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Protective scale variation on *Spodoptera* egg masses can potentially support the cost-effective use of *Trichogramma* parasitoids

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With 2 figures and 1 table

1 Introduction

Biological control methods have been utilized worldwide for over a century, providing sustainable control of multiple major agricultural pests (Heimpel & Mills 2017). Studies on egg parasitoids of the genus *Trichogramma* began in 1927, when Flanders discovered the possibility of rearing them on a factitious host, *Sitotroga cerealella* (Oliv.) (Parra & Zucchi 2004). Since then, there has been significant interest in these parasitoids because of their efficiency and ease of multiplication (Parra & Zucchi 2004). In the 1990s, *Trichogramma* spp. were released on more than 16 million ha worldwide annually (van Lenteren 2000), mainly through inundative releases (Smith 1996). Since the beginning of the 21st century, *Trichogramma* has been successfully used in various parts of the world and makes up one of the most widely reared and used groups of natural enemies for biological control programs (Parra & Zucchi 2004; Huang et al. 2020; Zang et al. 2021a; Zhang et al. 2021).

However, when it comes to the management of *Spodoptera* species such as the fall armyworm, *S. frugiperda* (J. E. Smith), a polyphagous herbivore (e.g. Wu et al. 2021; Wang et al. 2022), which has become a major invasive pest and threat to global food security in the last decade (Kenis et al. 2023), the use of *Trichogramma* spp. is generally considered to be limited because, with the exception of a few species, e.g., *Tr. atopovirilia* (Oatman & Platner) or *Tr. pretiosum* (Riley), *Trichogramma* cannot easily oviposit through the hairs or scales on the egg masses when the layer is too thick (Beserra & Parra 2004, 2005; Kenis et al. 2023; Li et al. 2023a).

Updated studies report that the scales provided by *Spodoptera* females on egg masses are sometimes inadequate and vary over the lifetime of the female, in addition, the thin scales are not sufficient to resist attack by *Trichogramma* spp. (Hou et al. 2022; Li et al. 2023b). These studies cast doubt on the stereotype of scales on *Spodoptera* spp. egg masses as a defense against *Trichogramma* spp. and make it necessary to re-evaluate the potential of *Trichogramma* spp. as biological control agents for *Spodoptera* pests, especially considering the cost-effective ones among them. Here, we analyze this briefly.

2 Variation of *Spodoptera* egg mass scale thickness

Female *Spodoptera*, e.g., *S. frugiperda*, *S. exigua* (Hübner), and *S. litura* (F.), can lay their eggs in multiple layers, leaving scales (hairs, setae) deposited around and/or over the eggs at the time of oviposition, which acts as a physical defense (Dong et al. 2021; Kannan et al. 2021). The scales often originate from an anal tuft at the tip of the female abdomen, but some could fall off from the hind margin of the wing (Powell & Common 1985). They can protect eggs through various mechanisms (i) as physical barriers or (ii) as an aposematic warning against various natural enemies, and (iii) by reducing the risk of eggs being washed away by rain (Floater 1998). Recent studies have also reported that these scales (hairs, setae) can (iv) sting or irritate the skin of the predators, parasitoids and also (v) facilitate protection from sunlight rays as well as (vi) ovicidal insecticides (Kannan et al. 2021).

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However, based on their origin, it is logical to assume that these scales are non-renewable resources for *Spodoptera* females and will gradually decrease due to age-related consumption. Recent studies provide support for this speculation. Although the scale thickness of *S. frugiperda* ranged from ~0 μm to over 300 μm (Fig. 1), the thickest scale (> 180 μm) egg masses account for only 9.9% during the lifetime of *S. frugiperda* females, while thin (< 80 μm) or no scale egg masses account for 51.9% during the lifetime of females (Hou et al. 2022). Although the lifespan of most *Spodoptera* adults may be shorter in the field than in the laboratory, these proportions of field populations need to be re-examined. In general, *S. frugiperda* scale thickness decreased with the increasing age of egg-laying females, with the earlier-laid eggs covered with thicker scales and the later-laid eggs covered only with thinner or no scales (Hou et al. 2022; Li et al. 2023b). Similar performance was also found in *S. exigua* and *S. litura* (Li et al. 2023b). These results suggest that the egg parasitoids may behave differently on eggs laid by *Spodoptera* females of different ages due to variations in scale thickness.

3 Performance of *Trichogramma* spp. on *Spodoptera* egg masses with different scales

Without a detailed differentiation of scale thickness, researchers once briefly concluded that the proportion of parasitism by *Tr. pretiosum* and *Tr. dendrolimi* (Matsumura) on egg masses with scales was significantly lower than that on egg masses without scales, thus excluding *Trichogramma* species, such as *Tr. dendrolimi*, from the dominant parasitoid wasps of *S. frugiperda* (Dong et al. 2021). However, re-examining the performance of *Trichogramma* spp. based on different egg scale thicknesses may provide a new perspective to evaluate their control potential on *Spodoptera* pests.

Consistent with earlier reports, the thickest scales (> 180 μm) prevented *Tr. dendrolimi* from parasitizing *S. frugiperda* eggs (parasitism rate: eggs: 1.9%; egg masses: 23.1%). However, *Tr. dendrolimi* performed similarly on eggs with thin scales (< 80 μm) and eggs without scales, which significantly improved the parasitism rate (eggs:

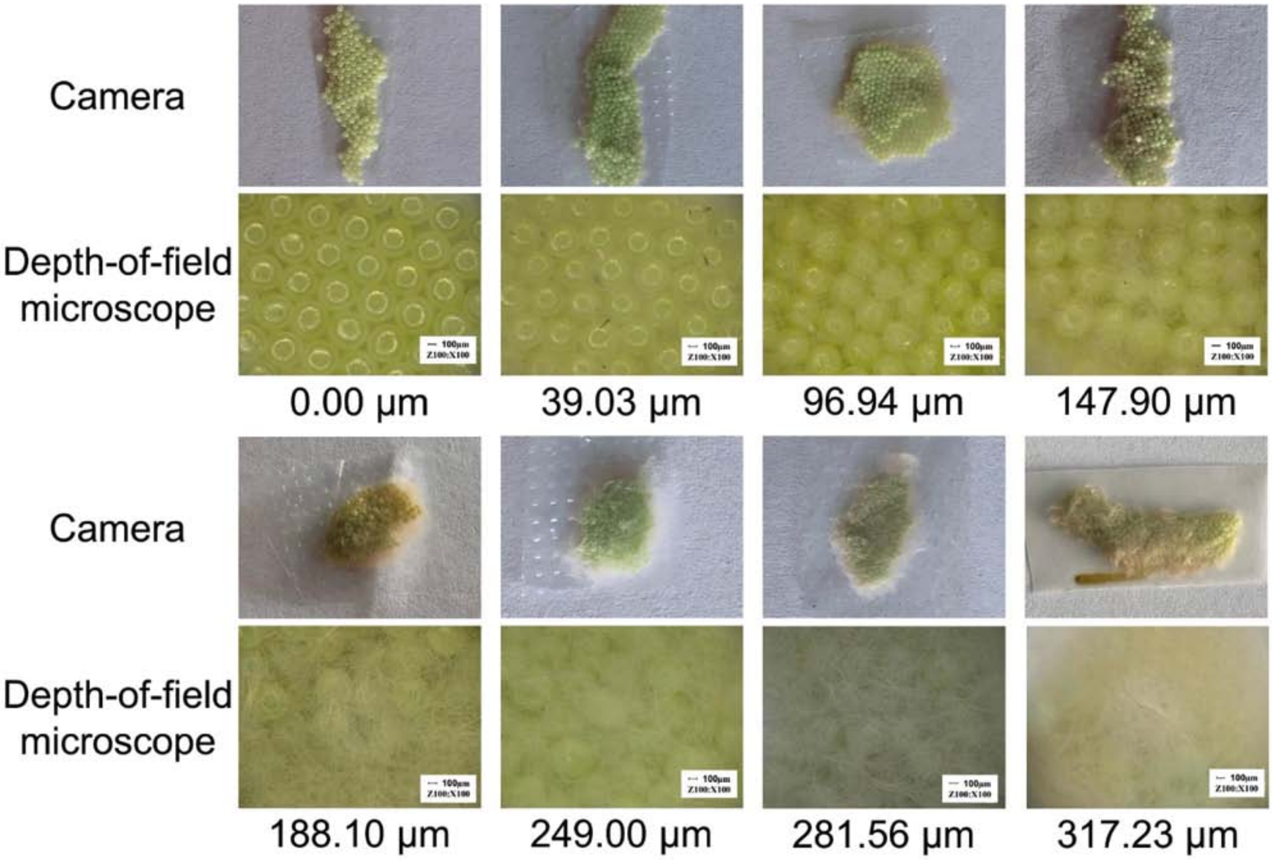

Fig. 1. Egg masses of *Spodoptera frugiperda*. The thicknesses of egg mass scales are shown. Camera photos show the overall appearance of the egg mass and depth-of-field microscope (VHX-2000, Keyence, Keys Ltd, Japan) photos show localized details. (credit: Yue Ma).

31.6%; egg masses: 78.3%) (Hou et al. 2022) (Fig. 2). It is also known that the egg masses with the thickest scales accounted for only 9.9% of the total eggs laid by *S. frugiperda* females, and the eggs covered with thin scales or no scales accounted for 51.9% of them (Hou et al. 2022). Those results together suggest that more *S. frugiperda* eggs could be attacked by *Tr. dendrolimi* than originally thought.

This case is not unique, as *Tr. chilonis* (Ishii) exhibits a similar pattern of behavior towards *S. exigua* eggs. The thickest scales (137.2 μm on average) also prevented *Tr. chilonis* from parasitizing *S. exigua* eggs (parasitism rate: eggs: 14.9%; egg masses: 87.5%), but when it came to the eggs with thin scales (approximately 10 μm on average), *Tr. chilonis* showed a significantly improved performance (parasitism rate: eggs: 36.5%; egg masses: 100%) (Li et al. 2023b). In addition, although the scale would hinder parasitism by *Tr. pretiosum*, this parasitoid can still use chemical clues in the scales to enhance the search for *S. frugiperda* eggs (Vargas et al. 2021). This parasitoid ability indicates that scales can be a barrier to *Trichogramma* spp. parasitism, but could also be employed by *Trichogramma* species to enhance their host-finding. The trade-off result of this interaction (scales-parasitism) is unclear and more complex than it could appear. Further studies analyzing the scales-parasitism interaction seem warranted due to the potential significance in terms of host-parasitoid coevolution.

The above studies provide positive support for re-evaluating the use of *Trichogramma* spp. for *Spodoptera* pest management. However, it should be noted that in the study by Li et al. (2023b), the key parasitoid wasp of *Spodoptera* species, *Telenomus remus* (Nixon), showed stable and higher parasitism on egg masses with different scale thicknesses. The parasitism rate of *Te. Remus* for *S. exigua* egg masses with thin scales was: eggs: 54.9%; egg masses: 100% (adequate 200 eggs were offered to a mated female parasitoid). Although these key parasitoids usually have better parasitic performance on *Spodoptera* spp. than *Trichogramma* (Kenis et al. 2023), after nearly one hundred years of biological control application, *Trichogramma* spp. have significant advantages over other parasitoids in many aspects, one of which is cost efficiency.

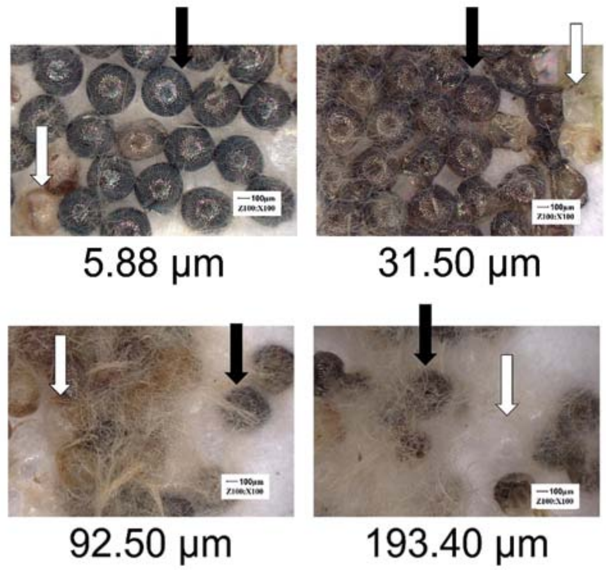

Fig. 2. *Spodoptera frugiperda* egg masses parasitized by *Trichogramma dendrolimi*. The thicknesses of egg mass scales are shown. As scale thickness increased, the proportion of parasitized eggs decreased. Black arrows indicate parasitized eggs, white arrows indicate egg chorions left behind after hatching of *S. frugiperda* larvae (credit: Zhen Shen).

4 Cost comparison of *Spodoptera* key parasitoids

Mass-rearing systems are crucial for cost efficiency and a key step to achieve field success of augmentative biological control programs using parasitoids (Parra 2010; Zang et al. 2021a). The lack of cost effectiveness can make the application of dominant parasitoids a dilemma, and *Chelonus* species currently appear to be in such a position. *Chelonus* species are an important *S. frugiperda* parasitoid group. They have been found on the larvae of *S. frugiperda* in the field of the Americas, Africa and Asia (Kenis et al. 2023). In Mexico, the parasitism of *Ch. insularis* (Cresson) reached 86% in some regions of the State of Morelos (Paredes-Sánchez et al. 2021). However, although there have been cases of in-lab rearing of *Chelonus* spp. (Padilla-Cortes & Martínez-Martínez 2022), successful mass rearing of these parasitoids is still lacking.

Meanwhile, in Latin America (van Lenteren & Bueno 2003), where *S. frugiperda* originated from, and even around the world (Kenis et al. 2023), *Te. remus* has been one of the most reported species studied and used for *S. frugiperda* control, and even so, it is still hard to deny that cost is not a limitation for large-scale applications of *Te. remus* (Queiroz et al. 2017).

Detailed economic studies on parasitoids are still limited. We collected information on the costs of key parasitoid wasps of *Spodoptera* spp. as well as *Trichogramma* spp. with potential for use in *Spodoptera* pest control (Table 1). Although there were some inconsistencies between the reported cost data, such as rearing *Tr. pretiosum* on *Anagasta kuehniella* (Zeller) eggs and *Te. remus* on *S. frugiperda* eggs (Table 1), the cost advantage of some *Trichogramma* spp. over the key parasitoid of *Spodoptera* spp. *Te. remus* seems clear. In the case of *S. frugiperda* control, for example, the number of *Tr. dendrolimi* released can be 760% of *Te. remus* and 2375% of *Ch. bifoveolatus* for the same investment (Table 1), whereas only the same level (760% and 2375% of *Tr. dendrolimi*, respectively) or more of *S. frugiperda* eggs parasitized by *Te. remus* and *Ch. bifoveolatus* can compensate for their cost disadvantages.

Table 1. Cost comparison of key parasitoids.

Parasitoids	Host stage[1]	Factitious hosts	US$ / 1000 parasitoids		Control cost per area		References
			Released[2]	Reared[3]	US$ / ha	Parasitoids / ha	
Trichogramma pretiosum (Riley)	Egg	*Anagasta kuehniella* (Zeller)	0.0074	–	0.74	100000	Tavares 2010[4]
Tr. chilonis (Ishii)	Egg	*Samia cynthia ricini* (Boisduval)	–	0.0093	–	35000–40000	Manisha et al. 2020[4]
Tr. dendrolimi (Matsumura)	Egg	*Antheraea pernyi* (Guérin-Méneville)	0.026	–	5.80	225000	Zang et al. 2021a
Tr. chilonis (Ishii)	Egg	*Corcyra cephalonica* (Stainton)	–	0.029	–	–	Manisha et al. 2020[4]
Tr. pretiosum	Egg	*Anagasta kuehniella*	0.16	–	15.8[5]	100000	Figueiredo et al. 2015
Telenomus remus (Nixon)	Egg	*Co. cephalonica*	–	0.20	–	–	Vieira et al. 2017
Te. remus	Egg	*Spodoptera frugiperda* (J. E. Smith)	–	0.40	–	–	Vieira et al. 2017
Chelonus bifoveolatus (Szépligeti)	Egg-larval	*Co. cephalonica*	–	0.67	–	–	Zang et al. 2021b, 2022[4]
Te. remus	Egg	*S. frugiperda*	1.89	–	15.1	8000	Colmenarez et al. 2022
Ch. bifoveolatus	Egg-larval	*S. litura*	–	4.55	–	–	Zang et al. 2021b[4]
Ch. bifoveolatus	Egg-larval	*S. frugiperda*	–	12.5	–	–	Zang et al. 2021b[4]

[1] Where the host is attacked and killed.
[2] Total cost of rearing and release, including materials, transportation, labor, etc.
[3] Rearing costs. Lack of cost coverage of field releases.
[4] Exchange rates used in the calculation: BRL: USD =1: 0.1888; INR: USD = 1: 0.0122; RMB: USD =1: 0.1379.
[5] Commercial release, whether it was the cost or the selling price was not specified.

Although deeper post-release studies are needed, analysis of parasitoid performance and survival is required for being conclusive on this. However, the relatively mature technology of *Trichogramma* production, mass rearing, release or even long-term storage should be considered.

The genus *Spodoptera* includes many species that are among the most important crop pests in the world. Moreover, *Spodoptera* spp. have developed resistance to all chemical families and 3 of them are in the top 15 most resistant arthropods in the Arthropod Pesticide Resistance Database: *S. litura*, *S. frugiperda* and *S. exigua* (Sparks et al. 2020). Controlling these world's major pests is a long and widespread war of attrition, and it is essential that the cost efficiency of parasitoids be taken into account.

5 Conclusion and outlooks

The aforementioned studies reveal that although control of *Spodoptera* spp. eggs with thick scales is less than ideal, *Trichogramma* spp. could be used as an economical biological control agent for the majority of *Spodoptera* eggs with medium and thin scales. Considering the low-cost advantages of *Trichogramma* spp. for mass rearing, long-term storage, and release, etc., it seems practical to use key parasitoids of *Spodoptera* spp. in combination with cost-effective *Trichogramma* wasps. This is already being supported by field studies (Xie et al. 2022). A study in China found that when *Te. remus* and *Tr. chilonis* coexist, the highest performance was achieved when they parasitized the same *S. frugiperda* egg mass together (84.4% eggs parasitized), better than when each was parasitized separately (66.7% for *Te. remus* and 52.2% for *Tr. chilonis*) (Xie et al. 2022). A field survey in Brazil also demonstrated the coexistence of *Te. remus*, *Tr. pretiosum*, and *Tr. atopovirilia* (Oatman & Platner) on *S. frugiperda* eggs (Da Silva et al. 2015). Overall, this commentary provides evidence that justifies rethinking the use of *Trichogramma* sp. for *Spodoptera* sp. control. Furthermore, it proposes new research ideas to define the best use of these *Trichogramma* species together with other key species such as *Telenomus* sp. or *Chelonus* sp. These parasitoids should be also considered for optimizing Integrated Pest Management programs, for example by combining together with entomopathogens such as *Beauveria bassiana* (Wang et al. 2021) and ensuring that their effectiveness is not compromised by side effects of pesticides (Desneux et al. 2007).

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