Natural Enemies of the Fall Armyworm, Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) in Ghana

Authors: Koffi, Djima, Kyerematen, Rosina, Eziah, Vincent Y., Agboka, Komi, Adom, Medetissi, et. al.

Source: Florida Entomologist, 103(1) : 85-90

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.103.0414
Natural enemies of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in Ghana

Djima Koffi*, Rosina Kyerematen†, Vincent Y. Eziah‡, Komi Agboka§, Medetissi Adom¶, Georg Goergen∥, and Robert L. Meagher, Jr.

Abstract

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is an invasive insect pest attacking maize in Ghana and sub-Saharan Africa countries. Biological control will need to be an important management strategy, and a first step was to identify potential natural enemies. Sampling was conducted in different localities of the 10 regions of Ghana from May to Nov 2017. A total of 1,062 larvae were collected from 106 maize farms, and the presence of natural enemies was recorded in 18 (17.0%) farms. Among natural enemies recorded, 7 species were parasitoids: *Chelonus bifoveolatus* Szpligeti, *Cocc ygium luteum* (Brull), *Cotesia icpe Fernandez, Meteoridea testacea* (Granger), and *Bracon* sp. (all Hymenoptera: Braconidae), *Anatrichus erinaceus* Loew (Diptera: Chloropidae), and an undetermined tachinid fly (Diptera: Tachinidae). The parasitism rate was 3.58%. Three predator species were collected: *Pheidole megacephala* (F.) (Hymenoptera: Formicidae), *Haematochares obscuripennis* Stål, and *Peprius nodulipes* (Signoret) (both Heteroptera: Reduviidae). The 2 most abundant parasitoids were *C. bifoveolatus* and *C. luteum* with a relative abundance of 29.0% and 23.7%, respectively, and a parasitism rate of 1.04% and 0.85%, respectively. However, *C. bifoveolatus* was the most dispersed parasitoid, found in 6.6% of the inspected sites within all the agroecological zones of Ghana. This species is a good candidate as a biological control agent for fall armyworm in Africa. The predator that was most abundant (46.0%) and dispersed (3.8% of the farms) was *P. megacephala*.

Key Words: biological control; *Cotesia bifoveolatus*; *Pheidole megacephala*; *Cocc ygium luteum*. 

Resumen

El cogollero, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), es una plaga de insectos invasora que ataca el maíz en Ghana y los países de África subsahariana. El control biológico deberá ser una estrategia de manejo importante, y un primer paso es identificar los enemigos naturales potenciales. Se realizó el muestreo en diferentes localidades de las 10 regiones de Ghana desde mayo hasta noviembre del 2017. Se recolectó un total de 1.062 larvas de 106 granjas de maíz, y se registró la presencia de enemigos naturales en 18 granjas (17.0%). Entre los enemigos naturales registrados, 7 especies fueron parasitoides: *Chelonus bifoveolatus* Szpligeti, *Cocc ygium luteum* (Brull), *Cotesia icpe Fernandez, Meteoridea testacea* (Granger) y *Bracon* sp. (todos los Hymenoptera: Braconidae), *Anatrichus erinaceus* Loew (Diptera: Chloropidae) y una mosca tachinida indeterminada (Diptera: Tachinidae). La tasa de parasitismo fue del 3.58%. Se recolectaron tres especies de depredadores: *Pheidole megacephala* (F.) (Hymenoptera: Formicidae), *Haematochares obscuripennis* Stål y *Peprius nodulipes* (Signoret) (ambos Heteroptera: Reduviidae). Los 2 parasitoides más abundantes fueron *C. bifoveolatus* y *C. luteum* con una abundancia relativa del 29.0% y 23.7%, respectivamente, y una tasa de parasitismo del 1.04% y 0.85%, respectivamente. Sin embargo, *C. bifoveolatus* fue el parasitoide más disperso, encontrado en el 6.6% de los sitios inspeccionados dentro de todas las zonas agroecológicas de Ghana. Esta especie es un buen candidato como agente de control biológico para el cogollero en África. El depredador que fue más abundante (46.0%) y disperso (3.8% de las granjas) fue *P. megacephala*.

Palabras Claves: control biológico; *Cotesia bifoveolatus*; *Pheidole megacephala*; *Cocc ygium luteum*.

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is an important pest of many crops including maize (*Zea mays* L.; Poaceae), sorghum (*Sorghum bicolor* [L.] Moench; Poaceae), cotton (*Gossypium hirsutum* L.; Malvaceae), and diverse pasture grasses. It is widely distributed in the Americas (Sparks 1979) and recently has become a pest of concern in Africa (Goergen et al. 2016; Nagoshi et al. 2017). Given the importance of maize in these regions, this pest has become one of the most serious problems on both continents. The yield losses caused by fall armyworm vary and depend on various factors, but can range from 19 to 100% in Brazilian plantations (De Almeida Sarmento et al. 2002).

After severe outbreaks in Africa, control of fall armyworm has been based principally on the use of chemical insecticides. However, biological control is a highly desirable management alternative for controlling this pest in the long term. The success of any biological control project depends on appropriate biological, ecological, and population studies of the species involved (Miller 1983).

There have been surveys for natural enemies of fall armyworm in the USA (Hogg et al. 1982; Ashley 1986; Meagher et al. 2016), Mexico and Central America (Castro & Pitre 1989; Molina-Ochoa et al. 2003), and South America (Beserra et al. 2002; Murúa et al. 2009). Although some species exist throughout the Western Hemisphere, most species...
distribution generally is defined by their geographic areas (Ashley 1979). Since fall armyworm is new to Africa, it is not known which local natural enemy species will use it as a host, although a recent report identifies parasitoids found in eastern Africa (Sisay et al. 2018). Successful biological control management programs for fall armyworm will be those that incorporate multiple natural enemy species (Gross & Pair 1986; Riggin et al. 1993; Figueiredo et al. 2006; Wyckhuys & O’Neill 2006, 2007).

Materials and Methods

SAMPLING SITES

Surveys were conducted twice in 2017 to cover both maize seasons. The first period covered May to July, and the second period covered August to November. A total of 106 maize sites or farms were sampled from different localities of the 10 regions of Ghana. The sites were geographically positioned between latitudes 4.733333°N and 11.183333°N, and between longitudes 3.183333°W and 1.183333°E (MoFA 2016), with the highest point being Mount Afadjato (880 masl). The sandy coastline is backed by plains and scrub, intersected by several rivers and streams. A tropical rain forest belt (central and east), interrupted by heavily forested hills and many streams and rivers, extends northward from the coastline. The north of the country varies from 91 to 396 masl and is covered by low bush, park-like savanna, and scattered grassy plains. The country is divided into 6 agroecological zones: Sudan Savannah, Guinea Savannah, Forest Transitional, Deciduous Forest, Rain Forest, and Coastal Savannah (MoFA 2016). The natural vegetation is determined by the different climatic conditions and is influenced by different soil types.

COLLECTION AND REARING OF NATURAL ENEMIES

Predators and parasitoids were collected from the field. Predators that were found preying on the larvae of S. frugiperda were directly collected and preserved in 70% ethanol; parasitoids were larval endoparasitoids which developed inside S. frugiperda larvae. Therefore, S. frugiperda larvae were collected from selected sites on infested maize plants, which were identified by the presence of larval feeding injury in the whorls and newly deposited frass.

| Region         | Sites                     | Coordinates                           | Species (Order: Family)                                                                 |
|----------------|---------------------------|---------------------------------------|----------------------------------------------------------------------------------------|
| Greater Accra  | Legon                     | 5.6477778°N, 0.1691667°W              | Coccygidium luteum, Bracon sp., Chelonus bifoveolatus Szpilgert (Hymenoptera: Braconidae) |
|                | Sege                      | 6.4905556°N, 0.6138889°W              | Meteoridea testacea (Granger) (Hymenoptera: Braconidae)                                 |
| Central        | Ayensu                    | 5.0944444°N, 1.4291667°W             | Pheidole megacephala (F.) (Hymenoptera: Formicidae); C. bifoveolatus                   |
| Western        | Dunkwan                   | 5.1108333°N, 1.6327778°W             | P. megacephala, M. testacea                                                            |
| Ashanti        | Kumasi                    | 6.1913889°N, 2.0263889°W             | C. bifoveolatus                                                                        |
|                | KNUST                     | 7.1347222°N, 1.9747222°W             | Anaotrictus erinaceus Loew (Diptera: Chloropidae); P. megacephala                      |
|                | Agogo Aburkyi             | 7.4030556°N, 1.1472222°W             | C. bifoveolatus                                                                        |
| Brong Ahafo    | Ejura                     | 7.4038889°N, 1.3455556°W             | C. bifoveolatus                                                                        |
| Eastern        | Kpong                     | 6.2316667°N, 0.1169444°W             | Bracno sp., Cotesia icipe, C. bifoveolatus, A. erinaceus, Haematocares obscuripennis    |
| Volta          | Agove                     | 6.8397222°N, 0.6419444°W             | StaI, Peprins nudulipes (Signoret) (Heteroptera: Reduviidae); P. megacephala          |
| Northern       | Tamale                    | 9.6377778°N, 1.4733333°W             | Cotesia icipe, Coccygidium luteum                                                     |
|                | Savelugu                  | 10.0716667°N, 1.4733333°W            | C. bifoveolatus                                                                        |
|                | Kilomposible              | 9.6797222°N, 2.7866666°W             | Undetermined sp. (Diptera: Tachinidae)                                                 |
|                | Kukpehi                   | 9.4163889°N, 0.9702778°W             | Coccygidium luteum                                                                    |
|                | Sango                     | 9.4319444°N, 0.9488889°W             | Coccygidium luteum                                                                    |
| Upper East     | Bolga1                    | 11.4713889°N, 1.4508333°W            | A. erinaceus                                                                           |
|                | Bolga2                    | 11.4150000°N, 1.3058333°W            | Bracno sp., C. bifoveolatus                                                            |

Fall armyworm larvae collected from the field were morphologically identified and placed individually in conical transparent rearing containers (8.5 × 5.5 × 11 cm³). Rearing containers were fitted with a black mesh cover at the top to allow ventilation and to prevent escape of larvae. Tissue paper was placed at the base of the containers to absorb moisture produced by the diet (maize leaves) and larvae (transpiration and frass). The larvae were reared in the laboratory under room conditions (27 ± 4 °C, 80 ± 8% RH, and 12:12 h [L:D] photoperiod). Parasitoids that emerged from the collected larvae were recorded every 24 h and placed in 70% ethanol. Natural enemies were identified by G. Goergen, Curator at the Biodiversity International Institute of Tropical Agriculture Benin.

DATA ANALYSIS

Larval mortality due to unknown factors, adult emergence rate and larval parasitism rate were calculated for all sites. The formula $Pr = \frac{Ni}{Nt} \times 100$ (Van Driesche 1983; Pair et al. 1986; Legaspi et al. 2001) was used to determine the parasitism rate (Pr), where Ni is the number of parasitized individuals of species i, and Nt is the total number of individuals collected. Relative abundance (RA) of each natural enemy species was calculated using the following formula developed and used by Canal Daza (1993) and Molina-Ochoa et al. (2001, 2004): $RA = \frac{Ni}{Nt} \times 100$, where Ni is the number of individuals of species i, and Nt is the total number of all individuals collected. The different localities from which parasitoids were obtained were grouped according to the biogeographic region to which they belong (Table 1).

All analyses were conducted using SAS vers. 9.4 (SAS 2012). Data were first analyzed using Box-Cox (PROC TRANSREG) and PROC UNIVARIATE to find the optimal normalizing transformation (Osborne 2010). Differences in percent parasitism, mortality due to other factors, and adult emergence were first compared between growing seasons, then compared across regions using PROC GLM. In all analyses LSMEANS with an adjusted Tukey test was used to separate variable means.

Results

Fall armyworm larvae were collected from all maize fields across Ghana during both cropping seasons. Natural enemies of fall army-
worm occurred in 17.0% (18 of 106) of the inspected sites, including 8 sites that were sprayed with insecticides. For this study, a total of 1,062 *S. frugiperda* larvae were collected and 38 were parasitized, yielding a parasitism rate of 3.6%. There was no difference in parasitism between the major (4.8 ± 2.3%) and minor (3.2 ± 0.9%) cropping systems ($F_{1,18} = 0.61; P = 0.4465$). There also was no difference in parasitism among regions, with a range from 0% in the Upper West to 7.8% in the Northern region ($F_{9,18} = 0.58; P = 0.7870$) (Table 2).

The collection of fall armyworm during the major cropping season from May to Jul included 29 farms from the 10 regions, but natural enemies of fall armyworm were recorded only in 8, representing 27.6% of the sites. Even though parasitoids were not found in the Greater Accra, Central, Western, Brong Ahafo, and Upper West regions, a total of 306 larvae were collected from the field, and only 12 were parasitized giving a 3.9% parasitism rate. For the 8 sites that contained parasitoids, a parasitism rate of 17.4 ± 3.41% was recorded (Table 3).

The minor cropping season collections were carried out from the end of Aug to Nov on 77 farms from the 10 regions. Larval natural enemies of fall armyworm were recorded in 10 sites representing 13.0% of sampled farms. During this season, 756 *S. frugiperda* larvae were collected, and 26 larvae were parasitized representing a parasitism rate of 3.4%. Parasitoids were not found in the Upper West, Upper East, and Volta regions, but among sites that contained parasitoids, Agogo Aburkyi, Legon, Kpong, and Sanga were not sprayed with insecticides and had the highest parasitism rates of 60%, 55.6%, 33.3%, and 23.8%, respectively (Table 4).

Seven species of parasitoids were identified: *C. bifoveolatus*, *C. icipe*, *Coccycgidium luteum*, *M. testacea*, and *Bracon sp.*, *A. erinaceus*, and an undetermined Tachnidae species. The 2 most abundant parasitoids were *C. bifoveolatus* and *Coccycgidium luteum*, with parasitism rates of 1.04% and 0.85%, respectively, and relative abundance of 29.0% and 23.7%, respectively. *Chelonius bifoveolatus* was the most dispersed parasitoid, found in 7 of the inspected sites (Table 5). Three species of predators were identified: *P. megacephala*, *H. obscuripennis*, and *P. nodulipes* (Table 1). The predator most abundant and most dispersed nationwide was *P. megacephala*, with a relative abundance of 46.0% collected from 4 of the inspected sites (Table 5).

In total, larval mortality due to unknown factors was 63.8%, and was not different between the major (65.6%) and minor (61.8%) cropping seasons ($F_{1,18} = 0.61; P = 0.4460$). Larval mortality due to unknown factors ranged from 55.3% in the Eastern Region to 73.8% in the Greater Accra Region (Table 2); however, there was no difference among regions ($F_{9,18} = 1.52; P = 0.2612$; Table 2). Only 32.7% of larvae collected from fields completed development in the laboratory, and there was no difference between the major (29.5%) and minor (34.9%) cropping seasons ($F_{1,18} = 2.05; P = 0.1689$). The Greater Accra region had the lowest development rate (20.6%), which was significantly lower than the Eastern (40.8%) and Upper West (42.6%) regions ($F_{2,18} = 4.0; P = 0.0208$; Table 2).

### Table 2. Fate of fall armyworm larvae collected during the major and minor maize seasons in different regions of Ghana, 2017.

| Region      | Larvae collected | Mortality by parasites (%) | Mortality by other factors (%) | Emerging adults (%) |
|-------------|------------------|----------------------------|-------------------------------|---------------------|
| Greater Accra | 107              | 6 (5.6)                    | 79 (73.8)                     | 22 (20.6)           |
| Central     | 98               | 1 (1.0)                    | 67 (68.4)                     | 30 (30.6)           |
| Western     | 107              | 3 (2.8)                    | 68 (63.6)                     | 36 (33.6)           |
| Ashanti     | 136              | 5 (3.7)                    | 90 (66.2)                     | 41 (30.1)           |
| Brong-Ahafo | 90               | 1 (1.1)                    | 56 (62.2)                     | 33 (36.7)           |
| Northern    | 166              | 13 (7.8)                   | 108 (65.1)                    | 45 (27.1)           |
| Upper West  | 68               | 0 (0)                      | 38 (55.9)                     | 29 (42.6)           |
| Upper East  | 67               | 4 (6.0)                    | 42 (62.7)                     | 21 (31.3)           |
| Eastern     | 103              | 4 (3.9)                    | 57 (55.3)                     | 42 (40.8)           |
| Volta       | 120              | 1 (0.8)                    | 71 (59.2)                     | 48 (40.0)           |
| Total       | 1062             | 38 (3.6)                   | 676 (63.6)                    | 347 (32.7)          |

### Discussion

The parasitism rate ranged from 6.25% at the Kwame Nkrumah University of Science and Technology site in the Ashanti Region, to 60% at the Bolga 2 site in the Upper East Region, and Agogo Aburkyi in the Ashanti Region. All 3 sites were not sprayed with chemical insecticides. The variations in parasitism is due to natural and cultural practices that can negatively or positively affect natural enemy populations (Kogan et al. 1999). The average parasitism across the country was lower than the previous findings in the Americas (8.1%, Ordóñez-Garcia et al. 2015; 13.8%, Molina-Ochoa et al. 2004; 15.5%, Wheeler et al. 1989; 18.3%, Murúa et al. 2009; 28.3%, Meagher et al. 2016; 35%, Rios-Velasco et al. 2011; 39%, Murúa et al. 2009). This low parasitism rate of *S. frugiperda* is due to the aspect of new pest introductions in Ghana. Biological control of fall armyworm requires mass rearing of introduced parasitoids in the laboratories in Africa with field releases to increase parasitism. We believe that parasitism of fall armyworm will increase as the pest continues to be present. However, high applications of chemical insecticides will negatively affect the natural enemies. Therefore, parasitoids must be preserved (Pair et al. 1986; Molina-Ochoa et al. 2004) by using selective systemic insecticides (Figueiredo et al. 2006).

*Chelonius bifoveolatus* was the most abundant parasitoid collected from larvae. *Chelonius* spp. are typical of egg-larval solitary koinobiont endoparasitoids that attack Noctuidae and Pyralidae (Marsh 1978; Vir-la et al. 1999; Murúa et al. 2009) by ovipositing into host eggs (Pierce & Holloway 1912; Rechav & Orion 1975). The parasitized host larvae exhibited reduced growth rates and weight compared to unparasitized larvae (Ables & Vinson 1981; Ashley et al. 1983). In the Western Hemisphere, *Chelonius* spp. appear to be the most geographically dispersed parasitoid of fall armyworm (Ashley et al. 1982, 1983; Meagher et al. 2016) and were reported to be present in 12 countries of the Caribbean, and South and Central America (Molina-Ochoa et al. 2003). In many areas, *Chelonius* spp. were reported to be the most common species collected (Wheeler et al. 1989; Cortez-Mondaca et al. 2010, 2012; Rios-Velasco et al. 2011; Estrada-Virgen et al. 2013). *Chelonius bifoveolatus* was found in 7 of the 10 regions (Greater Accra, Central, Eastern, Volta, Ashanti, Brong Ahafo, and Northern) and was recorded in all agroecological zones of Ghana (Coastal Savannah, Evergreen, Equatorial Forest, Transition Zone, and Guinea Savannah). These results suggest that this species is adapted to all sub-Saharan Africa agroecological zones. Therefore, this species can be a good agent for biological control of...
fall armyworm in Africa. However, the most efficient biological control programs for fall armyworm are ones that use and amplify several parasitoid species rather than programs that rely on an individual natural enemy species (Riggin et al. 1993). Therefore, we believe that adding New World parasitoids that are known to attack fall armyworm (classical biological control), plus preserving the parasitoids that are already active in Africa (conservation biological control), will contribute to reducing pest populations. The other active parasitoids included C. icipe, which is the koinobiont endoparasitoid that attacks lepidopteran larvae (Quicke 1997; Whitfield 1997). Cotesia spp. also are reported parasitoids of fall armyworm in the Americas (Ashley 1983; Meagher et al. 2016). These species may parasitize both eggs (Ruberson & Whitfield 1996), and the first and second instar larvae (Loke et al. 1983). Cotesia icipe was reported to be a successful parasitoid of a major maize pest in West Africa and in Mediterranean countries (Kaiser et al. 2017). Coccygidium luteum, as all members of this genus, is an internal koinobiont parasitoid of larval Noctuidae (Sharkey et al. 2009). Bracon sp. is an idiobiont ectoparasitoid that attack larvae with hidden behaviors, such as cereal stem borers and cereal stored products borers (Moolman et al. 2013; Souobou et al. 2015). Meteoridea testacea is a gregarious endoparasitoid that was defined as an egg-larval parasitoid of Lepidoptera (Achterberg 1993). The grass fly, A. erinaceus is widespread in Africa, but its parasitic status report is controversial (Upadhyay et al. 2001). However, it is documented as a parasitoid of sugarcane borers. Tachinidae species are almost all parasitoids. In Africa, they are usually collected from cereal stem borer larvae (Moolman et al. 2013; Chinwada et al. 2014).

Pheidole megacephala, the most abundant and most dispersed predator, prefers humid forest habitats (Hoffmann et al. 1999; Wilson 2003; Burwell et al. 2012). When introduced into a new area, P. megacephala...
Pheidole megacephala expanded its range and invaded into the forest interiors, where it attacked and displaced other introduced and naturally occurring ant species (Hoffmann 1998; Burwell et al. 2012). But the efficacy of P. megacephala as a biological agent is a challenge due to its generalist behavior and ecological disaster. However, it is a good predator with an efficient nest mate recruitment that enables the species to dominate baits and to retrieve prey too large for single workers to carry (Dejean et al. 2007, 2008). Therefore, P. megacephala must be protected as a complementary biological agent of S. frugiperda in forest zones, as well as the other 2 species of predators: H. obscuripennis and P. nodulipes, which also were found in the Equatorial Forest of the Eastern Region. The 2 Reduviids were found in the collection of true bugs sampled from Lama Forest in southern Benin (Attignon 2004).

Acknowledgments

We thank the German Academic Exchange Service (DAAD) for financing part of this research. We appreciate the help of the Government of Ghana for its contributions for field work; thanks also to Kwame Afreh-Nuamah and Ebenezer Abaoagye for their contributions during the surveys. We appreciate the contribution of the International Institute of Tropical Agriculture (IITA), Cotonou, Benin, for identifying natural enemies of fall armyworm. We appreciate and thank African Regional Postgraduate Programme in Insect Science via its Coordinator, Maxwell Billah for the use of laboratory facilities during the rearing periods. We appreciate the advice and contributions of Astrid T. Groot from the University of Amsterdam, The Netherlands, and Sabine Hänigger from Max Planck Institute for Chemical Ecology, Department of Entomology, Jena, Germany.

References Cited

Ables JR, Vinson SB. 1981. Regulation of host larval development by the egg larval endoparasitoid Chelonus insularis (Hym.: Braconidae). Entomophaga 26: 453–458.

Achterberg CV. 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen Leiden 283: 1–189.

Ashley TR. 1979. Classification and distribution of fall armyworm parasites. Florida Entomologist 62: 114–123.

Ashley TR. 1986. Geographical distribution and parasitization levels for parasitoids of the fall armyworm, Spodoptera frugiperda. Florida Entomologist 69: 516–524.

Ashley TR, Barfield CS, Waddill VH, Mitchell ER. 1983. Parasitization of fall armyworm larvae on volunteer corn, bermedagrass, and paragrass. Florida Entomologist 66: 267–271.

Ashley TR, Waddill WH, Mitchell ER, Rye J. 1982. Impact of native parasites on the fall armyworm, Spodoptera frugiperda (Lepidoptera: Noctuidae), in south Florida and release of the exotic parasite, Ephesia kuehniella (Hymenoptera: Ichneumonoidea). Environmental Entomology 11: 835–837.

Attignon EK. 2004. Invertebrate diversity and ecological role of decomposer assemblages in natural and plantation forests in southern Benin. Erlangen der Würde eines Doktors der Philosophie vorgelegt der Philosophisch-Naturwissenschaftlichen Fakultät der Universität Basel, Basel, Switzerland.

Besseira EB, Dias CT, Parra JRP. 2002. Distribution and natural parasitism of Spodoptera frugiperda (Lepidoptera: Noctuidae) eggs at different phenological stages of corn. Florida Entomologist 85: 588–593.

Burwell CJ, Nakamura A, McDougall A, Neldner W. 2012. Invasive African big-headed ants, Pheidole megacephala, on coral cays of the southern Great Barrier Reef: distribution and impacts on other ants. Journal of Insect Conservation 16: 777–789.

Canal Daza NA. 1993. Especies de parasitoides (Hymenoptera: Braconidae) de moscas-das-frutas (Diptera: Tephritidae) em quatro locais do estado do Amazonas. Tesis de Maestría ESALQ/USP, Piracicaba, São Paulo, Brazil.

Castro MT, Pite RN. 1989. Populations of fall armyworm, Spodoptera frugiperda (J. E. Smith), larvae and associated natural enemies in sorghum and maize cropping systems in southern Honduras. Tropical Agriculture 66: 259–264.

Chinwada P, Nyamutukwa S, Murandure A, Zitsanza ES. 2014. Biology and development of Sturmiopsis parasitica (Diptera: Tachinidae) on different species and populations of maize stem borers in Zimbabwe and an assessment of its suitability for redistribution in Africa. African Entomology 22: 828–837.

Cortez-Mondaca E, Armenta-Cárdenas I, Bahena-Juárez F. 2010. Parasitoids and percent parasitism of the fall armyworm (Lepidoptera: Noctuidae) in southern Sonora, Mexico. Southwestern Entomologist 35: 199–203.

Cortez-Mondaca E, Pérez-Márquez J, Bahena-Juárez F. 2012. Natural biological control of fall armyworm (Lepidoptera: Noctuidae) in maize and sorghum in northern Sinaloa, Mexico. Southwestern Entomologist 37: 423–428.

De Almeida Sarmento R, de Souza Aguiar RW, Vieira SMJ, de Oliveira HG, Holtz AM. 2002. Biology review, occurrence and control of Spodoptera frugiperda (Lepidoptera, Noctuidae) in corn in Brazil. Bioscience Journal 18: 41–48.

Dejean A, Moreau CS, Kenne M, Leponce M. 2008. The raiding success of Pheidole megacephala on other ants in both its native and introduced ranges. Comptes Rendus Biologies 331: 631–635.

Dejean A, Moreau CS, Uzac P, Le Breton J, Kenne M. 2007. The predatory behavior of Pheidole megacephala. Comptes Rendus Biologies 330: 701–709.

Estrada-Virgen O, Cambero-Campos J, Robles-Bermudez A, Rios-Velasco C, Carvajal-Cazola C, Isiodria-Aquino N, Ruiz-Cancino E. 2013. Parasitoids and entomopathogens of the fall armyworm Spodoptera frugiperda (Lepidoptera: Noctuidae) in Nayarit, Mexico. Southwestern Entomologist 38: 339–344.

Figueiredo MLC, Martins-Dias AMP, Cruz I. 2006. Relationship between fall armyworm and their natural biological control agents in the maize crop. Pesquisa Agropecuária Brasileira 41: 1693–1698.

Goergen G, Kumar PL, Sankung SB, Togola A, Tamo M. 2016. First report of outbreaks of the fall armyworm Spodoptera frugiperda (J. E. Smith) (Lepidoptera: Noctuidae), a new alien invasive pest in West and Central Africa. PLoS ONE 11: e0156532. doi:10.1371/journal.pone.0156532.

Gross HR, Pair SD. 1986. The fall armyworm: status and expectations of biological control with parasitoids and predators. Florida Entomologist 69: 512–515.

Hoffmann BD. 1998. The big-headed ant Pheidole megacephala: a new threat to monsoonal northwestern Australia. Pacific Conservation Biology 4: 250–255.

Hoffmann BD, Andersen AN, Hill GJE. 1999. Impact of an introduced ant on native rain forest invertebrates: Pheidole megacephala in monsoonal Australia. Oecologia (Berlin) 120: 595–604.

Hogg DB, Anderson RE, Pite RN. 1982. Early-season parasitization of fall armyworm (Lepidoptera: Noctuidae) larvae in Mississippi. Florida Entomologist 65: 584–585.
Kaiser L, Fernandez-Triana J, Capdevielle-Dulac C, Chantre C, Bodet M, Kaoula F, Benoist R, Calatayud P, Dupas S, Herniou EA, Jeannette R, Obonyo J, Silvain JF, Le Ru B. 2017. Systematics and biology of Cotesia typhae sp. n. (Hymenoptera: Braconidae, Microgastrinae), a potential biological control agent against the noctuid Mediterranean corn borer, Sesamia nonagrioides. ZooKeys 682: 105–136.

Kogan M, Gerling D, Maddox JV. 1999. Enhancement of biological control in annual agricultural environments, pp. 789–818 in Bellows T, Fisher T [eds.], Handbook of Biological Control. Academic Press, New York, USA.

Legaspi JC, French JV, Zuniga AG, Legaspi BC. 2001. Population dynamics of the citrus leafminer, Phyllocnistis citrella (Lep.: Gracillariidae), and its natural enemies in Texas and México. Biological Control 21: 84–90.

Loke WH, Ashley TR, Sailer RL. 1983. Influence of fall armyworm, Spodoptera frugiperda, (Lepidoptera: Noctuidae) larvae and corn plant damage on host finding in Apanteles marginiventris (Hymenoptera: Braconidae). Environmental Entomology 12: 911–915.

Marsh PM. 1978. The braconid parasites (Hymenoptera) of Heliocistis species (Lepidoptera: Noctuidae). Proceedings of the Entomological Society of Washington 80: 15–36.

Meagher RL, Nuesly G, Nagoshi RN, Hay-Roe MM. 2003. Parasitoids attacking fall armyworm (Lepidoptera: Noctuidae) in sweet corn habitats. Biological Control 95: 66–72.

Miller JC. 1983. Ecological relationships among parasites and the practice of biological control. Environmental Entomology 12: 620–624.

MoFA – Ministry of Food and Agriculture. 2016. Agriculture in Ghana. Statistics, Research and Information Directorate, Accra, Ghana.

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

Molina-Ochoa J, Carpenter JE, Lezama-Gutiérrez R, Foster JE, González-Ramírez M, Ángel-Sahagún CA, Fariñas-Larios J. 2004. Natural distribution of hymenopteran parasites of Spodoptera frugiperda (Lepidoptera: Noctuidae) larvae in México. Florida Entomologist 87: 461–472.

Molina-Ochoa J, Hamm J, Lezama-Gutiérrez R, López-Edwards M, González-Ramírez M, Pescador-Rubio A. 2001. A survey of fall armyworm (Lepidoptera: Noctuidae) parasites in the Mexican states of Michoacán, Colima, Jalisco, and Tamaulipas. Florida Entomologist 84: 31–36.

Moolman HJ, Van den Berg J, Conlong D, Cugala D, Siebert SJ, Le Ru BP. 2013. MoFA – Ministry of Food and Agriculture. 2016. Agriculture in Ghana. Statistics, Research and Information Directorate, Accra, Ghana.

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

Molina-Ochoa J, Carpenter JE, Lezama-Gutiérrez R, Foster JE, González-Ramírez M, Ángel-Sahagún CA, Fariñas-Larios J. 2004. Natural distribution of hymenopteran parasites of Spodoptera frugiperda (Lepidoptera: Noctuidae) larvae in México. Florida Entomologist 87: 461–472.

Molina-Ochoa J, Hamm J, Lezama-Gutiérrez R, López-Edwards M, González-Ramírez M, Pescador-Rubio A. 2001. A survey of fall armyworm (Lepidoptera: Noctuidae) parasites in the Mexican states of Michoacán, Colima, Jalisco, and Tamaulipas. Florida Entomologist 84: 31–36.

Moolman HJ, Van den Berg J, Conlong D, Cugala D, Siebert SJ, Le Ru BP. 2013. Diversity of stem borer parasites and their associated wild host plants in South Africa and Mozambique. Phytoparasitica 41: 89–104.

Murúa MG, Molina-Ochoa J, Fidalgo P. 2009. Natural distribution of parasitoids of larvae of the fall armyworm, Spodoptera frugiperda, in Argentina. Journal of Insect Science 9: 20. doi: 10.1673/031.009.2001

Nagoshi RN, Koffi D, Agboka K, Tounou KA, Banerjee R, Jurat-Fuentes JL, Mea-Murúa MG, Molina-Ochoa J, Fidalgo P. 2009. Natural distribution of parasitoids on five corn genotypes in South Georgia. Florida Entomologist 76: 292–302.

Rios-Velasco C, Gallegos-Morales G, Cambero-Campos J, Cerna-Chávez E, Del Rincón-Castro MC, Valenzuela-García R. 2011. Natural enemies of the fall armyworm Spodoptera frugiperda (Lepidoptera: Noctuidae) in Coahuila, México. Florida Entomologist 94: 723–726.

Ruberson JR, Whitfield JB. 1996. Facultative egg-larval parasitism of the beet armyworm, Spodoptera exigua (Lepidoptera: Noctuidae) by Cotesia marginiventris (Hymenoptera: Braconidae). Florida Entomologist 79: 296–302.

SAS. 2012. SAS for Windows, vers. 9.4. SAS Institute, Cary, North Carolina, USA.

Sharkey MJ, Yu DS, Noort SV, Seiltmann K, Penev L. 2009. Revision of the Oribatida genera of Agathidinae (Hymenoptera, Braconidae) with an emphasis on Thailand including interactive keys to genera published in three different formats. ZooKeys 21: 19–54.

Siaya B, Simiyu J, Malusi P, Likayo P, Mendesil E, Elibariki N, Wakgari M, Ayalew G. 2018. First report of the fall armyworm, Spodoptera frugiperda (Lepidoptera: Noctuidae), natural enemies from Africa. Journal of Applied Entomology 142: 800–804.

Soumbou M, Nacro S, Ouattara D. 2015. Natural enemies associated with rice stem borers in the Kou Valley, Burkina Faso. International Journal of Tropical Insect Science 35: 164–171.

Sparks A. 1979. A review of the biology of the fall armyworm. Florida Entomologist 62: 282–287.

Upadhyay RK, Mukerji KG, Chamola BP [eds.]. 2001. Biocontrol Potential and its Exploitation in Sustainable Agriculture. Springer (India) Private Ltd. New Delhi, India.

Van Driesche RG. 1983. Meaning of percent parasitism in studies of insect parasitoids. Environmental Entomology 12: 1611–1621.

Vira EG, Colomo MV, Berta C, Valverde L. 1999. El complejo de los parasitoides del “gusano cogollero” del maíz, Spodoptera frugiperda, en la República Argentina (Lepidoptera: Noctuidae). Neotrópica 45: 3–12.

Wheeler GS, Ashley TR, Andrews KL. 1989. Larval parasitoids and pathogens of the fall armyworm in Honduran maize. Entomophaga 34: 331–340.

Whitfield JB. 1997. Subfamily Microgastrinae, pp. 333–364 in Wharton RA, Marsh PM, Sharkey MJ [eds.], Manual of the New World Genera of the Family Braconidae (Hymenoptera): Special Publication No. 1. International Society of Hymenopterists, Washington, DC, USA.

Wilson EO. 2003. Pheidole of the New World: a dominant, hyperdiverse ant genus. Harvard University Press, Cambridge, Massachusetts, USA.

Wyckhuys KAG, O’Neil RJ. 2006. Population dynamics of Spodoptera frugiperda Smith (Lepidoptera: Noctuidae) and associated arthropod natural enemies in Honduran subsistence maize. Crop Protection 25: 1180–1190.

Wyckhuys KAG, O’Neil RJ. 2007. Influence of extra-field characteristics to abundance of key natural enemies of Spodoptera frugiperda Smith (Lepidoptera: Noctuidae) in subsistence maize production. International Journal of Pest Management 53: 89–99.