



Research Article

Incidence of egg and larval parasitoids of *Chilo partellus* on *Kharif* maize

JASWINDER KAUR¹, PRADYUMN KUMAR^{1*}, S. B. SUBY², J. C. SEKHAR³, ANJALI UPADHYAYA⁴, J. K. BANA⁵ and S. R. YADAV⁶

¹Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi - 110012, India

²ICAR-Indian Institute of Maize Research, Pusa Campus, New Delhi - 110012, India

³ICAR-Winter Nursery Centre, Rajendernagar, Hyderabad - 500030, Telangana, India

⁴9/3, Grainger Avenue, Ashfield-2131, NSW, Australia

⁵Agricultural Experimental Station, At and Post Paria-396145, Valsad, Gujarat, India

⁶Harnathpura, Post-Jorpura-303328, Via Jobner, Rajasthan, India

*Corresponding author E-mail: pradyumn.kumar@gmail.com

ABSTRACT: The incidence of egg and larval parasitoids of *Chilo partellus* was monitored in insecticide free maize fields at the Indian Agricultural Research Institute, New Delhi, for three *Kharif* seasons of 2013 to 2015. The hymenopteran parasitoid, *Trichogramma* sp. was recorded to be the only egg parasitoid in this area, while a good number of larvae were parasitized by braconid, *Cotesia flavipes*. The egg parasitism was recorded on the freshly laid eggs of stem borer obtained by artificially releasing the adults of *C. partellus* on maize cultivars, HQPM1 and PMH1, at 12 days after germination. There was no egg parasitism recorded during *Kharif* 2013 and 2014, whereas 5.6 percent egg-mass parasitism by *Trichogramma* sp. was recorded during *Kharif*, 2015. The larval parasitoids were monitored by artificially infesting the maize plants with neonates of laboratory reared *C. partellus*. The larvae were allowed to develop on maize plants under field conditions for 20 days. The plants showing stem borer damage were cut and brought to the laboratory. The larvae collected from infested maize plants were reared in the laboratory. The maggots of *C. flavipes* recovered from parasitized larvae ranged from 29-100, 41-50 and 20-80 percent during *Kharif* 2013, 2014 and 2015, respectively. The result of this study indicated that parasitism by *Cotesia* was influenced by age of plants damaged by *C. partellus*. The young maize plants seemed to be more attractive to the foraging of *Cotesia* and more stem borer larvae were parasitized on these plants as the maximum (58 percent) parasitism was observed at 40-day-old crop. The parasitoid was found to be active on maize from 40-60 days after germination and the incidence decreased thereafter. Insecticides should not be used during this period. The current studies also revealed that host densities had no significant effect on percentage parasitism by *Cotesia*.

KEY WORDS: Biocontrol, *Chilo partellus*, *Cotesia*, Maize, *Trichogramma*

(Article chronicle: Received: 07-08-2019; Revised: 10-03-2020; Accepted: 15-03-2020)

INTRODUCTION

Lepidopteran stem borers are among the most damaging pests of maize in semi-arid countries and are a major constraint in realizing the yield potential of the crop. In India, the stem borer, *Chilo partellus* (Swinhoe) (Crambidae: Lepidoptera) is one of the serious insect pests causing 24.3 to 36.3 % yield loss in different agro-climatic regions of the country (Ganguli *et al.*, 1997). A large number of insecticides belonging to different groups have been widely used to control the pest (Dharmasena, 1993; Teli *et al.*, 2007), but with limited success. Long-term overuse of stem borer-targeting insecticides has not only resulted in pest resistance, but is also associated with severe risks posed to humans, non-target organisms and the environment (Desneux *et al.*, 2007). Also, chemical control

is often effective on the neonate instars, before the larvae enter the stem (Reyes, 1987). Thus, as an alternative, to other control measures, the use of natural has been considered an essential component in its management strategy (Jalali and Singh, 2006). Exploiting biocontrol in maize ecosystem could reduce pesticide application, conserve the endemic natural enemy complex, reduce the need for additional treatments to control secondary pests, and reduce pesticide-associated risks to humans and environmental health (Van Lenteren, 2000).

Among the various biocontrol agents, *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) are the polyphagous endoparasitoids of lepidopteran eggs commonly used for biological control of economic pests around the world

(Hoffmann *et al.*, 2001, Kuhar *et al.*, 2004; Zhang *et al.*, 2010; Wang *et al.*, 2014, Kumar *et al.*, 2013). These can be easily reared in the insectaries on hosts other than the field hosts and have a broad host range of target pests, hence, play an important role in pest control (Mills, 2010). *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae), a gregarious larval endo-parasitoid, has been widely used in maize, sorghum and sugarcane ecosystems (Kalra and Srivatsava, 1996; Tanwar and Varma, 2002). It is found in nature during *Kharif* season throughout India, and has proven as a dominant larval parasitoid of *C. partellus* by reducing the population to the range of 32-55 per cent (Divyal *et al.*, 2009; Padmaja and Prabhakar, 2004). Though the egg and larval parasitoids are present in nature, the detailed information of their incidence and degree of parasitism during different months of crop period is not available on maize. Keeping this in view, the present investigations were carried out for the three *Kharif* seasons from 2013 to 2015. The results of this study are expected to provide valuable information for effective control of *C. partellus* particularly when integrating biological control agents in IPM program. The findings can also be used by the researchers to take initiative for conservation of available fauna for pest management and also to advise the farmers for judicious use of insecticides on the crop.

MATERIALS AND METHODS

Rearing of *Chilo partellus*

The nucleus culture of *Chilo partellus* was collected from the fields of ICAR- Indian Agricultural Research Institute, New Delhi. The culture was multiplied and maintained in the Entomology Laboratory of Directorate of Maize Research under the controlled temperature of $26 \pm 2^\circ\text{C}$ and relative humidity of $65 \pm 5\%$. The field collected larvae were reared on fresh maize stalk till pupation. Further, generations of *C. partellus* were multiplied on artificial diet (Siddiqui *et al.*, 1977). When most of the larvae turned into pupae, they were collected and kept for emergence. Adults were paired in oviposition jar ($26\text{ cm} \times 16\text{ cm}$) and kept at for egg laying. The egg laying was complete in five days. The eggs were laid in masses on the butter paper. Egg bearing area of butter paper was cut and kept in petri dish with moist cotton kept beside. The eggs, when reached black-head stage, were used for artificial infestation of plants in the field for evaluation of larval parasitoids.

Evaluation of egg parasitoids

Five beds of $2\text{m} \times 2\text{m}$ were prepared with $30\text{cm} \times 15\text{cm}$ row to row and plant to plant distance. In each bed, three rows, each of maize cultivar HQPM1 and PMH 1 were used for egg laying by *C. partellus*. Before releasing adults, the plots were covered by $2\text{m} \times 2\text{m} \times 2\text{m}$ walk-in cage made of

net which is permeable to *Trichogramma* but impermeable to *C. partellus* adults. The adults were released in the cages at 12 DAG (days after germination). Freshly emerged *C. partellus* adults in ratio of 1:4 (adult pair: plants) were released in the evening as standardized by Kumar *et al.*, (2012). The plants were cut from the base after four days during which the female finished laying eggs and brought to laboratory. Each plant was observed thoroughly for eggs. The egg masses were collected and kept in glass vial under ambient conditions to observe the emergence of any parasitoids. The parasitoid emerged from egg masses were counted and number was recorded.

Evaluation of larval parasitoids

For evaluating larval parasitoids, 12-15 day old 600 maize plants were infested by placing 10 black head stage eggs of *C. partellus* in each plant whorl. The larvae on hatching fed on the tender leaves of whorl and made their way in the stem. Twenty days after infestation, the plants showed symptoms of stem borer feeding. The visibly infested plants were harvested at 40, 50, 60, and 70 DAG and brought to the laboratory. The plants were dissected to recover the developing larvae/pupae/parasitoids. The recovered larvae were further reared on baby corn to observe the emergence of parasitoid/formation of *Chilo* pupa. The parasitized larvae were kept individually in glass vials to observe the emergence of the parasitoid. The emerged parasitoids were identified and their number was calculated and recorded.

RESULTS AND DISCUSSION

The results on incidence of egg and larval parasitoids are presented as below.

Egg parasitoids of *Chilo partellus*

No parasitism of the eggs of *C. partellus* was recorded during *Kharif* 2013 and 2014, whereas in *Kharif* 2015, 5.6 percent egg masses were parasitized (Table 1). From the parasitized egg mass, 32 percent eggs were observed to be parasitized by *Trichogramma* sp.

Larval parasitoids of *Chilo partellus*

The larval parasitism was assessed by destructive sampling during all the three years. *Cotesia flavipes* was found to be parasitizing the larvae of *C. partellus* in each year of observation (Table 2). In 2013, till 40 DAG, the plants showed infestation symptoms but no larva was recovered, but in 50 and 60 DAG plants, they were found to harbour 0.35 and 0.07 *C. partellus* larva per infested plant, respectively, out of which 28.6 and 100 percent larvae, respectively, were parasitized by *C. flavipes*. In 70 DAG, none of the infested plants yielded *C. partellus* larvae.

Table 1. Percent parasitism incidence and numbers of *Trichogramma* sp. in *Kharif* maize during 2013-2015

Cultivar	No. of egg masses	No. of egg mass parasitized	Number of parasitoid	% parasitization	Severity of parasitization
<i>Kharif, 2013</i>					
PMH 1	0	0	0	0	0
HQPM 1	0	0	0	0	0
<i>Kharif, 2014</i>					
PMH 1	9	0	0	0	0
HQPM 1	11	0	0	0	0
<i>Kharif, 2015</i>					
PMH 1	10	1 (50 eggs)	16	5.6	32
HQPM 1	8	0	0	0	0

Table 2. Percent parasitism of *Chilo partellus* by *Cotesia flavipes* during *Kharif* maize in 2013-2015

Plant Age	No. of plants	No. of larvae recovered	No. of infested larvae	Percent Incidence	
				<i>Chilo partellus</i>	<i>Cotesia flavipes</i> sp.
<i>Kharif, 2013</i>					
40	8	0	0	0.0	0.0
50	20	7	2	35.0	28.6
60	15	1	1	6.7	100.0
70	9	0	0	0.0	0.0
<i>Kharif, 2014</i>					
40	25	29	12	100.0	41.4
50	100	4	2	4.0	50.0
60	20	0	0	0.0	0.0
70	262	0	0	0.0	0.0
<i>Kharif, 2015</i>					
40	20	20	16	100.0	80.0
50	45	4	2	8.9	50.0
60	30	10	2	33.3	20.0
70	30	0	0	0.0	0.0

In 2014, 1.16 and 0.04 *C. partellus* larvae per plant were recovered per plant only from the infested plants of 40 and 50 DAG, respectively, whereas no larva was recovered from 60 and 70 DAG infested plants. Larvae recovered from 40 and 50 DAG plants were parasitized to the extent of 41 and 50 percent by *C. flavipes*. In 2015, 1.00, 0.09 and 0.33 larvae from 40, 50 and 60 DAG plants were recovered, respectively. The infested plants harvested 70 DAG did not yield any larva. The larvae recovered for 40, 50 and 60 DAG plants were parasitized to the extent of 80, 50 and 20 percent.

Biocontrol is one of the major components of Integrated Pest Management (IPM), which seeks to maximize the contribution of naturally occurring parasitoids, predators and pathogens to the reduction of pest population. The potential of natural parasitoids

present in maize ecosystem to manage stem borer population was monitored for three years, and the finding of which can be utilized for the timing of pesticide application, if at all required.

The egg and larval parasitism of *C. partellus* in the present studies resulted in variable parasitism during the three *Kharif* seasons from 2013-2015. From the egg parasitoids, *Trichogramma* sp. was found to be the only egg parasitoid during the study. *Trichogramma* spp. have successfully been used world-wide in inundative releases for the biological control of insect pests (Li, 1994; Smith, 1996; van Lenteren, 2000) as well as for the European corn borer, *Ostrinia nubilalis* (Hübner), (Wright *et al.*, 2002; Hoffmann *et al.*, 2006).

The consistent occurrence of larval parasitoids in all the three years of study confirmed *C. flavipes* as the major

parasitoid controlling the stem borer in maize ecosystem. In 2013, no larva was recovered from infested plants at 40 DAG, hence parasitism was observed only in plants harvested after 50 and 60 days of germination, while in 2014, the parasitoid were recovered in 40 and 50, DAG plants only, whereas in 2015, the parasitism occurred from 40 to 60 DAG. The data is indicative that the parasitoid coincides with first generation of *C. partellus* in maize. The crop happens to be the most susceptible for *C. partellus* in this stage. Accordingly, the most active time of parasitoid is 40-50 days of crop considering 2014-2015 assuming that the first brood of *Cotesia* coincide with first brood of *C. partellus* at 40-50 DAG which is depended upon the time we infested the plants artificially which usually extend from 12-16 days. In 2014 and 2015, the number of larvae recovered and the number of infested larvae were maximum at 40 DAG, the most reliable sampling data.

The present data suggests *Cotesia* to be active from July to mid-September with peak activity observed in first week of August during all these years. Dev and Raj (1996) reported 35 to 50% parasitism by *Cotesia* (= *Apanteles*) sp. on larvae of *C. partellus* during the second week of October in sorghum in Himachal Pradesh. Peak activity of *Cotesia* during July-August may be due to availability of host, i.e., *Chilo* larvae inside the plant. The activity period of *Cotesia* observed in the present studies is in close agreement with the results of Chaudhary and Sharma (1987) and Kishore (1986) who also recorded the highest percent parasitization (32%) during *Kharif* season in sorghum. Also, the young plants are more inducible and effective in emitting volatile organic compounds as well as secondary metabolites in defense to pest. This could be the cause of attraction of female which later led to their oviposition choice (Amalina *et al.*, 2016).

The year wise trend of parasitization indicated maximum parasitization in *Kharif* 2013 which may be due to the better synchrony of *Cotesia* with *C. Partellus*

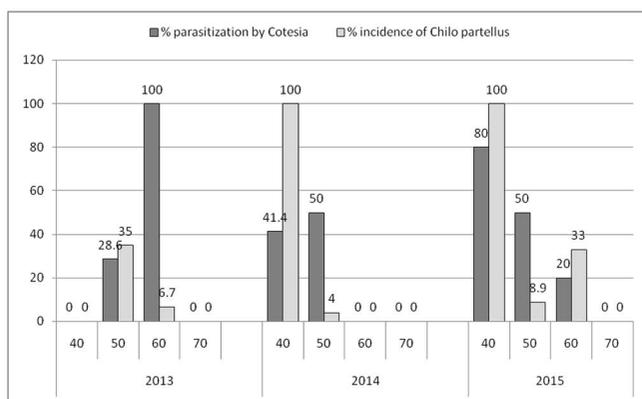


Fig. 1. Year wise percent incidence of *Chilo partellus* and *Cotesia flavipes* at different plant ages of maize

(Fig. 1). The parasitization ranged from 41.4-50 and 20-80 percent in *Kharif* 2014 and 2015, respectively. *Cotesia* has been found to be permanently established in East Africa, reducing borer densities by 50% and increasing maize yields by 10%, on an average (Overholt *et al.*, 1997; Zhou *et al.*, 2001). There was significant positive correlation of (0.87) between larval density and percent parasitization by *Cotesia*, whereas the larval density resulted in negative correlation (-0.14) with severity of parasitization by *Cotesia*. There were studies that showed parasitism by *Cotesia* responds in both density dependence (Sow *et al.*, 2013), and inversely density dependence (Talekar, 1997; Lim, 1982; Ooi, 1979). The correlation of -0.14 between host density and severity of parasitism may be because of more number of eggs laid by *Cotesia* in each larva in the absence of optimum number of hosts available. This is required to be studied in future.

REFERENCES

- Altieri MA, Nicholls CI. 2004. *Biodiversity and Pest Management in Agroecosystems* (2nd eds.). Food Products Press®, an imprint of The Haworth Press, Inc., 10 Alice Street, Binghamton, 13904-1580, New York, USA. <https://doi.org/10.1201/9781482277937>
- Amalina S, Mohd Hanifah Y, Mohamad Roff MN, Idris AB. 2016. Effects of plant age and insect densities on parasitism by *Cotesia vestalis* (Haliday). *Middle-East J Sci Res.* **24**: 1839-1846.
- Chaudhary RN, Sharma VK. 1987. Parasitization in diapausing larvae of *Chilo partellus* (Swinhoe) by *Apanteles flavipes* (Cameron). *Ind J Ecol.* **14**: 155-157.
- Desneux N, Decourtye A, Delpuech JM. 2007. The sub-lethal effects of pesticides on beneficial arthropods. *Annu Rev Entomol.* **52**: 81-106. <https://doi.org/10.1146/annurev.ento.52.110405.091440> PMID:16842032
- Devi N, Raj D. 1996. Extent of parasitization of *Chilo partellus* (Swinhoe) on maize by *Apanteles* sp. in mid hill zone of Himachal Pradesh (India). *J Entomol Res.* **30**: 171-172.
- Dharmasena CMD. 1993. Chemical control of maize stem borer, *Chilo partellus* (Swinhoe). *Pestology* **17**: 25-27
- Divyal K, Marulasiddesa KN, Karupanidhi K, Sankar M. 2009. Population dynamics of stem borer, *Chilo partellus* (Swinhoe) and its interaction with natural enemies in sorghum. *Ind J Sci Tech.* **3**: 1-2.
- Ganguli RN, Chaudhary RN, Ganguli Jayalakshmi. 1997. Effect of time of application of chemicals on

- management of maize stem borer, *Chilo partellus* (Swinhoe). *Int J Pest Manage.* **43**: 253-259. <https://doi.org/10.1080/096708797228546>
- Hoffmann MP, Ode PR, Walker DL, Gardner J, van Nouhuys S, Shelton AM. 2001. Performance of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) reared on factitious hosts, including the target host, *Ostrinia nubilalis* (Lepidoptera: Crambidae). *Biol Control* **10**: 1–10. <https://doi.org/10.1006/bcon.2000.0912>
- Hoffmann MP, Pitcher SA, Cheever SA, Gardner J, Losey JE, Kuhar TP, Laub CA, Youngman RR. 2006. Efficacy of inoculative releases of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) against European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae) in field corn. *Biol Control* **36**: 345-349. <https://doi.org/10.1016/j.biocontrol.2005.10.008>
- Jalali SK, Singh SP. 2006. Biological control of *Chilo partellus* using egg parasitoid *Trichogramma chilonis* and *Bacillus thuringiensis*. *Ind J Agric Res.* **40**: 184-189.
- Kalra AN, Srivastava RC. 1996. Biology of *Apanteles flavipes* Cameron (Braconidae: Hymenoptera), a parasite of moth borers of sugarcane, under micro-ecological conditions, pp. 606-609. IN: Proc Vth All India Conf on Sugarcane Research Workshop, Coimbatore, Tamil Nadu, India.
- Kishore P. 1986. Studies on natural enemies of spotted stem borer. *Sorghum Newslett.* **29**: 65-66.
- Kishore P. 1986. Studies on natural enemies of spotted stem borer. *Sorghum Newslett.* **29**: 65-66.
- Kuhar TP, Barlow VM, Hoffmann MP, Fleischer SJ, Groden E, Gardner J, Hazzard R, Wright MG, Pitcher SA, Speese J. 2004. Potential of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) for biological control of European corn borer (Lepidoptera: Crambidae) in solanaceous crops. *J Econ Entomol.* **97**: 1209–1216. <https://doi.org/10.1093/jee/97.4.1209>
- Kumar P, Sekhar JC, Kaur Jaswinder. 2013. Trichogrammatids: Integration with other methods of pest control. 410 pp. In: Sithanatham S, Ballal CR, Jalali SK, Bakthavatsalam N. (Eds.). *Biological Control of Insect Pests Using Egg Parasitoids*. 12 illus. Springer Science Publications.
- Kumar P, Sekhar JC, Kaur Jaswinder, Bana JK, Suby SB. 2012. Screening techniques in maize germplasm, 2012. Directorate Maize Research, Indian Council of Agricultural Research, Tech Bull. 2012/10, 40 pp.
- Landis DA, Wratten SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu Rev Entomol.* **45**: 175– 201. <https://doi.org/10.1146/annurev.ento.45.1.175> PMID:10761575
- Li LY. 1994. Worldwide use of *Trichogramma* for biological control of different crops: A survey, pp. 37-54. In: Biological control with egg parasitoids, (Wajnberg E, Hassan SA. (Eds.), CAB International, Wallingford, England. PMID:PMC159496
- Lim GS. 1982. The biology and effects of parasite on diamondback moth, *Plutella xylostella* (L.). Ph.D. thesis, University of London, United Kingdom.
- Mills N. 2010. Egg parasitoids in biological control and integrated pest management, pp. 389–411. In: Egg parasitoids in agro-ecosystems with emphasis on *Trichogramma* (Consoli F, Parra J, Zucchi R. (Eds.). Springer, New York, USA. PMID:21415890
- Ooi ACP. 1979. Incidence of *Plutella xylostella*. (Lepidoptera: Yponomeutidae) and its parasites, *Apanteles plutellae* Kurdj. (Hymenoptera: Braconidae) in Cameron Highlands, Malaysia. *Malaysian App Biol.* **8**: 131-143
- Overholt WA, Ngi-Song AJ, Omwega CO, Kimani-Njogu SW, Mbapila J, Sallam MN, Ofomata VC. 1997. A review of the introduction and establishment of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) in East Africa for biological control of cereal stem borers. *Insect Sci Appl.* **17**: 79–95.
- Padmaja PG, Prabhakar M. 2004. Natural parasitization of spotted stem borer, *Chilo partellus* (Swinhoe) on sweet sorghum in Andhra Pradesh. *Ind J Entomol.* **66**: 285–286.
- Reyes R. 1987. Sorghum stem borer in central and South Africa, pp. 49-58. In: Proc Int Workshop on sorghum stem borer, 17-20 November, ICRISAT Centre, Patancheru, AP, India.
- Siddiqui KH, Sarup P, Panwar VPS, Marwaha KK. 1977. Evolution of base gradients to formulate artificial diets for mass rearing of *Chilo partellus* (Swinhoe). *J Entomol Res.* **1**: 117-131.
- Smith SM. 1996. Biological control with *Trichogramma*: advances, successes and potential of their use. *Annu Rev Entomol.* **41**: 375-406. <https://doi.org/10.1146/annurev.en.41.010196.002111> PMID:15012334

- Sow G, Diarra K, Arvanitakis L, Bordat D. 2013. The relationship between the diamondback moth, climatic factors, cabbage crops and natural enemies in a tropical area. *Folia Hort.* **25**: 3-12 <https://doi.org/10.2478/fhort-2013-0001>
- Talekar NS. 1997. Characteristics of parasitism of diamondback moth by *Oomyzus sokolowskii* (Hymenoptera: Eulophidae), pp. 97-103. In: the Proceedings of Third International Workshop on Management of Diamondback Moth and other Crucifer Pests, Kuala Lumpur, Malaysia 29 October-1 November, 1996.
- Tanwar RK., Varma A. 2002. Field Trials with *Cotesia flavipes* Cameron against sugarcane borers in sub tropical India. *Sugar Tech.* **4**: 153-156. <https://doi.org/10.1007/BF02942698>
- Teli VS, Chavan BP, Ankalkoppe MN, Khot RB, Harers PN. 2007. Evaluation of some insecticides for the control of maize stem borer, *Chilo partellus* (Swinhoe). *J Entomol Res.* **31**: 323-326.
- Van Lenteren JC. 2000. Measures of success in biological control of arthropods by augmentation of natural enemies, pp. 77-103. In: Gurr G, Wratten S. (Eds.). *Measures of success in biological control*. Kluwer Academic; Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-011-4014-0_3
- Wang ZY, He KL, Zhang F, Lu X, Babendreier D. 2014. Mass rearing and release of *Trichogramma* for biological control of insect pests of corn in China. *Biol Control* **68**: 136–144. <https://doi.org/10.1016/j.biocontrol.2013.06.015>
- Wright MG, Kuhar TP, Hoffmann MP, Chenus SA. 2002. Effect of inoculative releases of *Trichogramma ostriniae* on populations of *Ostrinia nubilalis* and damage to sweet corn and field corn. *Biol Control* **23**: 149-155. <https://doi.org/10.1006/bcon.2001.0993>
- Zhang F, Babendreier D, Wang ZY, Il KS, Zheng L, Pyon YC, Bai SX, Song K, Ri J O, Grossrieder M, Kuhlmann U. 2010. Mass releases of *Trichogramma ostriniae* increase maize production in DPR Korea. *J App Entomol.* **134**: 481–490. <https://doi.org/10.1111/j.1439-0418.2010.01512.x>
- Zhou G, Baumgartner J, Overholt WA. 2001. Impact assessment of an exotic parasitoid on (Hymenoptera: Braconidae) stem borer (Lepidoptera) population dynamics in Kenya. *Ecol Appl.* **11**: 1554–1562. [https://doi.org/10.1890/1051-0761\(2001\)011\[1554:IAOAE\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1554:IAOAE]2.0.CO;2)