



Current status of the biological control of the fall armyworm *Spodoptera frugiperda* by egg parasitoids

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Abstract

The fall armyworm (FAW) is native to the Americas. It has invaded more than 100 countries worldwide since its first observation in West Africa in 2016. FAW is a highly polyphagous pest species, feeding on more than 350 plants species, including important staple and fiber crops. FAW has developed resistance to all chemical families and its eating behavior causes the larvae to be “protected” by the inner leaves of the plant, making interaction with pesticides difficult. Therefore, IPM strategies based on biological control have been emphasized. In this article, we review the progress of egg parasitoids of the FAW, including their biodiversity and bio-ecology, the impacting biotic and abiotic factors, the mass rearing and field application, and put forward prospects and suggestions. So as to provide systematic information for egg parasitoids joining the IPM strategy of FAW, and enhance the sustainable management of FAW in invaded regions.

Keywords Invasive species · Biological control · *Telenomus* · *Trichogramma* · *Chelonus*

Key messages

- *Spodoptera frugiperda* (FAW) females leave scales on egg masses as a defense against egg parasitoids

- 28 species of *S. frugiperda* egg and egg-larval parasitoids were recorded in 33 countries
- Mass rearing, quality control & release methods of egg parasitoids are key steps for augmentative biocontrol strategy
- Key information for using egg parasitoids against FAW under IPM are provided

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Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is native from tropical and subtropical America (Sparks 1979) and has become a major invasive pest around the world in the last decade (Kenis et al. 2023), threatening food security globally (Sagar et al. 2020). Since its first observation in West Africa in 2016, the FAW has invaded more than 100 countries worldwide, including most of sub-Saharan Africa, parts of West, East, and South Asia, and parts of Oceania, including southern Australia (Kenis et al. 2023) and New Zealand (MPI 2023). It is a highly polyphagous pest, feeding on more than 350 plants species, including important staple crops (e.g., maize, sorghum, rice, soybean) and fiber crops (e.g., cotton) (Montezano et al. 2018; Overton et al. 2021; Wu et al. 2021; Wang et al. 2022). Maize yield reduction of up to 70% can be recorded when plants are attacked during early stages (Ayala et al. 2013; Hruska 2019). In Africa, FAW has the potential to reduce maize yields by 8.3–20.6 million metric tons per year, accounting for 21–53% of the annual production of the crop (Day et al. 2017). This represents an annual economic loss estimated at US \$9.4 billion (Eschen et al. 2021).

Chemical insecticides have been used since 1940 as the most common tool for FAW control in agriculture because they are effective, offering relatively quick and easy solution with enough satisfactory results (van den Berg et al. 2021) at least at short-term scenario. Despite some disadvantages, modern agriculture can hardly maintain high yields without chemical inputs (Paredes-Sánchez et al. 2021). However, the overuse of chemical pesticides are known to trigger various negative side-effects on beneficial arthropods (Desneux et al. 2007), as well as the selection of resistant pest populations (Chen et al. 2017; Yao et al. 2017; Paula et al. 2021; Li et al. 2022) including FAW populations (Carvalho et al. 2013; Kenis et al. 2023). Not only have FAW but also other *Spodoptera* species developed resistance to different chemical groups (e.g. *Spodoptera eridania*, Weinberg et al. 2022) and three of the four *Spodoptera* species present in the Arthropod Pesticide Resistance Database are in the top 15 most resistant arthropods: *S. frugiperda*, *S. litura* (F.) and *S. exigua* (Hübner) (Sparks et al. 2020). Moreover, FAW's eating behavior enables its larvae to be "protected" by inner leaves of the maize whorl, usually covered with excrements of the insect, which reduces even more direct insecticide contact and therefore, its efficacy (Paredes-Sánchez et al. 2021). Thus, the development of different methods to control FAW is crucial in order to promote its sustainable management. Transgenic crops can also be adopted to manage the pest. A recent review found that maize yield

losses attributed to FAW were 13% for *Bt* maize without insecticides, 21% for non-*Bt* maize with insecticides, and 25% for unmanaged non-*Bt* maize (Overton et al. 2021).

Among the most sustainable pest management strategies, there are plenty of new opportunities for biological control which has been studied and used in agriculture for more than 100 years worldwide (Heimpel and Mills 2017). There are some promising reports reviewing the application potential of microorganisms such as entomopathogenic fungi, baculoviruses and entomopathogenic bacteria in the control of FAW (Hussain et al. 2021; Kenis et al. 2023). However, there are still some challenges associated with fungal production and storage (Fronza et al. 2017; Grijalba et al. 2018; Bateman et al. 2021), high virus production costs (Haase et al. 2015) among other limitations of microbiologicals (Paredes-Sánchez et al. 2021; Kenis et al. 2023). In addition, field surveys demonstrated that natural predatory and parasitic enemies can constrain the development of FAW population to some extent (Tang et al. 2019; Zhou et al. 2021). However, somewhat unexpectedly, as one of the classic biological control agents, data on FAW predators are relatively scarce. Although it is very frequent to find various species preying on eggs and larvae (Firake and Behere 2020a; Koffi et al. 2020; Kenis et al. 2023), only a few of them are considered to have the potential to prey on FAW, e.g., *Orius insidiosus* (Say), *Orius similis* (Zheng) and *Eocanthecona furcellata* (Wolff) (Isenhour et al. 1990; Keerthi et al. 2020; Zeng et al. 2021; Ren et al. 2022). Moreover, as well known, predators of FAW are too polyphagous to be considered for introduction (Kenis et al. 2023). Thus, due to insufficient data support, the importance of predators in the population dynamics of FAW is still unclear and deserves further study to assess their potential as biological control agents in augmentative or conservation biological control (Kenis et al. 2023).

As another important biological control agents, parasitoids get more attention than FAW predators. As the native region for FAW, the Americas have the most abundant parasitoid numbers (~ 150 taxa) of FAW, which have been recorded from 13 families, nine in Hymenoptera, and four in Diptera (Molina-Ochoa et al. 2003). However, studies of parasitoids vary widely due to significant differences in FAW host stages. The pupal stage of FAW is spent in the soil (Shi et al. 2021), and accordingly, pupal parasitism has been poorly studied due to the difficulty in collecting large numbers of pupae (Kenis et al. 2023). Larvae of FAW has received the most attention due to their active feeding behavior, however, although still controversial (Allen et al. 2021), several studies have provided natural larval parasitism rates, typically below 30% (e.g. Pair et al. 1986; Molina-Ochoa et al. 2004; Murúa et al. 2009; Virgen et al. 2013; Ordóñez-García et al. 2015; Ghosh et al. 2022; Lekha priyanka et al. 2022). Thus, more recently, egg parasitoids have been highlighted as key biological control agents, especially

considering augmentative biological control programs for being easily reared in large numbers in small spaces and being able to control pests in its first stage of development (egg), before any injury be caused to the plants (Parra and Coelho 2019).

FAW females lay their eggs almost all on the undersides of leaves (Kasige et al. 2022), where parasitoids are not difficult to approach. Nevertheless, it was generally believed that a high amount of scales and hair left on FAW egg mass by moths during oviposition could hinder the parasitism of some egg parasitoids, especially those from the genus *Trichogramma* (Beserra and Parra 2005; Goulart et al. 2011a). However, a more recent report noted that the proportion of the thick scales ($> 180 \mu\text{m}$) decreased with FAW moth aging, whereas *Trichogramma dendrolimi* (Matsumura) could attack FAW eggs with thin scales ($< 80 \mu\text{m}$) or no scale coverage (31.6% eggs and 78.3% egg masses were parasitized) (Hou et al. 2022). Egg parasitoids, especially species from the genus *Trichogramma*, make up one of the most commonly used groups of natural enemies for biological control programs worldwide (Zang et al. 2021). In addition to *Trichogramma* spp., the egg parasitoid *Telenomus remus* Nixon has been studied and released against various pest species of the genus *Spodoptera* (Colmenarez et al. 2022). Despite the parasitism potential of *Trichogramma* spp. as well as *T. remus*, we note that the lack of systematic information will limit the research and application of those egg parasitoids on FAW. Therefore, here, we review the progress of FAW egg parasitoids worldwide to provide more diversified options for integrated management of this key pest.

Biodiversity of FAW egg parasitoids

Since most of the key parasitoids of FAW occur at the egg stage, here we discuss the egg parasitoids and the egg-larval parasitoids together. More than 18 species of egg parasitoids and 10 species of egg-larval parasitoids from 5 genera were recorded in FAW in the field or laboratory in 33 countries (Table 1), in addition to a number of parasitoids that have not been identified. In the Americas, as the place where FAW was firstly recognized as a destructive agricultural pest (Luginbill 1928), the research on FAW parasitoids has been more detailed, despite many of these parasitoids distribution only being restricted to this area (Tang et al. 2019).

After the invasion and rapid spread of FAW in West Africa in 2016 (Kenis et al. 2023), the attention of countries in the Old World to the parasitoids of FAW continued to increase. As the most studied and used egg parasitoids, *Trichogramma* species have received priority attention (Parra and Zucchi 2004; Jin et al. 2019). *Trichogramma* spp. are known to parasitize eggs of more than 200 insect species (Polaszek 2010; Zucchi et al. 2010). Therefore, some

Trichogramma spp. that are even not natural enemies of FAW have also been tested to assess their potential to be used against FAW (Table 1).

Chelonus species is another important FAW parasitoid group. They were found on larvae of FAW in fields from America, Africa and Asia (Table 1). As egg-larval parasitoids, *Chelonus* species, such as *C. insularis* (Cresson) and *C. bifoveolatus* (Szépligeti), have a much larger body size and more egg-carrying capacity than other egg parasitoids (e.g., *Te. remus* and *Trichogramma* spp.) and are believed to have promising potential in Augmentative Biological Control programs (Tang et al. 2019; Zang et al. 2022).

Among all those parasitoids, *Trichogramma pretiosum* Riley and *Telenomus remus* Nixon were the most used in biological control of FAW in Latin American countries such as Venezuela, Colombia, and Brazil (van Lenteren and Bueno 2003; Colmenarez et al. 2022). *Telenomus remus* has received more attention than *Trichogramma* spp. in biocontrol programs of FAW due to its capability of parasitizing inner layers of the egg masses (Tepa-Yotto et al. 2022). Moreover, *Te. remus* was even considered as one of the most effective augmentative biological control agents due to its high fecundity, its ability to parasitize all layers in an egg mass (Cave 2000; Bueno et al. 2014; Colmenarez et al. 2022) and its high dispersing and searching capacities (Pomari et al. 2013; Pomari-Fernandes et al. 2018). Meanwhile, in China, *Tr. dendrolimi* is considered as a promising (Hou et al. 2022; Li et al. 2023) and cost-effective biocontrol agent choice due to its huge production capacity of 200 billion parasitoids per year in one production line (Zang et al. 2021).

Bio-ecology of key egg parasitoids of FAW

Telenomus remus

Telenomus remus is an egg parasitoid of lepidopterous insects, including the families Noctuidae, Pyralidae, and Arctiidae, especially those of the genus *Spodoptera* (Cave 2000), such as *S. albula* Walker, *S. cosmioides* Walker, *S. eridania* Cramer and *S. frugiperda* (Pomari et al. 2012). It has been the most reported species studied and used for FAW control (Table 1). The natural parasitism of *Te. remus* on FAW eggs was about 30%, and the developmental time 9.6 days at 26 °C, one single adult parasitoid emerged per egg and the female ratio was about 76.0% (Tang et al. 2020). Functional response of *Te. remus* was type II which parasitism stabilized at a density of 150-egg per parasitoid female and reached an in-lab parasitism rate of 68.0% (Carneiro et al. 2010). *Telenomus remus* female longevity varied from 15.7 to 7.7 days from 15 to 31 °C. When the temperature reached 35 °C, female longevity was greatly reduced

Table 1 Reported parasitoids attacking *S. frugiperda* at the egg stage

Species	Biology ¹	Countries	Natural parasitoids of FAW or not (Y/N)	References
Hym: Braconidae				
<i>Chelonus antillarum</i> (Marshall)	Egg-larval	Barbados	Y	Molina-Ochoa et al. (2003)
<i>Chelonus bifoveolatus</i> (Szépligeti)	Egg-larval	Benin, Burkina, China, Faso, Ghana, Senegal, Uganda, Zambia	Y	Tendeng et al. (2019); Agboyi et al. (2020); Koffi et al. (2020); Ahissou et al. (2021b); Durocher-Granger et al. (2021); Otim et al. 2021; Shen et al. (2023)
<i>Chelonus cautus</i> (Cresson)	Egg-larval	Mexico	Y	Gutiérrez-Ramírez et al. (2015)
<i>Chelonus curvinaculatus</i> (Cameron)	Egg-larval	Kenya, Zambia	Y	Sisay et al. (2019); Koffi et al. (2020); Durocher-Granger et al. (2021)
<i>Chelonus formosanus</i> (Sonan)	Egg-larval	China, India	Y	Firake and Behere (2020a, b); Gupta et al. (2020); Tang et al. (2020); Sagar et al. (2022)
<i>Chelonus insularis</i> (Cresson)	Egg-larval	Colombia, Mexico	Y	Zenner et al. (2006); López et al. (2018); García-González et al. (2020); Jaraleño-Teniente et al. (2020)
<i>Chelonus intermedius</i> (Thomson)	Egg-larval	Egypt	Y	Youssef (2021)
<i>Chelonus munakatae</i> (Munakata)	Egg-larval	China	Y	Li et al. (2019a)
<i>Chelonus</i> nr. <i>blackburni</i> (Cameron)	Egg-larval	India	Y	Sagar et al. (2022)
<i>Camptolepis sonorensis</i> (Cameron)	Egg-larval	Mexico	Y	García-González et al. (2020)
<i>Chelonus</i> sp.	Egg-larval	Brazil, Mexico, Niger	Y	Molina-Ochoa et al. (2003); Amadou et al. (2018)
Hym: Scelionidae				
<i>Telenomus remus</i> (Nixon)	Egg	Bangladesh, Benin, Brazil, Cameroon, China, Côte d'Ivoire, Ecuador, Ghana, Honduras, India, Kenya, Nepal, Niger, Nigeria, Pakistan, South Africa, Tanzania, Uganda, US, Zambia	Y	Hay-Roe et al. (2015); Kenis et al. (2019); Liao et al. (2019); Sisay et al. (2019); Agboyi et al. (2020); Elibariki et al. (2020); Firake and Behere (2020a); Laminou et al. (2020); Abang et al. (2021); Otim et al. (2021); Wengrat et al. (2021); Kenis et al. 2023
<i>Telenomus</i> sp.	Egg	Brazil, Colombia, Cuba, Guadeloupe, Mexico	Y	Molina-Ochoa et al. (2003)
Hym: Trichogrammatidae				
<i>Trichogramma atopovirilia</i> (Oatman & Platner)	Egg	Brazil, Mexico	Y	Beserra and Parra (2004); Dequech et al. (2013); Jaraleño-Teniente et al. (2020)
<i>Trichogramma bilinegensis</i> (He & Pang)	Egg	China	N	Tian et al. (2020)
<i>Trichogramma chilonis</i> (Ishi)	Egg	Cameroon, China, India, Kenya, Nepal	Y	Shylesha et al. (2018); Sisay et al. (2019); Elibariki et al. (2020); Tang et al. (2020); Abang et al. (2021); Navik et al. (2021)
<i>Trichogramma chilostraeae</i> (Nagaraja & Nagar-katti)	Egg	Indonesia	Y	Sari et al. (2021)
<i>Trichogramma confusum</i> (Viggiani)	Egg	China	N	Jin et al. (2021)
<i>Trichogramma dendrolimi</i> (Matsumura)	Egg	China	N	Hou et al. (2022)

Table 1 (continued)

Species	Biology ¹	Countries	Natural parasitoids of FAW or not (Y/N)	References
<i>Trichogramma embryophagum</i> (Htg.)	Egg	China	N	Jin et al. (2021)
<i>Trichogramma exitum</i> (Pinto and Platner)	Egg	Colombia	N	Díaz et al. (2012)
<i>Trichogramma fasciatum</i> (Perkins)	Egg	Barbados, Nicaragua, US	Y	Young and Hamm (1967); Molina-Ochoa et al. (2003)
<i>Trichogramma japonicum</i> (Ashmead)	Egg	China	N	Sun et al. (2021)
<i>Trichogramma leucaniae</i> (Pang & Chen)	Egg	China	N	Sun et al. (2021)
<i>Trichogramma minutum</i> (Riley)	Egg	Nicaragua, US	Y	Molina-Ochoa et al. (2003)
<i>Trichogramma mwanzai</i> (Schulten & Feijen)	Egg	Tanzania, Zambia	Y	Elibariki et al. (2020); Sun et al. (2021)
<i>Trichogramma ostriniae</i> (Pang & Chen)	Egg	China	N	Sun et al. (2021)
<i>Trichogramma pretiosum</i> (Riley)	Egg	Bangladesh, Brazil, China, India, Mexico, Nicaragua, Venezuela	Y	Molina-Ochoa et al. (2003); van Lenteren and Bueno (2003); Dequech et al. (2013); Ballal et al. (2016); Zhu et al. (2019); Huda et al. (2020); Jaraletio-Teniente et al. (2020)
<i>Trichogramma rojasi</i> (Nagaraja & Nagarkatti)	Egg	Brazil	Y	Camera et al. (2010)
<i>Trichogramma</i> sp.	Egg	Argentina, Benin, Brazil, Colombia, Cuba, Ghana, Guadeloupe, Indonesia, Mexico, Nicaragua, US	Y	Molina-Ochoa et al. (2003); Agboyi et al. (2020); Tawakkal et al. (2021)
<i>Trichogrammatoidea lutea</i> (Girault)	Egg	Zambia	Y	Sun et al. (2021)
<i>Trichogrammatoidea</i> sp.	Egg	Niger	Y	Amadou et al. (2018); Laminou et al. (2020)

¹Host stage, where the host is attacked and killed

(1.7 days) and egg viability was null (Bueno et al. 2010b). *Telenomus remus* can be reared on eggs of *Corcyra cephalonica* (Stainton) with lower costs than using FAW eggs (Vieira et al. 2017), and the offspring parasitoids showed no preference between eggs of *C. cephalonica* and FAW in a free choice test, which indicated that there was no parental preference when using *C. cephalonica* as an alternative host (Queiroz et al. 2017c). However, *C. cephalonica* has only been used so far for research purposes (Colmenarez et al. 2022). In addition, reports from China have argued that it is infeasible to rear *Te. remus* with *C. cephalonica* (Chen et al. 2021). Those differences might be due to different strains of the parasitoid indicating that *C. cephalonica* population or more likely *Te. remus* population has differentiated among different geographical areas (Colmenarez et al. 2022). Consequently, it triggers some concerns about the effectiveness and overall cost-benefits of the use of *C. cephalonica* to massively rear *Te. remus* (Colmenarez et al. 2022). *Spodoptera litura*, a close relative of FAW, was shown to also serve as an alternative host for *Te. remus* (Chen et al. 2021).

Trichogramma species

Species of *Trichogramma* play an important role in dampening pest oscillations (Yang et al. 2022). They are regarded as generalist parasitoids, attacking a wide range of host species, primarily lepidopteran eggs (Bai et al. 1995). Tests on *Trichogramma* spp. as candidate natural enemies of FAW have been conducted in many countries (Table 1). Some *Trichogramma* species that are not FAW natural enemies in the native or invaded range also showed significant potential. For example, the total number of FAW eggs parasitized in laboratory by *Tr. chilonis* and *Tr. pretiosum* (natural enemies of FAW in the native or invaded range), *Tr. ostriniae* and *Tr. confusum* (no reported association with FAW in nature) within the first 96 h were 180 and 169, 139 and 191.3, respectively (Jin et al. 2021). *Trichogramma mwanzai* has also showed promising results in Tanzania with about 70% parasitism of FAW eggs (Elibariki et al. 2020). The natural occurrence of *Trichogramma* spp. begins about two days after FAW egg occurrence (Dequech et al. 2013). Similar to *Te. remus*, some *Trichogramma* species (e.g., *Tr. pretiosum*), can also parasitize the eggs of a range of *Spodoptera* species, such as *S. frugiperda*, *S. abula* and *S. eridania* (Siqueira et al. 2012). However, given the wide range of hosts of *Trichogramma* spp., the effects on non-target insects when introducing *Trichogramma* species need to be studied. It is recommended to give preference to native *Trichogramma* species for FAW control (Heimpel and Mills 2017).

Some species from the genus *Trichogramma* showed different adaptability to *Spodoptera* spp. eggs. The average number of FAW eggs parasitized by a single *Tr. bilinealis*

female increased from 9.6 to 13.4 after 4 generations of successive rearing on FAW eggs (Tian et al. 2020). When *Tr. pretiosum* was reared on eggs of *S. litura*, the body size of offspring parasitoids was larger than when the parasitoids were reared on FAW eggs (Zhu et al. 2019). After parasitizing FAW eggs, the developmental time of *Tr. dendrolimi* was only 9.5 days at 25 °C, shorter than figures recorded for *Tr. leucaniae*, *Tr. japonicum* and *Tr. ostriniae* at the same temperature (Sun et al. 2020). *Trichogramma pretiosum* lives 7.2 times longer with access to the host and a source of food (pure honey) than those without access to host or food (Bleicher and Parra 1991). Although some *Trichogramma* species, such as *Tr. brassicae* and *Tr. turkestanica*, have host-feeding behaviors (Ferracini et al. 2006; Lessard and Boivin 2013), whether FAW eggs are killed by host-feeding or ovipositing behaviors of *Trichogramma* or other parasitoid wasps has not been studied in detail. It is not clear whether there is a non-consumptive ‘risk effect’ of *Trichogramma* species on FAW eggs.

Chelonus species

Despite being egg-larval parasitoids, *Chelonus* species firstly attack the host at the egg stage. *Chelonus insularis* females are attracted to volatiles emitted by FAW egg masses, FAW females, and maize seedlings (Roque-Romero et al. 2020). Females of *C. insularis* lay their eggs in host egg masses and only will emerge from FAW larvae of 4th instar when then it finally leads host to death (Zenner et al. 2006). Despite not killing the pest immediately after parasitism, parasitized FAW larvae gradually reduce their food intake, consuming less than 10% of the biomass consumed by a healthy larva (Prasanna et al. 2018). Consequently, *Chelonus* species have received much attention worldwide as candidate parasitoids for FAW control (Table 1).

There is no pre-oviposition period for adults of *C. insularis*, and the mean incubation period is about 1.8 days. The larval period varies from 17 to 23 days at 25 ± 2 °C, with an average of 20.4 days. The mean pupal period is 6.2 days. The average duration of the total cycle is 28.6 days. The average longevity of mated females is, on average, 11.6 days, with a maximum of 18 and a minimum of 5 days. The number of parasitized eggs and the longevity varied greatly between female individuals, and the parasitic capacity is reduced considerably near death. The highest rate of parasitism occurs when females are three days old, with a maximum of 92.2 and a minimum of 48.1 eggs parasitized on that day. In the interval between the 3rd and 6th day, the females had a 72% to 80% parasitism rate (Prasanna et al. 2018). The parasitism of *C. insularis* to FAW under natural conditions ranged from 6.63% to 21.96% (Tang et al. 2019). In a study in the United States, 8353 FAW larvae were collected from 3 south

Florida counties to identify the most common parasitoids. *Chelonus insularis* was one of the most common detected species. It was present in 18 of the 25 sampled sites (Meagher Jr et al. 2016). Similarly, in Mexico, FAW parasitism by *C. insularis* reached 86% in some regions of the State of Morelos (Paredes-Sánchez et al. 2021). Moreover, *C. bifoveolatus* was one of the most abundant FAW parasitoids in West Africa (Ahissou et al. 2021a). Despite such high biological control potential as herein discussed, *Chelonus* species uses in Augmentative Biological Control or Conservation Biological Control programs are still a challenge and need to be further studied in future researches.

Biotic and abiotic factors impacting biocontrol efficiency of egg parasitoids

Presence of scales and multiple layers in FAW eggs

FAW moths usually lay their eggs in multiple layers, leaving scales deposited around and/or over the eggs at the time of oviposition, what acts as a morphological or physical defense (Dong et al. 2021; Hou et al. 2022). This is usually an effective barrier to egg parasitism, although it can be used by some parasitoids such as *Te. remus* and *Tr. pretiosum* as chemical clues to search for FAW eggs (Nordlund et al. 1983; Vargas et al. 2021). It is also important to mention that some *Trichogramma* species are not sensitive to scales compared to their counterparts. *Trichogramma atopovirilia* females, with a higher parasitism capacity in eggs laid with different physical barriers, were more aggressive and showed higher specificity to FAW eggs than *Tr. pretiosum* (Beserra and Parra 2004). However, the number of egg layers can still affect its performance. Parasitism rate of *Tr. atopovirilia* on egg masses with one, two, and three layers was 66.2%, 45.2%, and 40.1%, respectively (Beserra and Parra 2005).

A recent report hinted that FAW scale thickness decreased with increasing age of egg laying FAW females, the earlier laid eggs covered with thicker scales and the later laid eggs covered with only thinner or no scales. In contrast, the parasitic performance of *Trichogramma* spp. (e.g., *Tr. dendrolimi*) increased as the scales decreased. During FAW female lifetime, the thinner (< 80 µm) or no scales egg masses showed the highest proportion (51.9%) while the thicker scales (> 180 µm) egg masses showed the lowest (9.9%) (Hou et al. 2022).

Telenomus remus has relatively ideal adaptability to FAW egg mass. Its females often crept into the scale layer covering the egg masses, whereas *Tr. dendrolimi* and *Tr. pretiosum* females did not, and *Te. remus* had a similar proportion of parasitism on egg masses with or without scales. Residence time, oviposition time, oviposition frequency, risk of host being found, and risk of parasitism by *Te. remus* were

significantly higher than the corresponding parameters of *Tr. pretiosum* and *Tr. dendrolimi* (Dong et al. 2021).

Inter- or intra-specific competition and coexistence

Available reports indicate that despite belonging to different species and sometimes even different families, these parasitoids are able to recognize FAW eggs previously parasitized by others (Carneiro and Fernandes 2012). Females of *Tr. atopovirilia* and *Tr. pretiosum* were observed to recognize the parasitized FAW egg, which took place after the female drilled into the host egg (Beserra and Parra 2003). And the one of these two species that first reached the FAW egg mass will be dominant (Dequech et al. 2013). When *Te. remus* and *Tr. pretiosum* females were placed together with FAW eggs, *Te. remus* had greater parasitism rate. However, when FAW eggs were previously exposed to *Tr. pretiosum*, there was no emergence of *Te. remus* (Carneiro and Fernandes 2012). Previous report attribute this to indirect competition for host resources (Silva et al. 2015a; b). However, since none of these parasitoid wasps could fully occupy the entire egg mass, this competition for eggs instead promoted the coexistence of different parasitoids on the egg mass and increased the utilization of the entire FAW egg mass resource. A field survey in Brazil demonstrated this coexistence of *Te. remus*, *Tr. pretiosum* and *Tr. atopovirilia* on eggs of FAW (Silva et al. 2015a; b). In an in-laboratory test, higher parasitic performance on FAW eggs was also observed when *Tr. pretiosum* and *Te. remus* were mixed at a ratio of 10–20% of *Te. remus* (Goulart et al. 2011b). And when *Te. remus* and *Tr. chilonis* were released simultaneously, the highest performance occurred when they were parasitizing the same FAW egg mass together (84.4% FAW eggs parasitized), better than when each parasitized separately (66.7% for *Te. remus* and 52.2% for *Tr. chilonis*) (Xie et al. 2022). However, the interaction between parasitoids and predators will be different. When FAW eggs were parasitized by *Te. remus* previously, *Doru luteipes* Scudder, a predator of FAW, only eats FAW eggs that were parasitized within 3 days, because after 72 h, the parasitoid will start to occupy the entire host egg, probably reducing the prey quality of the parasitized egg. Moreover, *Te. remus* takes 12.5 times longer to find *D. luteipes* eggs compared to finding FAW eggs. Generally, female *D. luteipes* will repel parasitoids. *Telenomus remus* only attacked and parasitized *D. luteipes* eggs when predator females, which present parental care with eggs, were absent (Carneiro and Fernandes 2020).

Sensitivity of insecticides

Not only insecticides but also herbicides and fungicides have frequently been reported impacting egg parasitoids (Desneux et al. 2007), especially in agroecosystems where

multiple pests often occur and require various control strategies to be used simultaneously. However, in a sustainable FAW management approach, the use of the most selective pesticides available should always be prioritized over the less selective products (Torres and Bueno 2018). Overall, fungicides and herbicides are less harmful to egg parasitoids than insecticides (Torres and Bueno 2018). Among different herbicides examined, paraquat was the most harmful to *Te. remus* (Carmo et al. 2010). As well as herbicides and fungicides, biopesticides can be included among the most selective pesticides to egg parasitoids (Torres and Bueno 2018) and some of them have been explicitly tested against *Tr. pretiosum* (Amaro et al. 2015; Silva and Bueno 2015a, b) and *Te. remus* (Silva et al. 2016; Amaro et al. 2018). For example, some plant extracts (from *Eremanthus elaeagnus* and *Lychnophora ericoides*) have shown to be relatively safe to *Tr. pretiosum* and *Te. remus* (Tavares et al. 2009). Also, the essential oils from *Hyptis marruboides* and *Ocimum basilicum* were classified as harmless according to the International Organization for Biological Control criteria for *Tr. pretiosum* (Bibiano et al. 2022). In the case of interactions with transgenic insect-resistant crops, there were no direct and indirect effects of FAW eggs, from insects fed with *Bt* soybean, on the parasitoid fitness and acceptance. Also, *Tr. pretiosum* does not distinguish between FAW eggs oviposited on *Bt* and non-*Bt* soybean plants (Leite et al. 2020). In addition, *Bacillus thuringiensis* was among the most selectivity treatments evaluated for *Chelonus* spp. (Zenner et al. 2006), *Tr. pretiosum* (Amaro et al. 2015) and *Te. remus* (Amaro et al. 2018).

Even among the synthetic insecticides, some active ingredients, especially those belonging to the group of Insect Growth Regulators (IGRs), such as diflubenzuron, flufenoxuron and methoxyfenozide, are relatively more selective to the egg parasitoids when compared to other synthetic chemical groups (Torres and Bueno 2018). Methoxyfenozide, diflubenzuron, and flufenoxuron had no effect above *Te. remus* adults (Carmo et al. 2010). The tests of *Te. remus* larvae and pupae reared in eggs of FAW showed that flufenoxuron, diflubenzuron, and methoxyfenozide were harmless to the parasitoid immature stages (Carmo et al. 2009). Similarly, bioassays used *Anagasta kuehniella* eggs treated with insecticides which were afterwards exposed to parasitism showed that triflumuron was also selective to *Tr. pretiosum* (Souza et al. 2013).

In contrast, pyrethroids such as bifenthrin, gamma-cyhalothrin or beta-cyfluthrin, organophosphates such as chlorpyrifos and acephate as well as emulsifiable concentrates were frequently among the most harmful insecticides to the egg parasitoids, especially to adults, which is generally the most susceptible parasitoid stage (Hassan et al. 1985; Carmo et al. 2009, 2010) despite some variations in the reported results. For example, spinosad was classified as

harmless for larvae of *Te. remus* (Carmo et al. 2009). Chlorantraniliprole + lambda-cyhalothrin, abamectin + chlorantraniliprole, and alpha-cypermethrin + teflubenzuron were also classified as innocuous (class 1). Abamectin + chlorantraniliprole, although classified as harmless, did reduce the parasitism, longevity, and flight capability of the adult parasitoids (Paiva et al. 2020). Overall, it is important to emphasise that pesticides should only be applied in the field when strictly required. Furthermore, whenever possible, harmful pesticides should be replaced by more selective products (Torres and Bueno 2018). In addition, taking Augmentative Biological Control programs of FAW into consideration, the most harmful pesticides should be strongly avoided in the fields at least one and two weeks before and after *Tr. pretiosum* and *Tr. remus* releases, respectively (Bueno et al. 2022).

Polyculture

Intercropping is the agronomic practice of growing two or more crops in the same field at the same time (Smith and McSorley 2000). The broader term *polyculture* includes intercropping but also encompasses combining crops and weeds intentionally and combining crops with beneficial non-crop plants, such as cover crops or nursery crops (Andow 1991; Thomine et al. 2020a; 2020b; 2022). Some researchers have suggested that herbivore damage in diverse systems is reduced due to increased efficiency of natural enemies. It was hypothesized that diverse environments would provide a greater variety of habitats and victims to predators and parasitoids through time, as well as alternate food sources such as pollen and nectar, and so sustain more stable populations of natural enemies than monocultures (Smith and McSorley 2000). The establishment of a conservation planting of native wildflowers adjacent to high-bush blueberry (*Vaccinium corymbosum* L.) fields confirmed that provision of resources for natural enemies increases their abundance in adjacent crop fields without increasing the abundance of pest insects (Walton and Isaacs 2011). Similarly, infield diversity of FAW natural enemies may be enhanced through interventions such as residue retention (Rivers et al. 2016), intercropping (Smith and McSorley 2000) and weed management (Kenis et al. 2023). More *C. bifoveolatus* and higher parasitism rate on FAW were recorded in cowpea + maize intercropping plots as opposed to maize sole cropping systems. This is believed to be associated with high biodiversity in the intercropping systems (Ngangambe and Mwatawala 2020).

Abiotic environmental variables

Environmental variables markedly influence the egg parasitoid performance and must be considered when choosing the best parasitoid strain/species and its release strategy (Grande

et al. 2021). Temperature is one of the abiotic variables that certainly influence the most insect biology of different egg parasitoid species, what indicates this parameter might affect the success of a biological control program using those biocontrol agents in the field (Wu et al. 2016). Adults of most parasitoid species are incapable of lipogenesis (Denis et al. 2011) but, as ectotherm insects, temperature is inversely related to their metabolic-rate and lipid consumption (Huey and Berrigan 2001). However, adults of those parasitoids are usually incapable to synthesize lipids what makes them more vulnerable to an increase in temperature than most of the herbivorous species (Denis et al. 2011). Thus, for most of the parasitoid species, allocation of lipids accumulated during the parasitoid larval stage determines adult lifespan and fecundity (Visser and Ellers 2008) and, therefore, its lifetime reproductive success (Huey and Berrigan 2001).

Parasitoid emergence, developmental time among other traits is greatly impacted by temperature. The emergence of *Tr. pretiosum* on FAW eggs was influenced by temperature, being the lowest percentage of emergence observed at 32 °C (88.9%), and the highest ones at both 18 °C (100%) and 20 °C (99.5%) (Bueno et al. 2010a). *Telenomus remus* showed the same trend towards temperature and was more sensitive to relatively higher temperatures, considering the optimal temperatures for FAW egg hatching is about 30 °C (du Plessis et al. 2020). Parasitoid emergence was higher than 80% at temperatures from 19 to 28 °C when *Te. remus* was reared on eggs of FAW, but when at 34 °C, this parameter was lower than 6% (Pomari et al. 2012). Parasitoid developmental time is reduced at higher temperatures. The shortening of parasitoid developmental time, from egg to adult, inversely follows the increases in the temperature and is probably a consequence of the increase in the metabolic activity of the parasitoid species (Bueno et al. 2009). Another impact of temperature to be considered is the specific ability of egg parasitoids to introduce the ovipositor into the corium of the host eggs once these host eggs might gradually lose its turgidity following an increase in temperature (Bueno et al. 2009). The possible effects of temperature on this ability can be responsible for the differences in the quantity and uniformity of parasitism as previously reported by Pereira et al. (2004) for *Trichogramma exiguum* on *Plutella xylostella* eggs. Therefore, those egg parasitoids should be released in field in augmentative biological control programs preferable during the mildest temperature of day, usually the first hours of the morning.

It is worth emphasizing, though, that temperature is not the only variable responsible for changes in the development and survival of different egg parasitoid species. Other abiotic variables, such as photoperiod and relative humidity, as well as biotic variables like interspecific and intraspecific competition can also impact those egg parasitoid biological characteristics (Pratissoli and Parra 2000). In general, relative

humidity has no effect on the development of *Te. remus* on FAW eggs, but if *C. cephalonica* is used as an alternative host to rear *Te. remus*, 80% relative humidity is recommended for good performance (Pomari-Fernandes et al. 2015). Other weather factors can also play a role, such as the presence of light favored the parasitism of *Te. remus* on FAW (Grande et al. 2021). In the major and minor rainy seasons in Africa, *Te. remus* parasitized up to 33% and 72–100% of FAW egg masses, respectively (Agboyi et al. 2021). However, another field study conducted during the rainy season in China concluded that *Te. remus* performed better than *Tr. pretiosum* under hot and rainy conditions, which had higher egg mass and egg parasitism rates (100.0%, 50.3%, respectively), and better dispersal performance (Zhu et al. 2020). The differences in these studies may stem from differences in precipitation between regions.

Mass rearing

Mass rearing of egg parasitoids is a critical step to achieve field success of augmentative biological control programs using those biocontrol agents (Parra 2010). There are three different ways to massively rear egg parasitoids: (1) on the natural host, (2) on factitious hosts (both in vivo) and (3) on an artificial diet (in vitro) (Colmenarez et al. 2022). This has been an issue extensively reviewed and studied in the last decades reflecting both the importance and challenges of this subject (Parra 2010). Nevertheless, limited success has been reached with in vitro rearing of *Trichogramma* spp. (Lü et al. 2017) with those rearing still being restricted to research and development. Similarly, only in vivo *T. remus* rearing has been used so far with both advantages and disadvantages comparing natural and factitious hosts (Colmenarez et al. 2022). Although there were cases of in-lab rearing of *Chelonus* spp. (Padilla-Cortes and Martínez-Martínez 2022), successful large-scale rearing of those parasitoids is still lacking. This may be attributed to the lack of alternative hosts and the relatively long rearing calendar. Therefore, here in this review we will limit to briefly present the mass rearing of *Te. remus* and *Trichogramma* species most important updates.

Telenomus remus

In general, the rearing of *Te. remus* has been limited due to the difficulties and labor intensive requirements of its natural host production, the eggs of FAW (Pomari-Fernandes et al. 2015). Although *Te. remus* can be reared continuously and stably on FAW eggs for up to 250 generations (Pomari-Fernandes et al. 2016), alternative hosts are still sought to reduce costs and then allow to scale parasitoid production (Queiroz et al. 2017a). *Corcyra cephalonica* was proved to

be useful for rearing *Te. remus* up to 45 generations without *Te. remus* quality reduction (Queiroz et al. 2017a). Although the parasitoids reared on *C. cephalonica* were smaller than those on natural hosts (Pomari-Fernandes et al. 2016), their flight ability was not affected (Queiroz et al. 2017a). A laboratory simulation rearing study showed that the cost of production of *Te. remus* was US\$ 0.0004 per wasp when reared with FAW eggs and US\$ 0.0002 with *C. cephalonica* eggs (Vieira et al. 2017). *Spodoptera litura* can also serve as a factitious host for *Te. remus*. The number of parasitized eggs was greater for *S. litura* than for FAW. Meanwhile, the parasitoid emergence rate exceeded 86.6%, and it was significantly higher from *S. litura* eggs than from FAW eggs (Chen et al. 2021).

Since the production of biocontrol agents is often out of synchronization with the demands in the field. Appropriate cold storage techniques can drastically prolong their shelf-life to synchronize the release schedule with field needs and reduce production costs (Chen et al. 2022). The performance of *Te. remus* varies on different hosts. When reared on FAW eggs, the highest emergence rate was observed when the parasitized eggs were stored at 15 °C for ≤ 9 days (Salazar-Mendoza et al. 2020). The cold storage experience of *C. cephalonica* eggs can affected *Te. remus* parasitism. Viable stored *C. cephalonica* eggs were parasitized to the same degree or even higher than fresh eggs when stored until 14 days at 5 °C or until 21 days at 10 °C (Queiroz et al. 2017b). However, survival of *Te. remus* pupae declined with storage time of parasitized *C. cephalonica* eggs. When using *C. cephalonica* as alternative host, it is recommended that the maximal storage time at 10 °C is 7 days for *Te. remus* pupae, while parasitoid adults should not be stored for more than 4 days at either 5 or 10 °C (Queiroz et al. 2017b). When using *S. litura* as the host, the emergence percentage and parasitism capacity of parental parasitoids all decreased with increased storage duration and decreased storage temperature. However, the maternal female longevity, offspring emergence percentage and percentage of females were barely affected by cold storage. Storage of the first instar larvae at 14 °C for 21 days was the optimum storage scheme for *Te. remus* (Chen et al. 2022).

Trichogramma species

Egg parasitoids from the genus *Trichogramma* have been successfully reared and used in various parts of the world (Smith 1996). Several stages of the rearing process, e.g., cleaning and drying of host eggs, preparation of egg cards, parasitoid inoculation, and selection–collection of parasitized host eggs (Liu et al. 1991; Song et al. 1994; Mao et al. 1999), have been mechanized and/or automated, and cost efficiency depends on the possibility of using low-cost

factitious hosts for rearing the selected *Trichogramma* species (Zang et al. 2021). Four key factitious hosts, *Antheraea pernyi*, *C. cephalonica*, *Samia cynthia ricini*, and *Sitotroga cerealella*, have been studied (Zang et al. 2021). Up to 260 *Trichogramma* individuals could be produced per *A. pernyi* egg, with *Tr. dendrolimi* being reared on *A. pernyi* eggs and reaching 400 billion parasitoids production per year for a cost of US\$11.4 million (Zang et al. 2021). Interestingly, many other species can reach adulthood inside *A. pernyi* eggs (e.g., *Tr. ostrinae* and *Tr. leucaniae*), but they cannot emerge, failing to break through the egg chorion (Hassan et al. 2004; Li et al. 2019b; Iqbal et al. 2019). Recently, multiparasitism with *Tr. dendrolimi* and *Tr. chilonis* enabled emergence of *Tr. ostrinae* and *Tr. leucaniae*, respectively, the two latter species using holes made by *Tr. dendrolimi* and *Tr. chilonis* (Li et al. 2019b; Iqbal et al. 2019; Zhang et al. 2021). This may open a way to use multiparasitism for mass rearing of high-potential species (Zang et al. 2021). And smaller lepidopteran eggs such as *C. cephalonica* and *S. cerealella* are also used worldwide, they are useful for rearing species showing a weak ovipositor and/or mouthparts, the drawback is mainly their high cost for mass rearing, as well as for *Trichogramma* rearing (Zang et al. 2021). In China, a *Tr. japonicum* production line using *C. cephalonica* egg as factitious host reached a production of 2 billion parasitoids at a cost of US\$0.43 million (Zang et al. 2021).

Relying on cold conditions proved possible only for short-term storage, and duration depended on the alternative host used (Zang et al. 2021). Last-day pupae of *Tr. pretiosum* could be stored from 4 to 10 days at 16.7 °C, and up to 12 days if temperature was lowered to 15 °C on the sixth day of exposure (Parra 2010). And longer-term cold storage will induce negative effects owing to reduced moisture content, dry matter, and pH in host eggs (Wu et al. 2018). Nonetheless, cold storage of *Trichogramma* developing in *A. pernyi* eggs proved possible for up to 40 days without negative impacts when stored at 2–7 °C (Zang et al. 2021). Beyond regular cold storage, diapause induction is key for efficient long-term storage of mass reared *Trichogramma*. Diapause occurs at prepupal stages and is regulated by particular temperature and photoperiodic conditions (Zang et al. 2021). *Trichogramma dendrolimi* can enter diapause both through a two-step temperature change (e.g., 40 h at 26 °C followed by 31 days at 10 °C) or continuous low temperature (Ma and Chen 2005; Zhou et al. 2014; Zang et al. 2021) and enables storage for up to 4 months without impairing *Trichogramma* traits (Zhou et al. 2014). Host species also affect diapause induction with high diapause rates (up to 98%) in *Tr. japonicum*, *Tr. ostrinae*, and *Tr. dendrolimi* when reared on *S. cerealella* eggs, but these rates are much lower in individuals raised on *C. cephalonica* (13–34%) (Li et al. 1992).

Quality control

In a very simple definition, quality control of egg parasitoid rearing is a protocol to be followed in order to guarantee the production of wasps intended for field releases that are efficient in the field, therefore, competitive in parasitism and surviving with wild individuals (Leppla and De Clercq 2019; Parra et al. 2022). It must provide not only production control of the egg parasitoid but also the whole process control which includes the product control and also the control of the use of the egg parasitoid under field conditions (Leppla and De Clercq 2019). Thus, the concepts of quality control were later expanded including the term “quality assurance” which encompasses not only factors linked to production, but also to the post-production process, including distribution, application and evaluation of the efficiency of natural enemies in field. Consequently, there must be such control in the laboratory and, later, in the field (Leppla 2023).

Quality control of natural enemies' production is certainly one of the most important steps for an augmentative biological control program to succeed (van Lenteren et al. 2003). Consequently, it has been a subject extensively studied since early stages of this area development with the book “Insect Colonization and Mass Production” published in 1966 (Smith 1966). Despite the long history of studies publications in the issue (Leppla and De Clercq 2019), quality of control of egg parasitoids is still a challenge because during rearing process, different problems might occur. Among the possible problems the egg parasitoid produced in controlled conditions might face: (1) Behavioral change; (2) Genetic deterioration and haplotype selection; (3) Infection by pathogens are highlighted by Parra et al. (2022). Therefore, parasitoid longevity, fecundity, sex ratio, adult size, emergence percentage, flight ability and parasitism capacity should be frequently evaluated during the insect rearing (van Lenteren et al. 2003). The frequency and methods to be adopted are very difficult to define for all parasitoid species given the biological characteristics of each one (Parra et al. 2022). For example, for *Trichogramma* species, the IOBC recommends that five parameters should be evaluated monthly, at a temperature of 25 °C and relative humidity between 60 and 70%, with the respective values expected for an insect to be considered of good quality: (a) Sex ratio: $\geq 50\%$ females; (b) Parasitism capacity: ≥ 40 eggs/7 days/parasitoid female; (c) Longevity: 80% of the females should live at least for 7 days; (d) Parasitism in the natural host: ≥ 10 parasitized eggs/4 h/female; (f) Flight test: $\geq 90\%$ flying insects according to Dutton and Bigler (1995), modified by Prezotti et al. (2002).

Field releases

Telenomus remus

A detailed review of *Te. remus* field releases is provided by Colmenarez et al. (2022). In general, an in-lab study suggested the optimal *Te. remus* release density when reared on *C. cephalonica* was between 0.133 and 0.150 female parasitoids/FAW (Queiroz et al. 2017c). However, *Telenomus remus* releasing numbers may vary depending on the crop, plant architecture and/or the plant phenological stage. The appropriated *Te. remus* releasing number might being higher in soybean and cotton compared to maize. In maize field, the maximum parasitism observed was 99.8% and 96.8% at a parasitoid releasing number of 0.231 and 0.264 *Te. remus* females per FAW egg, respectively. In cotton and soybean, the highest parasitism was recorded when using *Te. remus* releasing numbers at 0.297 parasitoid per FAW egg. In cotton, it was 77.8% and 73.1% at the vegetative and reproductive stages, respectively and in soybean, it was 77.3% and 54.4% also at the vegetative and reproductive stages (Pomari et al. 2013). Another field study carried out in Brazil suggested that *Te. remus* should be released at a minimum density of 35 points/hectare in soybean crops and 34 points/hectare in maize crops to ensure *Te. remus* dispersal over 100% of the area in the worst-case scenario. At each point, approximately 150,000 newly emerged (up to 24 h old) adults of *Te. remus* reared on eggs of *C. cephalonica* or *S. frugiperda* were released. And since wind direction influences the dispersal pattern of *Te. remus*, the release methodology should be determined according to wind conditions, possibly with preference for a perimetric distribution of the released insects (Pomari-Fernandes et al. 2018). *Telenomus remus* decreased linearly with increasing distance from the release point in maize field, but it was influenced by the crop's phenological stage. Egg parasitism of FAW was 28% higher at the older than younger growth stages, and dispersal distance and area of dispersal were 35% and 16% lower, respectively, at the older stage (Salazar-Mendoza et al. 2020).

Trichogramma species

Studies have pointed out that parasitoids should be released so that the majority emerge during daylight, especially for *Te. remus* and *Tr. pretiosum*, since parasitism was greatly reduced in dark environments (Grande et al. 2021). Although the adaptability to FAW egg mass is not as high as *Te. remus*, the addition of *Trichogramma* spp. can still improve the overall control of FAW and reduce

costs. The cost of *Tr. dendrolimi* release in maize fields is as low as US\$5.8/ha (225,000 wasps/ha) (Zang et al. 2021). Field trials of *Tr. chilonis*, *Tr. dendrolimi* and *Tr. pretiosum* were carried out in the tropical areas of China, parasitoids were released in field cages (2×2×2 m, covered 20–25 corn plants) using a ratio of parasitoids to FAW eggs of approximately 1:1, the parasitism rates of three parasitoids ranged from 10.7 to 31.4% (Yang et al. 2022). In another study carried out from June to August in a maize field (nearly 1200 m²) with FAW larva density occurs 300–400 individuals per 100 plants, nearly 1500 parasitized eggs of *C. cephalonica* that had been offered to *Tr. chilonis*, *Tr. ostrinae*, *Tr. confusum*, and *Tr. pretiosum* were released, the parasitism rate on the egg masses ranged from 61.5 to 87.5%. The rate that the egg masses did not hatch were 41.7%, 12.5%, 15.4%, and 15.4%, respectively. And the rate of plant damage ranged from 36.1 to 59.7%. The larvae density on the plants ranged from 0.43 to 0.83 individuals/plant, which was significantly lower than untreated control (95.6% and 1.37 individuals/plant) (Jin et al. 2021).

IPM case

A biocontrol-based integrated pest management (IPM) strategy was designed and evaluated in farmer's field during 2018–2019 in India. The strategy comprising installation of controlled release FAW pheromone traps, four releases of *Tr. pretiosum*, two sprays of neem oil, one spray of each *Bacillus thuringiensis* (NBAIR-BT25) and *Metarizium anisopliae* (NBAIR Ma-35) resulted in 71.6–76.0% egg mass; 74.4–80.0% larval population reduction at 60 days after treatment. Cob yield per acre in biocontrol-based IPM field was higher than the farmer's practice (6–7 sprays of emamectin benzoate 5% SG), and it resulted in 38.3–42.3% gain in yield per acre (Varshney et al. 2021).

Conclusion and perspectives

FAW invaded Africa, Asia and Oceania extremely rapidly due to its strong flight capability, polyphagy, lack of diapause and quick development of insecticide/virus-resistance (Kenis et al. 2023). In addition to the yield loss of local crops, especially maize and rice, some Asian and African countries invaded by the FAW are also important importers of wheat and will be exposed to higher food security risks due to the current heightened uncertainty in international wheat supply (Bentley et al. 2022). As FAW continues to spread into new territories, new settlements emerged, such as Southwest and South China (Zhou et al. 2021), and the risk of new insect source also arose. The rapid and frequent migration of FAW makes it impossible

to control it in an isolated single area, and none of the single methods reported so far is sufficient to manage the pest and keep the damage threshold below the economic injury level. So, it is foreseeable that an international cooperative IPM strategy will be the most promising solution to FAW threat, and such cooperation requires the organization and coordination of important international organizations such as FAO, USAID or CABI.

Here, we reviewed the main FAW egg parasitoid and egg-larval parasitoid species, as well as key parasitoids such as *Te. remus*, *Tr. pretiosum*, *Tr. dendrolimi*, *Tr. mwanzai* and *C. insularis*, which either have been used in the biological control of FAW, or have considerable production and promising control potential, or are frequently observed to parasitize FAW naturally in the field. We have also noticed some parasitoids, such as *Tr. atopovirilia*, *Tr. bilingensis*, *Tr. chilonis*, *Tr. confusum*, *C. bifoveolatus*, which showed FAW control potential in laboratory tests. We recommend mixing high-performing key parasitoids with native potential parasitoids to maximize FAW egg control, and developing IPM strategies in conjunction with multiple approaches such as natural enemies, green pesticides and agroecological pathways to form a diverse, environmentally friendly and sustainable global control of FAW.

Overall, it is important to point out that no ready-to-use package is available to advise farmers how to use parasitoids against FAW. Therefore, it is evident that new research is still needed in order to precisely determine egg parasitoid use recommendations. And those recommendations might be even different for place to place. Thus, the cost control (e.g., for *Te. remus* and *Chelonus* spp.), local factitious hosts selection (e.g., for *Chelonus* spp.), extension of parasitoid shelf life, optimal release rates, release times and frequencies, and also the best parasitoid stage (pupa or adult) and which equipment for the releases should be used are among the issues that still need research and field validations in different areas of the world where FAW threatens local agriculture.

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Declarations

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