* has proved very effective in South America and Florida to minimize the egg layers problems progressively superimposed on each other. Thus, a combined release of *Trichogramma* and *T. remus* could add a synergistic effect in egg parasitism, which may increase the efficacy of the biological control of FAW. Moreover, *Trichogramma* spp. parasitizes the upper layer of FAW egg masses, whereas *T. remus* can parasitize lower layers, thus, there may be a complementary effect towards egg parasitism (Bueno et al. 2023). Although both parasitoids may compete for FAW eggs from the upper layers, yet a complementary effect can still be expected (Bueno et al. 2023). Furthermore, the more frequent releases of well-fed parasitoids at the pupal or adult stages are crucial in achieving increased egg parasitism rates in the fields. In addition, parasitoid releases should be conducted based on moth catches in pheromone traps with intervals of three days, as the average incubation period of FAW eggs is three days (Cruz et al. 1999). This synchronization is crucial for successful parasitism by the *Trichogramma* species in fields for FAW management (Bueno et al. 2023).

Trichogramma species are generalist egg parasitoids of lepidopterans, concerns exist about possible detrimental effects of inundative releases on non-target native hosts and beneficial lepidopterans used for biological control of weeds (Paraiso et al. 2013). *Trichogramma* species reported that parasitizing FAW eggs are also known to parasitize the eggs of other lepidopteran pests (Navik et al. 2019). The inundative releases of *T. pretiosum* are widely adopted to control FAW in corn in Brazil (Parra et al. 2015) and *T. chilonis* in Asia against noctuid pests (Jin et al. 2021), both parasitoids have a wider host range (Jalali et al. 2017). Nevertheless, the *Trichogramma* species tend to show a strong preference for certain hosts, plants, and climatic conditions (Hassan and Gou 1991). Given that, *Trichogramma* are likely to have a limited host range in particular climatic conditions, decreasing the risk for non-target impacts (Orr et al. 2000). Babendreier et al. (2003a) reported the minimal (1% parasitism)

impact of inundative releases of *Trichogramma brassicae* Bezdenko on non-target butterflies including species endangered species in Switzerland and suggested the cautious release of parasitoids (Babendreier et al. 2003b). Similarly, the non-target impacts of inundative release of *Trichogramma nubilale* Ertle and Davis on endangered and threatened were minimal (Andow et al. 1995). While *Trichogramma fuentesi* Torre was not advocated for biological control of *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) due to a moderately high level of risk to native non-target cactus moth, *Melitara prodenialis* Walker (Lepidoptera: Pyralidae) which share the same habitat (Paraiso et al. 2013). Consequently, the specific research on the non-target impact of inundative releases of *Trichogramma* species used in biological control of FAW is still limited and research on this subject is urgently needed in the near future.

Conclusion and prospects

FAW is a serious pest of cereals and other economic crops in native and invaded regions of the world. None of the single methods is sufficient to control the pest spread in new territory and keep infestations below the economic injury level. Moreover, the egg parasitoids provide an opportunity but not below economic injury level as indicated by the low range of field parasitism to control pests at their egg stage before their larvae hatch out and cause crop damage. Of the various *Trichogramma* species, *T. pretiosum*, *T. mwanzai* and *T dendrolimi* have been mass-reared and exploited for augmentative biological control of FAW. In addition, several species of *Trichogramma* have been found naturally parasitized FAW eggs and also tested for laboratory efficacy. Furthermore, the integration of potent species of *Trichogramma* with other key parasitoids, such as *T. remus* or/and potential native parasitoids and predators in biological control or IPM strategies to achieve effective FAW control. As *Trichogramma* parasitoids find difficulty in penetrating egg mass covered with scales or deposited in multi-layered, it becomes essential to combine with other platygasterid parasitoids that can penetrate through scales and parasitize inner layers of FAW egg mass. Further, the integration of *Trichogramma* with safer and selective pesticides such as green pesticides that are considered environmentally friendly to habitats, and to the ecosystem and conservation of other natural enemies could help in sustainable and environment-friendly FAW control. However, there is a need to investigate more on release time, release rates, number of releases to be made and what stages of *Trichogramma* to be taken for field releases to maximize the efficacy of biological control or IPM strategies. Further, investigations are needed on release methods, mass rearing protocols and their validation at the field level, determined area-wise so that farmers can release *Trichogramma* parasitoids effectively to control FAW.

Abbreviations

FAW Fall armyworm
IPM Integrated pest management
UAS Unmanned aircraft systems

Acknowledgements

The senior author is thankful to the Director, ICAR-National Bureau of Agricultural Insect Resources (NBAIR), Bengaluru, for the constant support for research and providing research facilities. YY thanks the Director, ICAR–National Institute of Biotic Stress Management, Raipur, and SCK thanks the Director, CSIR-Central Institute of Medicinal and Aromatic Plants, Lucknow, for providing facilities for this work.

Author contributions

ON and SCK collected the data for writing the review under various headings. ON, SCK, YY and SNS participated in preparation and reviewing of the manuscript. All the authors have read and approved the final manuscript.

Funding

Not applicable.

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.

Author details

[1]ICAR–National Bureau of Agricultural Insect Resources, Bengaluru 560 024, India. [2]School of Crop Health Biology Research, ICAR–National Institute of Biotic Stress Management, Raipur 493 225, Chhattisgarh, India. [3]Entomology Laboratory, Crop Production and Protection Division, Council of Scientific and Industrial Research–Central Institute of Medicinal and Aromatic Plants (CSIR-CIMAP), Lucknow 226 015, Uttar Pradesh, India.

Received: 12 July 2023 Accepted: 2 December 2023
Published online: 13 December 2023

References

Abang AF, Nanga SN, Fotso Kuate A, Kouebou C, Suh C, Masso C, May-Guri S, Fiaboe KKM (2021) Natural enemies of fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in different agro-ecologies. Insects 12(6):509. https://doi.org/10.3390/insects12060509

Andow DA, Lane CP, Olson DM (1995) The use of *Trichogramma* in maize estimating environmental risks. In: Hokkanen HMT, Lynch JM (eds) Biological control: benefits and risks. Cambridge Univ, Press, pp 101–118

Andrews KL (1988) Latin American research on *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Fla Entomol 71(4):630–653. https://doi.org/10.2307/3495022

Atashi N, Shishehbor P, Seraj AA, Rasekh A, Hemmati SA, Riddick EW (2021) Effects of *Helicoverpa armigera* egg age on development, reproduction, and life table parameters of *Trichogramma euproctidis*. Insects 12(7):569. https://doi.org/10.3390/insects12070569

Babendreier D, Kuske S, Bigler F (2003a) Non-target host acceptance and parasitism by *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) in the laboratory. Biol Control 26(2):128–138. https://doi.org/10.1016/s1049-9644(02)00121-4

Babendreier D, Kuske S, Bigler F (2003b) Parasitism of non-target butterflies by *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) under field cage and field conditions. Biol Control 26(2):139–145. https://doi.org/10.1016/S1049-9644(02)00120-2

Beserra EB, Parra JRP (2004) Biologia e parasitismo de *Trichogramma atopovirilia* Oatman and Platner *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) em ovos de *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). Rev Bras Entomol 48:119–126

Beserra EB, Parra JRP (2005) Impact of the number of *Spodoptera frugiperda* egg layers on parasitism by *Trichogramma atopovirilia*. Sci Agric 62(2):190–193

Beserra EB, Dias CTDS, Parra JR (2002) Distribution and natural parasitism of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) eggs at different phenological stages of corn. Fla Entomol 85(4):588–593

Beserra EB, dos Santos Dias CT, Parra JRP (2003) Características biológicas de linhagens de *Trichogramma pretiosum* desenvolvidas em ovos de *Spodoptera frugiperda*. Acta Sci Agron 25(2):479–483

Beserra EB, Dias CT, Parra JRP (2005) Behaviour of Trichogramma atopovirilia Oatman and Platner and *T. pretiosum* Riley (Hymenoptera: Trichogrammatidae) on *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) egg masses. Braz J Biol 65(1):9–17. https://doi.org/10.1590/s1519-69842005000100003

Bueno RCOF, Parra JRP, Bueno AF (2009) Biological characteristics and thermal requirements of a Brazilian strain of the parasitoid *Trichogramma pretiosum* reared on eggs of *Pseudoplusia includens* and *Anticarsia gemmatalis*. Biol Control 51:355–361. https://doi.org/10.1016/j.biocontrol.2009.07.006

Bueno RCOF, Bueno AF, Parra JRP, Vieira SS, Oliveira LJD (2010) Biological characteristics and parasitism capacity of *Trichogramma pretiosum* Riley (Hymenoptera, Trichogrammatidae) on eggs of *Spodoptera frugiperda* (JE Smith) (Lepidoptera, Noctuidae). Rev Bras Entomol 54:322–327. https://doi.org/10.1590/S0085-56262010000200016

Bueno AF, Sutil WP, Maciel RMA, Roswadoski L, Colmenarez YC, Colombo FC (2023) Challenges and opportunities of using egg parasitoids in FAW augmentative biological control in Brazil. Biol Control. https://doi.org/10.1016/j.biocontrol.2023.105344

Burtet LM, Bernardi O, Adriano AM, Maiquel PP, Thiago TS, Guedes JVC (2017) Managing fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), with *Bt* maize and insecticides in south Brazil. Pest Manag Sci 73(12):2569–2577. https://doi.org/10.1002/ps.4660

Camera C, Dequech STB, Ribeiro LDP, Querino RB (2010) First report of *Trichogramma rojasi* parasitizing eggs of *Spodoptera frugiperda*. Ciência Rural 40(8):1828–1831

Carneiro TR, Fernandes OA (2012) Interspecific interaction between *Telenomus remus* (Hymenoptera: Platygastridae) and *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) on *Spodoptera frugiperda* (Lepidoptera: Noctuidae) eggs. An Acad Bras Cienc 84(4):1127–1135. https://doi.org/10.1590/s0001-37652012000400027

Chailleux A, Desneux N, Seguret J, Do Thi Khanh H, Maignet P, Tabone E (2012) Assessing European egg parasitoids as a mean of controlling the invasive south American tomato pinworm *Tuta absoluta*. PLoS ONE 7(10):e48068. https://doi.org/10.1371/journal.pone.0048068

Chen W, Li Y, Wang M et al (2021) Evaluating the potential of using *Spodoptera litura* eggs for mass-rearing *Telenomus remus*, a promising egg parasitoid of *Spodoptera frugiperda*. Insects 12:384. https://doi.org/10.3390/insects12050384

Coelho A, Reigada C, Haddad ML, Parra JRP (2016) Effects of temperature increase caused by larval metabolism on the reproduction of *Anagasta kuehniella* (Lepidoptera: Pyralidae), a factitious host for *Trichogramma*. Biocontrol Sci Technol 26:630–639. https://doi.org/10.1080/09583157.2016.1140125

Cruz I, Figueiredo MLC, Matoso MJ (1999) Controle biológico de *Spodoptera frugiperda* utilizando o parasitóide de ovos *Trichogramma*. Embrapa milho e sorgo, Sete Lagoas, MG, Brazil, Circ. Técn. n. 30, p 40

Dasilva CSB, Vieira JM, Loiácono M, Margaría C, Parra JRP (2015) Evidence of exploitative competition among egg parasitoids of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in maize. Rev Colomb Entomol 41(2):184–186

Day R, Abrahams P, Bateman M, Beale T, Clottey V, Cock M et al (2017) Fall armyworm: impacts and implications for Africa. Outlooks Pest Manag 28:196–201. https://doi.org/10.1564/v28_oct_02

De Sa LAN, Parra JRP (1994) Natural parasitism of *Spodoptera frugiperda* and *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs in corn by *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) in Brazil. Fla Entomol 77(1):185–188. https://doi.org/10.2307/3495886

Dequech STB, Camera C, Sturza VS, Ribeiro L, Querino RB, Poncio S (2013) Population fluctuation of *Spodoptera frugiperda* eggs and natural parasitism by *Trichogramma* in maize. Acta Sci Agron 35:295–300. https://doi.org/10.4025/actasciagron.v35i3.16769

Deshmukh S, Pavithra HB, Kalleshwaraswamy CM, Shivanna BK, Maruthi MS, Mota-Sanchez D (2020) Field efficacy of insecticides for management of invasive fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) on maize in India. Fla Entomol 103(2):221–227. https://doi.org/10.1653/024.103.0211

Diaz MF, Ramírez A, Poveda K (2012) Efficiency of different egg parasitoids and increased floral diversity for the biological control of noctuid pests. Biol Control 60:182–191. https://doi.org/10.1016/j.biocontrol.2011.11.001

Dong H, Zhu K, Zhao Q, Bai X, Zhou J, Zhang L (2021) Morphological defence of the egg mass of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) affects parasitic capacity and alters behaviours of egg parasitoid wasps. J Asia Pac Entomol 24(3):671–678. https://doi.org/10.1016/j.aspen.2021.05.015

Dupatne P, Venkatesan T, Navik O, Mohan M, Venugopal KM, Basavaarya V, Lalitha Y, Sivakumar G, Ashwini M (2023) Cross-resistance and biochemical mechanism in an insecticide-resistant population of *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) and its parasitizing efficiency against invasive fall armyworm. Curr Sci 124(1):115–122. https://doi.org/10.18520/cs/v124/i1/115-122

Durocher-Granger L, Mfune T, Musesha M et al (2021) Factors influencing the occurrence of fall armyworm parasitoids in Zambia. J Pest Sci 94:1133–1146. https://doi.org/10.1007/s10340-020-01320-9

Early R, González-Moreno P, Murphy ST, Day R (2018) Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm. NeoBiota 40:25–50. https://doi.org/10.3897/neobiota.40.28165

Elibariki N, Bajracharya ASR, Bhat B, Tefera T, Mottern JL, Evans G, Muniappan R, Yubak DG, Pallangyo B, Likhayo P (2020) Candidates for augmentative biological control of *Spodoptera frugiperda* (JE smith) in Kenya, Tanzania and Nepal. Indian J Entomol 82(4):606–608. https://doi.org/10.5958/0974-8172.2020.00088.7

FAO (2023) Map of the worldwide spread of fall armyworm since 2016 (as of July 2023). https://www.fao.org/fall-armyworm/monitoring-tools/faw-map/en/. Accessed 22 Sept 2023

Figueiredo MDLC, Della Lucia TMC, Cruz I (2002) Effect of *Telenomus remus* Nixon (Hymenoptera: Scelionidae) density on control of *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) egg masses upon release in a maize field. Rev Bras Milho Sorgo 1(02):12–19

Figueiredo MCD, Cruz I, Da Silva RB, Foster JE (2015) Biological control with *Trichogramma pretiosum* increases organic maize productivity by 19.4%. Agron Sustain Dev 35(3):1175–1183. https://doi.org/10.1007/s13593-015-0312-3

Flanders SE (1927) Biological control of the codling moth (*Carpocapsa pomonella*). J Econ Entomol 20:644

Floater JG (1998) Tuft scales and egg protection in *Ochrogaster lunifer* Herrich-Schäffer (Lepidoptera: Thaumetopoeidae). Aust J Entomol 37(1):34–39. https://doi.org/10.1111/j.1440-6055.1998.tb01540.x

Fortes ADR, Coelho A Jr, Amorim DJ, Demetrio CG, Parra JR (2023) Biology and quality assessment of *Telenomus remus* (Hymenoptera: Scelionidae) and Trichogramma spp. (Hymenoptera: Trichogrammatidae) in eggs of *Spodoptera* spp. for augmentative biological control programs. J Insect Sci 23(5):5. https://doi.org/10.1093/jisesa/iead047

Fukuda T, Wakamura S, Arakaki N, Yamagishi K (2007) Parasitism, development and adult longevity of the egg parasitoid *Telenomus nawai* (Hymenoptera: Scelionidae) on the eggs of *Spodoptera litura* (Lepidoptera: Noctuidae). Bull Entomol Res 97(2):185–190. https://doi.org/10.1017/S0007485307004841

Gomes SM, Parra JRP (1998) The parasitization as a tool for factitious host selection for *Trichogramma galloi* Zucchi and *T. pretiosum* Riley. Mitt Biol Bundesanst Land-Forstwirtsch 356:13–23

Goulart MMP, Bueno ADF, Bueno RCODF, Diniz AF (2011a) Host preference of the egg parasitoids *Telenomus remus* and *Trichogramma pretiosum* in laboratory. Rev Bras Entomol 55:129–133. https://doi.org/10.1590/S0085-56262011000100021

Goulart MMP, Bueno ADF, Bueno RCODF, Vieira SS (2011b) Interaction between *Telenomus remus* and *Trichogramma pretiosum* in the management of *Spodoptera* spp. Rev Bras Entomol 55:121–124. https://doi.org/10.1590/S0085-56262011000100019

Grande MLM, de Queiroz AP, Gonçalves J et al (2021) Impact of environmental variables on parasitism and emergence of *Trichogramma pretiosum*, *Telenomus remus* and *Telenomus podisi*. Neotrop Entomol 50:605–614. https://doi.org/10.1007/s13744-021-00874-2

Greenberg SM, Morrison RK, Nordlund DA, King EG (1998) A review of the scientific literature and methods for production of factitious hosts for use in mass rearing of *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) in the former Soviet Union, the United States, Western Europe and China. J Entomol Sci 33(1):15–32

Guo J, Wu S, Zhang F et al (2020) Prospects for microbial control of the fall armyworm *Spodoptera frugiperda*: a review. Biocontrol 65:647–662. https://doi.org/10.1007/s10526-020-10031-0

Hassan SA, Guo MF (1991) Selection of effective strains of egg parasites of the genus *Trichogramma* (Hym., Trichogrammatidae) to control the European corn borer *Ostrinia nubilalis* Hb. (Lep., Pyralidae). J Appl Entomol 111:335–341

Hoballah ME, Degen T, Bergvinson D, Savidan A, Tamo C, Turlings TC (2004) Occurrence and direct control potential of parasitoids and predators of the fall armyworm (Lepidoptera: Noctuidae) on maize in the subtropical lowlands of Mexico. Agric for Entomol 6(1):83–88. https://doi.org/10.1111/j.1461-9555.2004.00207.x

Hou YY, Yang X, Zang LS et al (2018) Effect of oriental armyworm *Mythimna separata* egg age on the parasitism and host suitability for five *Trichogramma* species. J Pest Sci 91:1181–1189. https://doi.org/10.1007/s10340-018-0980-2

Hou YY, Xu W, Desneux N, Nkunika PO, Bao HP, Zang LS (2022) *Spodoptera frugiperda* egg mass scale thickness modulates *Trichogramma* parasitoid performance. Entomol Gen 42(4):589–596. https://doi.org/10.1127/entomologia/2022/1443

Hruska AJ (2019) Fall armyworm (*Spodoptera frugiperda*) management by smallholders. CAB Reviews 14:043

Iqbal A, Hou YY, Chen YM et al (2020) Impact of *Trichogramma* parasitoid age on the outcome of multiparasitism in the factitious host eggs of Chinese oak silkworm, *Antheraea pernyi*. J Pest Sci 93:1347–1357. https://doi.org/10.1007/s10340-020-01239-1

Jalali SK, Sriram S, Venkatesan T, More RP, Navik O, Lalitha Y, Ojha R (2017) Host-insect and host-plant associated diversity in microbiota isolated from most important Oriental-Australian region egg parasitoid. J Biol Contr 31(4):229–239. https://doi.org/10.18311/jbc/2017/18228

Jaraleno-Teniente J, Lomeli-Flores JR, Rodríguez-Leyva E, Bujanos-Muñiz R, Rodríguez-Rodríguez SE (2020) Egg parasitoids survey of Spodoptera frugiperda (JE. Smith) (Lepidoptera: Noctuidae) in maize and sorghum in Central Mexico. Insects 3:157. https://doi.org/10.3390/insects11030157

Jaraleno-Teniente J, Lomeli-Flores JR, Rodríguez-Leyva E, Bujanos-Muñiz R, Rodríguez-Rodríguez SE (2021) Efficiency of three egg parasitoid species on fall armyworm (Lepidoptera: Noctuidae) in laboratory and field cages. J Entomol Sci 56(4):519–526. https://doi.org/10.18474/JES20-78

Jin T, Lin Y, Ma G, Liu J, Hao Z, Han S, Peng Z (2021) Biocontrol potential of *Trichogramma* species against *Spodoptera frugiperda* and their field efficacy in maize. Crop Prot 150:105790. https://doi.org/10.1016/j.cropro.2021.105790

Jing WAN, Huang C, Li CY, Zhou HX, Ren YL, Li ZY et al (2021) Biology, invasion and management of the agricultural invader: fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). J Integr Agric 20(3):646–663. https://doi.org/10.1016/S2095-3119(20)63367-6

Junce T, Yanhui LU, Wang G, Zheng X, Yang Y, Xu H, Zhongxian L (2020) The parasitic capability of five *Trichogramma* species on eggs of fall armyworm *Spodoptera frugiperda*. Chin J Biol 36(4):485

Kebede M, Shimalis T (2018) Out-break, distribution and management of fall armyworm, *Spodoptera frugiperda* JE smith in Africa: the status and prospects. Acad Agric J 3:551–568

Kenis M, Benelli G, Biondi A, Calatayud PA, Day R et al (2022) Invasiveness, biology, ecology, and management of the fall armyworm. Spodoptera Frugiperda Entomol Gen 43(2):187–241. https://doi.org/10.1127/entomologia/2022/1659

Ksentini I, Herz A (2019) Studies on interactions between parasitoids: the case of the idiobiont *Trichogramma cacoeciae* and the koinobiont *Ascogaster quadridentata* on *Cydia pomonella* eggs. Bull Insectol 72(2):207–218

Kumar RM, Gadratagi BG, Paramesh V, Kumar P, Madivalar Y, Narayanappa N, Ullah F (2022) Sustainable management of invasive fall armyworm. Spodoptera Frugiperda Agron 12(9):2150. https://doi.org/10.3390/agronomy12092150

Lacerda LFD, Coelho A, Paula PHD, Amorim DJ, Demetrio CGB, Parra JRP (2023) Biological basis for adoption of an isoline of *Telenomus remus* (Hymenoptera: Scelionidae) for an augmentative biological-control program for *Spodoptera frugiperda* (Lepidoptera: Noctuidae). J Insect Sci. https://doi.org/10.1093/jisesa/iead045

Lalitha Y, Navik O, Varshney R, Patel VN, Ballal CR (2023) Field efficacy of *Trichogramma chilonis* reared on different factitious hosts for the management of sugarcane stem borers. Bull Insectol 76(1):1–7

Laminou SA, Ba MN, Karimoune L, Doumma A, Muniappan R (2020) Parasitism of locally recruited egg parasitoids of the fall armyworm in Africa. Insects 11(7):430. https://doi.org/10.3390/insects11070430

Li ZG, Lv X, Xu QY, Ye JW, Han SC, Zhang CL, Li J (2019) The parasitism of *Telenomus remus* and *Trichogramma chilonis* on *Spodoptera frugiperda* found in the fields of Guangzhou and Hong Kong. J Environ Entomol 41:760–765

Li TH, Ma Y, Hou YY, Nkunika POY et al (2023) Variation in egg mass scale thickness of three *Spodoptera* species and its effects on egg parasitoid performance. J Pest Sci. https://doi.org/10.1007/s10340-023-01608-6

Loya J (1978) Estudio sobre el gusano cogollero, *Spodoptera frugiperda* (J.E. Smith), en Morelos. Informe Tecnico de la Coordinacion Nacional del Apoyo Entomologico. Seccion de Agric. y Recursos Hidraulicos. Inst Nac Invest Agric Mex 3:45–55

Mahanthi VTR, Venkatesan T, Ballal CR, Laxman K, Nagarjuna D, Chittibabu G, Venkatarao P, Jamuna P (2019) Report of the invasive fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) and its natural enemies on maize and other crops from Andhra Pradesh. India J Entomol Zool Stud 7(4):1348–1352

Martel V, Johns RC, Jochems-Tanguay L, Jean F, Maltais A, Trudeau S, St-Onge M, Cormier D, Smith SM, Boisclair J (2021) The use of UAS to release the egg parasitoid *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) against an agricultural and a forest pest in Canada. J Econ Entomol 114(5):1867–1881. https://doi.org/10.1093/jee/toaa325

Martinazzo T, Pietrowski V, Cordeiro ES, Eckstein B, Grisa S (2007) Release of *Trichogramma pretiosum* for biological control of *Spodoptera frugiperda* in corn. Rev Bras Agroecol 2(2):1657–1660

Mohamed HO, El-Heneidy AH, Dahi HF (2023) Impact of egg mass layers and scale thicknesses of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), on the parasitic performance of *Trichogrammatoidea bactrae* (Hymenoptera: Trichogrammatidae). Egypt J Biol Pest Control 33:89. https://doi.org/10.1186/s41938-023-00733-9

Molina-Ochoa J, Carpenter JE, Heinrichs EA, Foster JE (2003) Parasitoids and parasites of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas and Caribbean basin: an inventory. Fla Entomol 86:254–289

Monje JC, Zebitz CPW, Ohnesorge B (1999) Host and host age preference of *Trichogramma galloi* and *T. pretiosum* (Hymenoptera: Trichogrammatidae) reared on different hosts. J Econ Entomol 92:97–103. https://doi.org/10.1093/jee/92.1.97

Montezano DG, Specht A, Sosa-Gómez DR, Roque-Specht VF, Sousa-Silva JC, Paula-Moraes SVD, Peterson JA, Hunt TE (2018) Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. Afr Entomol 26:286–301. https://doi.org/10.4001/003.026.0286

Montoya JA (1980) Observaciones sobre la importancia de *Euplectrus* sp. en la integraci6n de los metodos de control de plagas del maiz. In: VIII Reuni6n Nacional de Control Biologico, Manzanilla, Col. Mex. 7

Morales J, Vásquez C, Pérez NL, Valera N, Ríos Y, Arrieche N, Querino RB (2007) Especies de *Trichogramma* (Hymenoptera: Trichogrammatidae)

parasitoides de huevos de lepidópteros en el Estado Lara, Venezuela. Neotrop Entomol 36:542–546
Navik O, Jalali SK, Lalitha Y (2019) Natural parasitism by trichogrammatids (Hymenoptera: Trichogrammatidae) on lepidopteran eggs under diverse cropping system. J Biol Contr 33:279–284. https://doi.org/10.18311/jbc/2019/24028
Navik O, Shylesha AN, Patil J, Venkatesan T, Lalitha Y, Ashika TR (2021) Damage, distribution and natural enemies of invasive fall armyworm *Spodoptera frugiperda* (J.E. smith) under rainfed maize in Karnataka. India. Crop Prot 143:105536. https://doi.org/10.1016/j.cropro.2021.105536
Navik O, Varshney R, Lalitha Y, Jalali SK (2023) Trichogrammatid parasitoids. In: Omkar (ed) Parasitoids in pest management. CRC Press, pp 227–263. https://doi.org/10.1201/9781003354239-9
Orr DB, GarciaSalazar C, Landis DA (2000) *Trichogramma* nontarget impacts: A method for biological control risk assessment. In: Follett PA, Duan JJ (eds) Non-target effects of biological control. Kluwer Academic Publishers, Norwell/USA, pp 111–125
Overton K, Maino JL, Day R, Umina PA, Bett B, Carnovale D, Ekesi S, Meagher R, Reynolds OL (2021) Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): A review. Crop Prot 145:105641. https://doi.org/10.1016/j.cropro.2021.105641
Paraiso O, Hight SD, Kairo MTK, Bloem S (2013) Host specificity and risk assessment of *Trichogramma fuentesi* (Hymenoptera: Trichogrammatidae), a potential biological agent of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Fla Entomol 96:1305–1310. https://doi.org/10.1653/024.096.0409
Parra JRP (2010) Mass rearing of egg parasitoids for biological control programs. In: Consoli F, Parra JRPP, Zucchi R (eds) Egg parasitoids in agroecosystems with emphasis on Trichogramma. Progress in Biological Control. Springer, Dordrecht, pp 325–342. https://doi.org/10.1007/978-1-4020-9110-0_10
Parra JRP, Coelho A (2022) Insect Rearing Techniques for biological control programs, a component of sustainable agriculture in Brazil. InSects 13(1):105. https://doi.org/10.3390/insects13010105
Parra JRP, Coelho JA, Geremias LD, Bertin A, Ramos CJ (2014) Criação de *Anagasta kuehniella*, em Pequena Escala, para Produção de *Trichogramma*. Occasio, Piracicaba, p 32
Parra JRP, Geremias LD, Bertin A, Colmenarez Y, Coelho A (2021) Small-scale rearing of *Anagasta kuehniella* for *Trichogramma* production. CABI, Wallingford UK
Parra JRP, Zucchi RA, Coelho Jr A, Geremias LD, Consoli FL (2015) *Trichogramma* as a tool for IPM in Brazil. In: Vinson SB, Greenberg SM, Liu T, Rao A, Volosciuk LF(eds.) Augmentative biological control using *Trichogramma* spp.: current status and perspectives Yangling: Nothwest A&F University Press, pp 472–496
Patil J, Linga V, Vijayakumar R, Subaharan K, Navik O, Bakthavatsalam N, Mhatre PH, Sekhar J (2022) Biocontrol potential of entomopathogenic nematodes for the sustainable management of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in maize. Pest Manag Sci 78:2883–2895. https://doi.org/10.1002/ps.6912
Peralta G, Delgado LG, Ramirez A (1981) Evaluacion de diferentes dosis del parasito *Trichogramma* sp. en los cultivos de la region Tamaulipas Norte. IX Reunion Nacional de Control Biol6gico, Oaxaca, Oax. Mex. pp 129–149
Pinto JRL, Fernandes OA (2020) Parasitism capacity of *Telenomus remus* and *Trichogramma pretiosum* on eggs of moth pests of peanut. Bull Insectol 73:71–78
Pinto ADS, Parra JR, Oliveira HND, Arrigoni ED (2003) Comparison of release techniques of *Trichogramma galloi* Zucchi (Hymenoptera: Trichogrammatidae) to control *Diatraea saccharalis* (Fabricius) (Lepidoptera: Crambidae). Neotrop Entomol 32:311–318. https://doi.org/10.1590/S1519-566X2003000200018
Pizzol J, Desneux N, Wajnberg E, Thiéry D (2012) Parasitoid and host egg ages have independent impact on various biological traits in a *Trichogramma* species. J Pest Sci 85:489–496. https://doi.org/10.1007/s10340-012-0434-1
Prasanna BM, Bruce A, Beyene Y et al (2022) Host plant resistance for fall armyworm management in maize: relevance, status and prospects in Africa and Asia. Theor Appl Genet 135:3897–3916. https://doi.org/10.1007/s00122-022-04073-4
Pratissoli D, Parra JRP (2000) Desenvolvimento e exigências térmicas de *Trichogramma pretiosum* Riley, criados em duas traças do tomateiro. Pesqui Agropecu Bras 35:1281–1288. https://doi.org/10.1590/S0100-204X2000000700001
Queiroz A, de Bueno AF, Pomari-Fernandes A et al (2017a) Low temperature storage of *Telenomus remus* (Nixon) (Hymenoptera: Platygastridae) and its factitious host *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). Neotrop Entomol 46:182–192. https://doi.org/10.1007/s13744-016-0442-6
Queiroz A, de Freitas BA, Pomari-Fernandes A et al (2017b) Quality control of *Telenomus remus* (Hymenoptera: Platygastridae) reared on the factitious host *Corcyra cephalonica* (Lepidoptera: Pyralidae) for successive generations. Bull Entomol Res 107:791–798. https://doi.org/10.1017/S0007485317000030X
Querino RB, Silva NNPD, Zucchi RA (2016) Natural parasitism by *Trichogramma* spp. in agroecosystems of the Mid-North. Brazil Ciência Rural 46:1521–1523. https://doi.org/10.1590/0103-8478cr20151352
Rane R, Walsh TK, Lenancker P et al (2023) Complex multiple introductions drive fall armyworm invasions into Asia and Australia. Sci Rep 13:660. https://doi.org/10.1038/s41598-023-27501-x
Ribeiro LP, Dequech STB, Camera C, Sturza VS, Poncio S, Vendramim JD (2014) Vertical and temporal distribution of *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) egg masses, parasitized and non-parasitized, on maize plants. Maydica 59:315–320
Rios VDM, Teran J (2003) Los *Trichogramma* (Hymenoptera: Trichogrammatidae) de la región noroccidental del estado Guárico, Venezuela. Entomotropica 18:127–145
Shylesha AN, Jalali SK, Gupta A, Varshney R, Venkatesan T, Shetty P, Ojha R, Prabhu C, Ganiger C, Navik O, Subaharan K, Bakthavatsalam N, Ballal CR (2018) Studies on new invasive pest *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) and its natural enemies. J Biol Control 32:1–7
Sisay B, Simiyu J, Mendesil E, Likhayo P, Ayalew G, Mohamed S, Subramanian S, Tefera T (2019) Fall Armyworm, *Spodoptera frugiperda* Infestations in East Africa: assessment of damage and parasitism. Insects 10(7):195. https://doi.org/10.3390/insects10070195
Sparks AN (1979) A review of the biology of the fall armyworm. Fla Entomol 62(2):82–87. https://doi.org/10.2307/3494083
Sun JW, Hu HY, Nkunika PO, Dai P, Xu W, Bao HP, Zang LS (2021) Performance of two trichogrammatid Species from Zambia on fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae). Insects 12(10):859. https://doi.org/10.3390/insects12100859
Tabebordbar F, Shishehbor P, Ebrahimi E, Polaszek A, Ugine TA (2022) Effect of different constant temperatures on life history and life table parameters of *Trichogramma euproctidis* (Hymenoptera: Trichogrammatidae). J Econ Entomol 115(2):474–481. https://doi.org/10.1093/jee/toac007
Tambo JA, Day RK, Lamontagne-Godwin J, Silvestri S, Beseh PK, Birgitta OM, Phiri NA, Matimelo M (2019) Tackling fall armyworm (*Spodoptera frugiperda*) outbreak in Africa: an analysis of farmers' control actions. Int J Pest Manag 66(4):298–310. https://doi.org/10.1080/09670874.2019.1646942
Tang J, Lyu B, Lu H, Ji X, Yang P, Su H, Cai B (2020) Investigation and preliminary study of biological characteristic of parasitic wasps of Spodoptera frugiperda in Hainan. Chin J Trop Agric 41:1189–1195. https://doi.org/10.3969/j.issn.1000-2561.2020.06.017
Tang LD, Sun JW, Dai P, Mu MY, Nkunika PO, Desneux N, Zang LS (2023) Performance of two dominant trichogrammatid species of fall armyworm from China and Africa under contrasted temperature and humidity regimes. Biol Control 179:105179. https://doi.org/10.1016/j.biocontrol.2023.105179
Toonders TJ, Sanchez JLC (1987) Evaluacion de la efectividad de *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) en el combate de *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) recomendaciones para su uso. Centro De Entomol y Acarol 67:75–84
Udayakumar A, Shivalingaswamy TM, Bakthavatsalam N (2021) Legume-based intercropping for the management of fall armyworm, *Spodoptera frugiperda* L. in maize. J Plant Dis Prot 128:775–779. https://doi.org/10.1007/s41348-020-00401-2
Vandekerkhove B, De Clercq P (2010) Pollen as an alternative or supplementary food for the mirid predator *Macrolophus Pygmaeus*. Biol Control 53(2):238–242. https://doi.org/10.1016/j.biocontrol.2010.01.005
Varshney R, Poornesha B, Raghavendra A, Lalitha Y et al (2021) Biocontrol-based management of fall armyworm, *Spodoptera frugiperda* (J.E. Smith)

(Lepidoptera: Noctuidae) on Indian Maize. J Plant Dis Prot 128:87–95. https://doi.org/10.1007/s41348-020-00357-3

Varshney R, Navik O, Jalali SK (2022) Reproductive strategies in parasitoids. In: Reproductive strategies in insects. CRC Press. pp. 283–305. https://doi.org/10.1201/9781003043195-14

Waddill HV, Whitcomb WH (1982) Release of *Telenomus remus* [Hym. scelionidae] against *Spodoptera frugiperda* [Lep.: Noctuidae] in Florida, USA. Entomophaga 27:159–162. https://doi.org/10.1007/BF02375224

Wang CL, Mao G, Gao Y, Li LJ, Cui DJ (1999) An instrument for selecting healthy parasitized host eggs. Chin J Biol Control 15:139–140

Yang L, Li F, Lü X, Xing B, Pan X, Shi X, Li J, Wu S (2022) Performance of three *Trichogramma* species as biocontrol agents on *Spodoptera frugiperda* eggs. Appl Entomol 146:1019–1027. https://doi.org/10.1111/jen.13042

Zang LS, Liu TX (2007) Intraguild interactions between an oligophagous predator, *Delphastrus catalinae* (Coleoptera: Coccinellidae), and a parasitoid, *Encarsia sophia* (Hymenoptera: Aphelinidae), of *Bemisia tabaci* (Homoptera: Aleyrodidae). Biol Control 41:142–150. https://doi.org/10.1016/j.biocontrol.2007.01.009

Zang LS, Wang S, Zhang F, Desneux N (2021) Biological control with *Trichogramma* in China: history, present status, and perspectives. Annu Rev Entomol 66:463–484. https://doi.org/10.1146/annurev-ento-060120-091620

Zucchi RA, Querino RB, Monteiro RC (2010) Diversity and hosts of *Trichogramma* in the new world, with emphasis in South America. In: Consoli F, Parra J, Zucchi R (eds) Egg parasitoids in agroecosystems with emphasis on *Trichogramma*. Progress in biological control, vol 9. Springer, Dordrecht, pp 219–236. https://doi.org/10.1007/978-1-4020-9110-0_8

Publisher's Note