OCCURRENCE OF ENTOMOPATHOGENS OF *SPODOPTERA FRUGIPERDA* (LEPIDOPTERA: NOCTUIDAE) IN THE MEXICAN STATES OF MICHOACÁN, COLIMA, JALISCO AND TAMAULIPAS

ROBERTO LEZAMA-GUTIÉRREZ[1], JOHN J. HAMM[2], JAIME MOLINA-OCHOA[1], MARILÚ LÓPEZ-EDWARDS[1], ALFONSO PESCADOR-RUBIO[3], MARTÍN GONZÁLEZ-RAMIREZ[1] AND ELOISE L. STYER[4]
[1]Facultad de Ciencias Biológicas y Agropecuarias, Universidad de Colima
Apartado Postal No. 36, Tecomán, Colima 28100, México

[2]Crop Protection and Management Research Unit, USDA-ARS, PO Box 748, Tifton, GA 31793-0748

[3]Centro Universitario de Investigación y Desarrollo Agropecuario, Universidad de Colima
Apartado Postal No. 36, Tecomán, Colima 28100, México

[4]Diagnostic and Investigational Laboratory, The University of Georgia, PO Box 1389, Tifton, GA 31793-1389

ABSTRACT

Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (FAW) larvae and soil samples were collected from corn and sorghum fields in the Mexican states of Michoacán, Colima, and Jalisco during August 1998. Additional FAW larvae were collected from a sorghum field in Tamaulipas, Mexico in September. A total of 2219 FAW larvae from 20 locations and 76 soil samples from 19 locations were examined for indigenous FAW biological control agents. Four species of entomopathogenic fungi representing two classes, Zygomycetes (Entomophthorales) and Hyphomycetes (*Beauveria bassiana, Nomuraea rileyi*, and *Hirsutella* sp.) were recovered from 43 (1.94%) of FAW larvae. An unidentified microsporidian was collected from 32 (1.44%) of FAW larvae, 29 from Colima, 2 from Jalisco, and 1 from Michoacán. Forty nine larvae (2.21%) parasitized by mermithid nematodes were collected in the state of Colima. Two (0.09%) larvae infected with ascovirus were collected in Tamaulipas. Three species of Hyphomycetes (*Paecilomyces fumosoroesus, B. bassiana*, and *Metarhizium anisopliae)* were isolated from soil samples using *Galleria mellonella* larval traps. Entomopathogenic nematodes (*Steinernema* sp. and *Heterorhabditis* sp.) were recovered from soil samples from 5 of 19 localities using *Galleria mellonella* larval traps. *Bacillus thuringiensis* was isolated from soil samples from 12 locations. The most widely distributed microbial control agent on FAW larvae in the Western Coast of Mexico was the fungus *N. rileyi*, and from soil were the bacterium *B. thuringiensis* and steinernematid nematodes. The microsporidian was found predominantly in Colima and the mermithid nematodes only in Colima. Thus, Colima had the highest total percent mortality (9.67%) due to fungi, microsporidia and mermithids.

Key Words: Fall armyworm, biological control, maize, *Nomuraea rileyi,* mermithid nematode, microsporidia

RESUMEN

Larvas de gusano cogollero, *Spodoptera frugiperda* (J. E. Smith) (FAW) y muestras de suelos fueron colectadas de campos cultivados de maíz y sorgo, en los estados mexicanos de Michoacán, Colima y Jalisco, durante Agosto de 1998. Más larvas de FAW fueron colectadas de sorgo en Tamaulipas, México en Septiembre. Un total de 2219 larvas de FAW provenientes de 20 localidades y 76 muestras de suelos de 19 localidades fueron examinadas en búsgueda de agentes locales de control biológico de FAW. Cuatro especies de hongos entomopatógenos de dos clases, Zygomycetes (Entomophthorales) e Hyphomycetes (*Beauveria bassiana, Nomuraea rileyi*, e *Hirsutella* sp.) fueron recuperados de 43 (1.94%) de las larvas. Un microsporidio no identificado fue colectado de 32 (1.44%) de las larvas, 29 de Colima, dos de Jalisco, y uno de Michoacán. Cuarenta y nueve larvas (2.21%) parasitadas por nematodos mermitidos fueron colectadas de Colima. Dos larvas (0.09%) infectadas con ascovirus fueron colectadas de Tamaulipas. Tres especies de Hyphomycetes (*Paecilomyces fumosoroseus, B. bassiana*, y *Metarhizium anisopliae*) se aislaron de muestras de suelos usando las trampas de larvas de *Galleria mellonella*. Nematodos entomopatógenos (*Steinernema* sp. y *Heterorhabditis* sp.) se recuperaron de muestras de suelos en 5 de 19 localidades usando las trampas de larvas de *G. mellonella*. La bacteria *Bacillus thruingiensis* fue aislada de muestras de suelos de 12 localidades. El agente de control microbiano más ampliamente distribuido sobre larvas de FAW en la Costa Occidental de México fue el hongo *N. rileyi* y del suelo, *B. thruingiensis* y *los nematodos entomopat*ógenos. El microsporidio fue encontrado predominante-

mente en Colima y los nematodos mermitidos sólo en Colima. Así, Colima tuvo el prociento de mortalidad más alto (9.67%) debido a hongos, microsporidios y mermitidos.

Corn or maize, *Zea mayz* L., is one of the major sources of animal and human foods in the Americas and is one of the most valuable field crops in the U.S.A. It is attacked by a variety of insect pests including, one of the more destructive of these pests, the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith). The FAW causes damage in all plant growth stages, often limiting production due to severe damage to, or complete destruction of, whorl-stage plants (Wiseman et al. 1967, 1996). The use of microbial control is a potentially valuable alternative to chemical pesticides with their high cost, possible pest resurgence, development of resistance, and environmental contamination. The strategies for using pathogens in biological control of insect pests are determined primarily by the interactions among pathogens, insect host, and environment, including the plant to be protected (Hamm 1984). Thus, a first step to develop a microbial control program is the knowledge of the occurrence of insect pathogens, in order to utilize them as a component of an integrated pest management scheme.

The FAW is reported to be susceptible to viruses, fungi, protozoa, bacteria, and nematodes (Steinhaus & Marsh 1962; Gardner & Fuxa 1980; Fuxa 1982; Hughes et al. 1984; Agudelo-Silva 1986; Remillet & Silvain 1988; Richter & Fuxa 1990; Raulston et al. 1992; Molina-Ochoa et al. 1996), but their occurrence and distribution may vary with their habitat. Geographical location and agricultural practices, as well as pesticide use, may have an impact on the occurrence of natural control agents in the host population or in the soils (Fargues et al. 1992; Rogers & Marti 1992; Sosa-Gomez & Moscardi 1994; Vanninen 1996; Mietkiewski et al. 1997).

There is an increased interest in developing biological control methods for FAW in Mexico, but its natural enemy complex (particularly pathogens) is poorly known. More than three decades ago a parasitic nematode (Mermithidae) was reported to infest 21-53% of FAW larvae from Cotaxtla, Veracruz, Mexico (Alcocer and Méndez 1965). More recently, Lezama-Gutiérrez et al. (1996) assessed the virulence of some isolates of *Metarhizium anisopliae* (Metch.) Sor., *Beauveria bassiana* (Bals.) Wuill., and *Nomuraea rileyi* (F.) Samson, obtained from FAW larvae collected in the state of Colima, Mexico, against eggs and neonates of FAW. However, no detailed studies have been conducted on the occurrence of FAW pathogens from Colima, Michoacán, Jalisco, or Tamaulipas, Mexico, although data from other countries suggest that many entomopathogenic fungi and nematodes are ubiquitous inhabitants of the soil (Chandler et al. 1997). This paper reports the natural occurrence of entomopathogens and nematodes on FAW larvae and in the soil of corn and grain sorghum fields from the states of Colima, Jalisco, Michoacán, and Tamaulipas, Mexico.

Materials and Methods

Isolation of Pathogens from FAW Larvae

During August of 1998 collections of FAW larvae were made from whorl-stage corn and grain sorghum fields in the states of Colima, Jalisco, and Michoacán, and 1 collection from fruiting corn in Jalisco. A single collection of FAW larvae was made from whorl-stage grain sorghum in Tamaulipas in September. Concurrently, four soil samples were obtained from each location in the first three states. Locations 12 and 18 comprise combinations of collections from adjacent fields of whorl-stage maize and sorghum. Sample size ranged from 25 to 300 FAW larvae per field. The number collected is corrected by subtracting the number that died from injury or unknown causes during the first days after collection. Collection data and percent infection by pathogens and nematodes is presented in Table 1. Larval mortality due to insect parasitoids is reported elsewhere (Molina-Ochoa et al., in press).

The larvae were placed individually in 30 cc plastic cups with pinto bean diet (Burton & Perkins 1989) and held in the laboratory to record the larvae infected by entomopathogens and mermithid nematodes. Mermithid nematodes that emerged from larvae were collected and placed in 70% alcohol. Larvae showing signs of virus infection or infection by microsporida were examined microscopically for occlusion bodies or spores. Microsporidian and virus infected tissues from field-collected insects were fixed in a modified Karnovsky's fixative, postfixed in OsO_4, and embedded in epoxy resin; sections were cut, stained and examined as described by Styer et al. (1987). The ascovirus was examined by negative-stain electron microscopy using methods described by Hamm et al. (1992). Ascovirus was diagnosed by the presence of vesicles in stunted larvae and transmitted to other larvae using a cactus spine (Hamm et al. 1986). Final identification was made by electron microscopy (Federici et al. 1991).

Dead larvae showing signs of fungus infection were placed in a plastic Petri dish (60 × 10 mm) lined with filter paper moistened with sterile distilled water, until the fungus sporulated on the insect surface. *Nomuraea rileyi* was isolated from dead larvae on medium composed of 200 ml of

TABLE 1. LOCATION, DATE, CROP, SAMPLE SIZE, AND TOTAL PERCENTAGE FALL ARMYWORM LARVAE INFECTED BY PATHOGENS AND MERMITHID NEMATODES COLLECTED FROM CORN (C) OR SORGHUM (S) IN THE MEXICAN STATES OF MICHOACÁN (M), COLIMA (C), JALISCO (J), AND TAMAULIPAS (T).

Code	Location	Date	Crop	No. coll.	Percentage infected
M 1	Jazmin	08/07/98	C	25	8.0
M 2	El Batillero	08/07/98	C	26	0.0
M 3	La Sidra	08/07/98	C	84	2.4
M 4	La Sidra	08/08/98	C	89	9.0
M 5	El Hueso	08/08/98	C	102	2.0
M 6	Carreras	08/08/98	C	109	0.9
C 7	Mezcales	08/12/98	C	143	3.5
C 8	Los Clomos	08/12/98	C	84	14.3
C 9	Cerro Colorado	08/13/98	C	121	9.2
C 10	El Bordo	08/13/98	C	114	17.5
C 11	Crucero de Tepames	08/13/98	C	89	10.1
C 12	Peña Blanca	08/13/98	C & S	219	13.2
C 13	El Narajito	08/14/98	C	171	6.4
J 14	Los Pozos	08/19/98	S	81	7.4
J 15	Apastepe	08/19/98	C	89	4.5
J 16	Los Depositos	08/19/98	C	89	3.4
J 17	Sayula	08/19/98	C	89	9.0
J 18	Sayula	08/20/98	C & S	177	4.5
J 19	Sayula	08/20/98	C (ears)	18	16.7
T 20	El Mante	09/22/98	S	300	0.3

"V8" vegetable juice, 3 g $CaCO_3$, 5 g glucose, 2 g yeast extract, 15 g agar, and 800 ml distilled water (Fargues & Rodriguez-Rueda 1980). Other fungal species were grown on Sabouraud-Dextrose agar enriched with 1% (w/v) yeast extract (SDAY), with 500 ppm chloramphenicol (Lezama-Gutiérrez et al. 1996) except the entomophthorales which were not isolated.

Isolation of Entomopathogens from Soil

Four soil samples, from corn or sorghum fields, were collected from each of 19 locations from the states of Michoacán, Colima, and Jalisco. In every location approximately 2 kg of soil was collected from four points a few meters apart by digging to a depth of 10-15 cm with a small spade. These subsamples were combined to form a sample. The soil samples were put in plastic bags and taken to the laboratory and stored at 25°C until processing. The storage time ranged from a few days to three weeks. For processing, the soil was thoroughly mixed and passed through a 0.4 mm mesh sieve to break or separate any coarse lumps of soil or litter.

In order to isolate the entomopathogenic fungi or nematodes, larvae of laboratory-reared *Galleria mellonella* (L.) were used as bait (Chandler et al. 1997; Bedding and Akhurst 1975). Four groups of sieved soil from each location were placed in plastic pots and five last instar bait larvae were released into each pot. Pots were incubated at room temperature (25°C) in the dark for 10 days (Zimmermann 1986; Woodring & Kaya 1988). Dead, intact larvae were removed and surface-sterilized in 1% sodium hypochlorite for 3 min, then washed three times in sterile distilled water and placed on damp filter paper within a sealed Petri dish 5.5 cm diameter, and incubated at 25°C for 12 days (Chandler et al. 1997). Entomopathogenic fungi were isolated from the bait larvae using SDAY, with 500 ppm of chloramphenicol (Lezama-Gutiérrez et al. 1996). The fungi were identified by microscopic inspection of morphological characteristics *in situ* or after isolation in SDAY, according to the criteria by Brady (1979) and Samson et al. (1988). Nematodes were separated to genera by identifying coloration of dead bait larvae according to Woodring and Kaya (1988).

To isolate *Bacillus thuringiensis* Berliner from the soil, 1 g samples from each location were placed in 50 ml of sterile distilled water in bioassay tubes, mixed for 3 min, and heated to 80°C for 10 min. After heating, 100 µl, of each sample, was placed on nutrient agar in four Petri dishes. Petri dishes were incubated at 30°C for 72 h, and colonies were microscopically examined after fixation and staining with methylene blue cotton. The presence of protein crystals was utilized as identification criteria of *B. thuringiensis*, according to Chaufaux et al. (1997).

RESULTS

Out of 2219 FAW larvae collected from 20 locations, the percentage infected by pathogens and mermithid nematodes ranged from 0 to 17.5 (Table

1), 77 larvae (3.47%) were killed by pathogens and 49 (2.21%) by mermithid nematodes. Four species of entomopathogenic fungi, represented by three Hyphomycetes, *Beauveria bassiana* (Bals.) Vuill., *Nomuraea rileyi* (F.) Samson, and *Hirsutella* sp., and one Zygomycete, Entomophthorales, were recovered (Table 2). *Nomuraea rileyi* was the most abundant and widely distributed fungus attacking FAW larvae in the three Western Mexican States and accounted for most of the pathogen-induced mortality of FAW larvae collected in Michoacán and Jalisco (Table 2). Two larvae infected with *B. bassiana* and a single larva infected by a member of the Entomophthorales were collected in Jalisco. A single larva infected with *Hirsutella* sp. was collected from Colima.

Mermithid infected FAW larvae were found only in the state of Colima and were more numerous than fungus infected larvae at 3 of the 7 locations.

Microsporida infected larvae were found predominately in Colima and were more numerous than fungus infected larvae at 4 of the 7 locations in Colima (Table 2). Collections from Michoacán and Jalisco had 1 and 2 microsporida infected larvae, respectively. All mortality appeared to be due to the same unidentified microsporidian which formed clumps of numerous thick-walled spores with no apparent sporophorous vesicle (Fig. 1A). The infected larvae showed no obvious symptoms prior to death, but after death were often dry and fragile, resembling the ash of a cigarette.

Four of five collections with rates of infection greater than ten percent were from the state of Colima (Table 1) and can be attributed to the higher rates of infection by mermithid nematodes and microsporidia in Colima than in the other states (Table 2). The only other collection with more than ten percent infection (J19) was a small collection of larvae from ears of corn in Jalisco which was entirely due to *Nomuraea rileyi*.

Two ascovirus infected larvae from Tamaulipas were the only virus infected larvae identified. The ascovirus (Fig. 1 B & C) resembled the ascovirus collected from FAW in Georgia and Florida, forming vesicles in the fat body but not in the epidermis or tracheal epithelium (Hamm et al. 1998).

Entomopathogens from Soil

The most numerous and widely distributed entomopathogen isolated from soil samples was *B. thuringiensis* which was isolated from 4 of 6 locations in Michoacán, 7 of 7 locations in Colima and 1 of 6 locations in Jalisco.

Three species of entomopathogenic fungi were recovered from soil samples. *Metarhizium anisopliae* was recovered from 5 locations, 2 of 7 from Colima and 3 of 6 from Jalisco. *Beauveria bassiana* was recovered from 4 locations, 1 from Michoacán, 1 from Colima, and 2 from Jalisco. *Paecilomyces fumosoroseus* was recovered from a single soil sample from Colima.

TABLE 2. PERCENTAGE OF FALL ARMYWORM LARVAE INFECTED BY VARIOUS PATHOGENS AT EACH LOCATION.

Code*	*N. r.*	*Ent.*	*Hir.*	*B. b.*	Mer.	Mic.	Asc.
M 1	8.0	0	0	0	0	0	0
M 2	0	0	0	0	0	0	0
M 3	2.4	0	0	0	0	0	0
M 4	9.0	0	0	0	0	0	0
M 5	1.0	0	0	0	0	1.0	0
M 6	0.9	0	0	0	0	0	0
C 7	2.1	0	0	0	1.4	0	0
C 8	9.5	0	0	0	2.4	2.4	0
C 9	0.8	0	0	0	4.1	4.1	0
C 10	0	0	0	0	14.9	2.6	0
C 11	0	0	0	0	0	10.1	0
C 12	1.4	0	0	0	9.1	2.7	0
C 13	1.8	0	0.6	0	1.8	2.3	0
J 14	6.2	0	0	1.2	0	0	0
J 15	3.4	0	0	0	0	1.1	0
J 16	2.2	0	0	0	0	1.1	0
J 17	6.7	1.1	0	1.1	0	0	0
J 18	4.5	0	0	0	0	0	0
J 19	16.7	0	0	0	0	0	0
T 20	0	0	0	0	0	0	0.7

*Locations are described in Table 1.

N. r. = *Nomuraea rileyi*, *Ent.* = *Entomophthora* sp., *Hir.* = *Hirsutella* sp., *B. b.* = *Beauveria bassiana*, Mer. = Mermithid nematode, Mic. = Microsporidia, Asc. = Ascovirus.

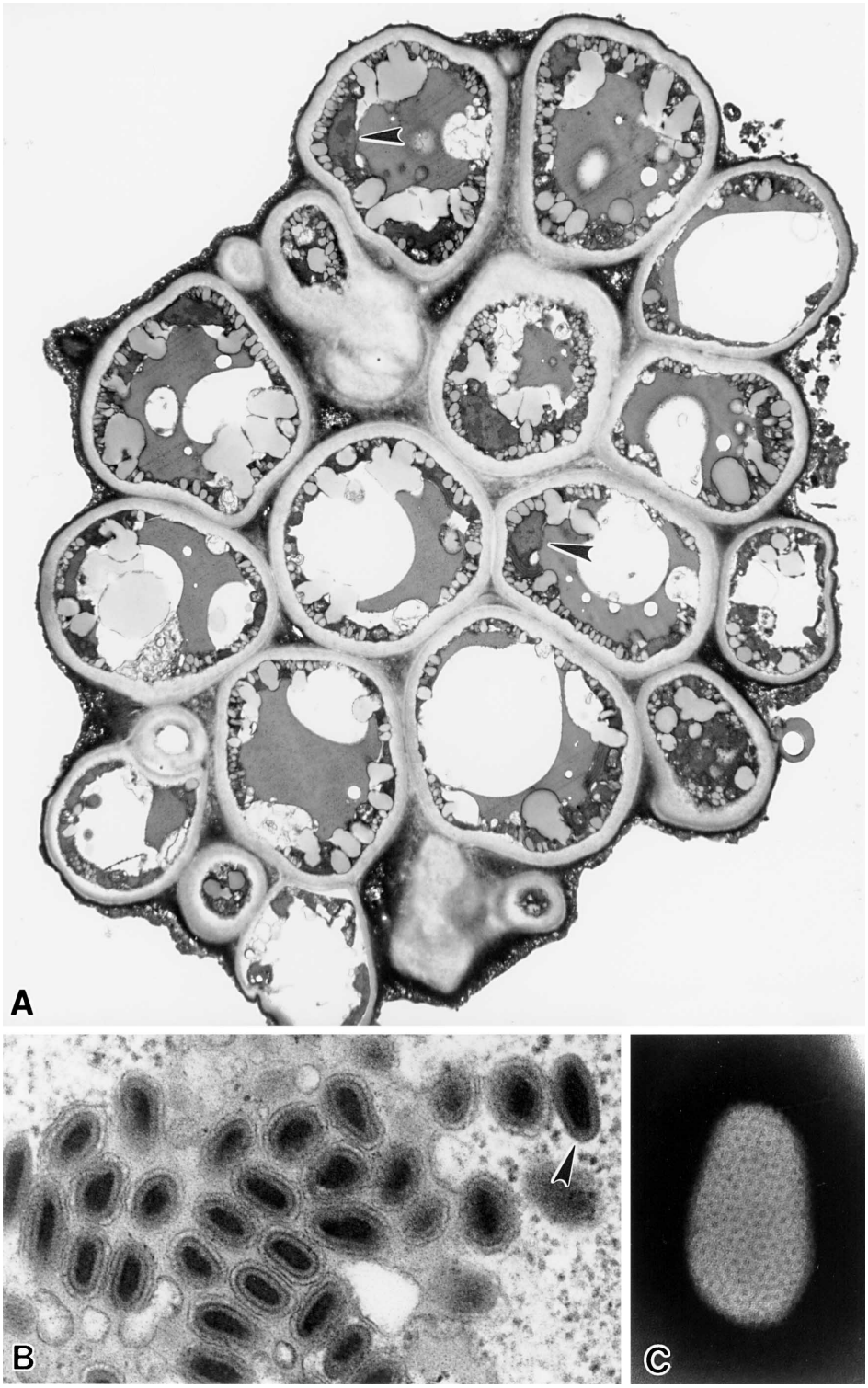

Fig. 1. A) Cluster of microsporidia spores from fall armyworm larva collected in Colima, Mexico, 6,200×, arrows pointing to nuclei. B & C) Ascovirus from fall armyworm larva collected in Tamaulipas, Mexico: B, Enlargement of viral inclusion body showing unenveloped virus (arrowhead) and enveloped virions 58,000×. C, negative stain of virion showing characteristic surface of envelop 150,000×.

Two genera of entomogenous nematodes were collected from soil samples. Steinernematid nematodes were collected from 3 of 4 locations in Michoacán and 1 location in Colima; heterorhabditid nematodes were collected from only one location in Colima.

DISCUSSION

Nomuraea rileyi is recognized as an important pathogen of many insect pests, especially lepidopteran larvae (Ignoffo 1981; Carruthers & Soper 1987), and has been reported infecting FAW in Puerto Rico, Colombia, Honduras, Mexico, and U.S.A. (Gardner & Fuxa 1980; Ignoffo 1981; Wheeler et al. 1989; Sánchez-Peña 1990; Pantoja & Fuxa 1992). *Entomophthora aulicae* was reported infecting FAW and other noctuid larvae in sorghum in Georgia (Hamm 1980). *Erynia radicans* was reported infecting FAW in Venezuela (Agudelo-Silva 1986).

Spodoptera frugiperda (= *Laphygma frugiperda*) has been reported to be infected by *Nosema laphygmae* Weiser, *Nosema trichoplusiae* Tanabe and Tamashiro and *Vairimorpha necatrix* (Kramer) (Bulla & Cheng 1977; Gardner & Fuxa 1980). *Nosema laphygmae* was described from larvae, pupae and adults from the vicinity of Caracas, Venezuela (Weiser 1959). *Vairimorpha necatrix* was reported naturally infecting FAW by Patel and Habib (1988). *Nosema trichoplusiae* was demonstrated to infect FAW in the laboratory. Unidentified microsporidia were reported from FAW in Louisiana by Fuxa (1982), in Venezuela by Agudelo-Silva (1986), and in Puerto Rico by Pantoja & Fuxa (1992). We did not find *Nosema* or *Vairimorpha* in our collections; the unidentified microsporidian that we found was obviously not in either of those genera based on the arrangement of spores. We were unable to infect FAW larvae using dried spores that were a few weeks old and thus were unable to study the developmental stages of the microsporidian.

The ascovirus isolated from FAW larvae collected in Tamaulipas is the first report of an ascovirus from Mexico. While the ascovirus can cause significant mortality in FAW (Hamm et al. 1986) it interferes with development of braconid parasitoids (Hamm et al. 1985). Although baculoviruses, nuclear polyhedrosis virus and granulosis virus, have been reported infecting FAW in many areas, they were not found in this survey. Fuxa (1982) reported that in Louisiana, NPV was more prevalent in fall armyworms infesting pastures than in those infesting corn or sorghum until mid July or early August, but the eventual infection rates were similar. He suggested that the lag in virus in corn and sorghum could be because rain and other physical agents cannot move the NPV from the soil reservoir to vegetation as easily as in grass. Also, the faster growth of corn or sorghum may produce more uncontaminated leaf surface and larvae may not move from plant to plant as readily as in pastures.

Mermithid nematodes have been reported infecting FAW in various parts of its range but have not been studied extensively. Valincente (1986) reported FAW attacked by mermithid nematodes in Brazil. Pair et al. (1986) reported an unidentified mermithid attacking FAW in South Carolina. Wheeler et al. (1989) reported *Hexamermis* sp. from FAW in Honduras where it made up 23% of the natural enemy complex of FAW on corn. *Hexamermis* has been reported to cause 8-100% FAW mortality in Mexico (Alcocer & Méndez 1965) and over 50% FAW mortality in Nicaragua (Van Huis 1981).

Steinernema riobravis is an important control agent for prepupae and pupae of FAW and corn earworm, *Helicoverpa zea* (Boddie), in cornfields of the Lower Rio Grande Valley (Raulston et al. 1992; Cabanillas et al. 1994) where the nematode appears to be naturally selected for the subtropical semi-arid environment.

The distribution of the various entomopathogens indicates a potential for increasing biological control by moving some of the pathogens and nematodes from one area to another. Additional research is needed on the identification and biology of the microsporidian and the mermithid nematode to determine their potential for biological control. Also, additional research is needed to determine the species and strains of the entomopathogenic nematodes, Steinernematidae and Heterorhabditidae, isolated from the soil and their potential for biological control of fall armyworm.

ACKNOWLEDGMENTS

This project was supported in part by Specific Cooperative Agreement #58-6602-7-F101 between the United States Department of Agriculture, Agricultural Research Service and the Universidad de Colima, Mexico.

REFERENCES CITED

AGUDELO-SILVA, F. 1986. Naturally occurring pathogens of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) larvae collected in Venezuela. Florida Entomol. 69: 768-769.

ALCOCER, G. L. AND V. M. MÉNDEZ. 1965. Estudios preliminares sobre parasitismo en larvas de *Laphygma frugiperda* Smith y Abbot, por un nemátodo de la familia Mermithidae. Fitófilo 18: 5-20.

BEDDING, R. A., AND R. A. AKHURST. 1975. A simple technique for the detection of insect parasitic rhabditid nematodes in soil. Nematologica 21: 109-110.

BRADY, B. L. K. 1979. CMI Description of Pathogenic Fungi and Bacteria, Sets 61 and 62 (Nos. 601-620), Commonwealth Mycological Institute, England, UK.

BULLA, L. A., JR., AND T. C. CHENG. 1977. Comparative Pathobiology Vol. 2 Systematics of the Microsporidia. Plenum Press, New York, 510 pp.

BURTON, R. L., AND W. D. PERKINS. 1989. Rearing the corn earworm and fall armyworm for maize resis-

tance studies. pp. 37-45. *In* CIMMYT. 1989. Toward insect resistant maize for the third world host plant resistance to maize insects. CIMMYT, Mexico.

CABANILLAS, H. E., G. O. POINAR JR. AND J. R. RAULSTON. 1994. *Steinernema riobravis* n. sp. (Rhabditida: Steinernematidae) from Texas. Fundam. Appl. Nematol. 17: 123-131.

CARRUTHERS, R. I., AND R. S. SOPER. 1987. Fungal Diseases. pp. 357-416. *In* J. R. Fuxa and Y. Tanada (eds.). Epizootiology of Insect Diseases. John Wiley & Sons, New York.

CHANDLER, D., D. HAY, AND A. P. REID. 1997. Sampling and occurrence of entomopathogenic fungi and nematodes in UK soils. Applied Soil Ecol. 5: 133-141.

CHAUFAUX, J., M. MARCHAL, N. GILOOIS, I. JEHANNO, AND C. BUISSON. 1997. Recherche de souches naturelles du *Bacillus thuringiensis* dans diféentes biotopes, à travers le monde. Canadian J. Mirobiol. 43: 337-343.

FARGUES, J., AND D. RODRIGUEZ-RUEDA. 1980. Sensibilité des larves de *Spodoptera littoralis* (Lepidoptera: Noctuidae) aux hyphomycètes entomopathogènes *Nomuraea rileyi* et *Pacilomyces fumosoroseus*. Entomophaga 25: 43-54.

FARGUES, J., N. K. MANIANIA, J. C. DELMAS, AND N. SMITS. 1992. Influence de la température sur la croissance *in vitro* d'hyphomycètes entomopathogènes. Agronomie 12: 557-564.

FEDERICI, B. A., J. J. HAMM, AND E. L. STYER. 1991. Ascoviridae. *In* J. R. Adams and J. R. Bonami (eds.). Atlas of Invertebrate Viruses. CRC Press Inc., Boca Raton.

FUXA, J. R. 1982. Prevalence of viral infection in populations of fall armyworm, *Spodoptera frugiperda*, in Southeastern Louisiana. Environ. Entomol. 11: 239-242.

GARDNER, W. A., AND J. R. FUXA. 1980. Pathogens for the suppression of the fall armyworm. Florida Entomol. 63: 439-447.

HAMM, J. J. 1980. Epizootics of *Entomophthora aulicae* in lepidopterous pests of sorghum. J. Invertebr. Pathol. 36: 60-63.

HAMM, J. J. 1984. Invertebrate pathology and biological control. J. Georgia Entomol. Soc. 19: 6-13.

HAMM, J. J., D. A. NORDLUND, AND O. G. MARTI. 1985. Effects of a nonoccluded virus of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on the development of a parasitoid, *Cotesia marginiventris* (Hymenoptera: Braconidae). Environ. Entomol. 14: 258-261.

HAMM, J. J., S. D. PAIR, AND O. G. MARTI. 1986. Incidence and host range of a new ascovirus isolated from fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Florida Entomol. 69: 524-531.

HAMM, J. J., E. L. STYER, AND W. J. LEWIS. 1992. Three viruses found in the braconid parasitoid *Microplitis croceipes* and their implications in biological control programs. Biol. Control 2: 329-336.

HAMM, J. J., E. L. STYER, AND B. A. FEDERICI. 1998. Comparison of field-collected ascovirus isolates by DNA hybridization, host range, and histopathology. J. Invertebr. Pathol. 72: 138-146.

HUGHES, P. R., H. A. WOOD, J. P. BURAND, AND R. R. GRANADOS. 1984. Quantification of the dose-mortality response to *Trichoplusia ni, Heliothis zea,* and *Spodoptera frugiperda* to nuclear polyhedrosis viruses: Applicability of an exponential model. J. Invertebr. Pathol. 43: 343-350.

IGNOFFO, C. M. 1981. The fungus *Nomuraea rileyi* as a microbial insecticide. pp. 513-538. *In* H. D. Burges (ed.). Microbial Control of Pests and Plant Diseases. Academic Press, New York.

LEZAMA-GUTIÉRREZ, R., R. ALTORRE-ROSAS, L. F. BOJALIL-JABER, J. MOLINA-OCHOA, M. ARENAS-VARGAS, M. GONZÁLEZ-RAMÍREZ, AND O. REBOLLEDO-DOMÍNGUEZ. 1996. Virulence of five entomopathogenic fungi (Hyphomycetes) against *Spodoptera frugiperda* (Lepidoptera: Noctuidae) eggs and neonate larvae. Vedalia 3: 35-39.

MIETKIEWSKI, R. T., J. K. PELL, AND S. J. CLACK. 1997. Influence of pesticide use on the natural occurrence of entomopathogenic fungi in arable soils in the UK. Field and laboratory comparisons. Biocontrol Sci. Technol. 7: 565-575.

MOLINA-OCHOA, J., J. J. HAMM, R. LEZAMA-GUTIÉRREZ, L. F. BOJALIL-JABER, M. ARENAS-VARGAS, AND M. GONZÁLES-RAMÍREZ. 1996. Virulence of six entomopathogenic nematodes (Steinernematidae and Heterorhabditidae) on immature states of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Vedalia 3: 25-29.

MOLINA-OCHOA, J., J. J. HAMM, R. LEZAMA-GUTIÉRREZ, M. LÓPEZ-EDWARDS, M. GONZÁLES-RAMÍREZ, AND A. PESCADOR-RUBIO. 2001. A survey of fall armyworm (Lepidoptera: Noctuidae) parasitoids in the Mexican states of Michoacán, Colima, Jalisco, and Tamaulipas. Florida Entomol. (in press).

PAIR, S. D., J. R. RAULSTON, A. N. SPARKS, AND P. B. MARTIN. 1986. Fall armyworm (Lepidoptera: Noctuidae) parasitoids: differential spring distribution and incidence on corn and sorghum in the Southeastern Unites States and Mexico. Environ. Entomol. 15: 342-348.

PANTOJA, A., AND J. R. FUXA. 1992. Prevalence of biotic control agents in the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). Folia Entomol. Mexico 84: 79-84.

PATEL, P. N., AND M. E. M. HABIB. 1988. Protozoosis caused by *Vairimorpha necatrix* Microsporida Nosematidae in larvae of *Spodoptera frugiperda* Lepidoptera Noctuidae. Rev. Bras. Zool. 5: 593-598.

RAULSTON, J. R., S. D. PAIR, J. LOREA, AND H. E. CABANILLAS. 1992. Prepupal and pupal parasitism of *Helicoverpa zea* and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) by *Steinernema* sp. in cornfields in the Lower Rio Grande Valley. J. Econ. Entomol. 85: 1666-1670.

REMILLET, M., AND J. F. SILVAIN. 1988. *Noctuidonema guyanense* n. g., n. sp. (Nematoda: Alphelenchoididae) ectoparasite de noctuelles du genre *Spodoptera* (Lepidoptera: Noctuidae). Revue Nématol. 11: 21-24.

RICHTER, A. R., AND J. R. FUXA. 1990. Effect of *Steinernema feltiae* on *Spodoptera frugiperda* and *Heliothis zea* (Lepidoptera: Noctuidae) in corn. J. Econ. Entomol. 83: 1286-1291.

ROGERS, C. E., AND O. G. MARTI. 1992. Infestation and dispersal of *Noctuidonema guyanense* (Nematoda: Aphelenchoididae) on *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Environ. Entomol. 21: 417-421.

SAMSON, R. A., H. C. EVANS, AND J. P. LATGÉ. 1988. Atlas of entomopathogenic fungi. 187 pp. Springer-Verlag, Berlin, Germany.

SÁNCHEZ-PEÑA, S. R. 1990. Some insect and spider pathogenic fungi from Mexico with data on their host ranges. Florida Entomol. 73: 517-522.

SOSA-GOMEZ, D. R., AND F. MOSCARDI. 1994. Effect of till and no-till soybean cultivation on dynamics of entomopathogenic fungi in the soil. Florida Entomol. 77: 284-287.

STEINHAUS, E. A., AND G. A. MARSH. 1962. Report of diseases of insects, 1951-1961. Hilgardia 33: 349-390.

STYER, E. L., J. J. HAMM, AND D. A. NORDLUND. 1987. A new virus associated with the parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae): Replication in noctuid host larvae. J. Invert. Pathol. 50: 302-307.

VALINCENTE, F. H. 1986. Occurrence of entomogenous nematode Mermithidae in fall armyworm *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae), in Sete Lagoas, MG. An. Soc. Entomol. Brazil 15: 391-393.

VAN HUIS, A. 1981. Integrated pest management in the small farmer's maize crop in Nicaragua. Med. Land. 81-6: 93-100.

VANNINEN, I. 1996. Distribution and occurrence of four entomopathogenic fungi in Finland: Effect of geographical location, habitat type and soil type. Mycol. Res. 100: 93-101.

WEISER, J. 1959. *Nosema laphygmae* n. sp. and the internal structure of the microsporidian spore. J. Insect Pathol. 1: 52-59.

WHEELER, G. S., T. R. ASHLEY, AND K. L. ANDREWS. 1989. Larval parasitoids and pathogens of the fall armyworm in Honduran maize. Entomophaga. 34: 331-340.

WISEMAN, B. R., C. F. WASSOM, AND R. H. PAINTER. 1967. An unusual feeding habit by the fall armyworm, *Spodoptera frugiperda* (J. E. Smith). Agron. J. 59: 279-281.

WISEMAN, B. R., F. M. DAVIS, W. P. WILLIAMS, AND N. W. WIDSTROM. 1996. Resistance of a maize population, FAWCC(C5), to fall armyworm larvae (Lepidoptera: Noctuidae). Florida Entomol. 79: 329-336.

WOODRING, J. L., AND H. K. KAYA. 1988. Steinernematid and Heteorhabditid Nematodes: A handbook of techniques. Southern Cooperative Series Bulletin 331. 30 pp. Arkansas Agricultural Experiment Station, Fayetteville, Arkansas.

ZIMMERMANN, G. 1986. *Galleria* bait method for detection of entomopathogenic fungi in soil. Zietschrift fur Argewandte Entomologie 2: 213-215.