SEASONAL CHRONOLOGY OF *NOCTUIDONEMA*, AN ECTOPARASITIC NEMATODE OF ADULT MOTHS, IN TROPICAL AND SUBTROPICAL AMERICA

A. M. Simmons, C. E. Rogers, K. U. Buckmire[1], B. Gray[2], K. D. Monkman[3], A. Pantoja[4], J. R. Raulston[5], and V. H. Waddill[6]
Insect Biology and Population Management Research Laboratory,
Agricultural Research Service, U.S. Department of Agriculture,
Tifton, Georgia 31793-0748

Abstract

Male moths of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), were examined for *Noctuidonema guyanense* Remillet and Silvain, an ectoparasitic nematode of adult Lepidoptera, during a 1-year (mid-September 1988 to mid-September 1989) study at locations in tropical and subtropical America (Hamilton, Bermuda; Belle Glade, Florida; St. Georges, Grenada; Panama, Republic of Panama; Isabela, Puerto Rico; and Weslaco, Texas) and in Tifton, Georgia. Host parasitism and nematode population density varied among locations and over time. Overall parasitism of *S. frugiperda* males averaged about 30%, with about 30 nematodes per parasitized moth. However, parasitism averaged 77% in Grenada, but only about 1% in Texas. Nematodes were more numerous at lower latitudes than higher latitudes. Nematode densities were correlated with temperature and humidity. However, because seasonal fluctuations of nematode populations occurred at locations with fairly stable climatic conditions, other factors (e.g., host migration and age of the host) may also affect the nematode populations.

Resumen

Machos adultos del gusano cogollero, *Spodoptera frugiperda* (J. E. Smith), fueron examinados para determinar la presencia de *Noctuidonema guyanense* Remillet y Silvain, un nematodo parasítico de adultos lepidopteros. El estudio se realizó durante un año (Septiembre 1988 a Septiembre 1989) en siete localidades de América tropical y subtropical (Hamilton, Bermuda; Belle Glade, Florida; Tifton, Georgia; St Georges, Grenada; Panama, Republic of Panama; Isabela, Puerto Rico; y Weslaco, Texas). El parasitismo y la densidad poblacional del nematodo fueron diferentes entre localidades y cambiaron a traves del tiempo. El promedio de parasitismo en machos de *S. frugiperda* fue del 30 % con approximadamente 30 nematodos por adulto. En contraste, el parasitismo alcanzó hasta el 77 % en Grenada, pero sólo 1 % en Texas. Se encontró un número mayor de nematodos en latitudes bajas que en latitudes altas. La población de nematodos está corelacionó con humedad y temperatura. Fluctuaciones estacionales observadas en la población de los nematodos en localidades con condiciones climáticas estables, sugieren que otros factores (migración y edad del hospedero) pueden también afectar las poblaciones del nematodo.

---

[1]Caribbean Agricultural Research & Development, Ministry of Agriculture Botanical Gardens, P. O. Box 431, St. Georges, Grenada, W. I.
[2]Universidad de Panama, Facultad de Ciencias Agropecuarias, CEIAT, Ciudad Universitaria Octavio Mendez Pereira, Panama City, Republic of Panama.
[3]Department of Agriculture & Fisheries, Botanical Gardens, P. O. Box HM834, Hamilton HJMCX, Bermuda.
[4]Formerly, University of Puerto Rico, Mayaguez Campus and Agricultural Experiment Station; Currently, CIAT Rice Program, Apartado Aereo 6713, Cali, Colombia, S. A.
[5]USDA-ARS-SARL, 2413 East Highway 83, P. O. Box 267, Weslaco, Tex. 78596.
[6]Everglades Research and Education Center, P. O. Box Drawer A, Belle Glade, Fla. 33430.

Ectoparasitic nematodes have rarely been found on adult insects. Hunt (1980) found the first known ectoparasitic nematode of an adult arthropod occurring on a cockroach (*Periplaneta americana* (L.)) in Saint Lucia, West Indies, but there was no additional published report regarding that nematode. Subsequently, an ectoparasitic nematode, *Noctuidonema guyanense* Remillet and Silvain (Nematoda: Aphelenchoididae), was found on adults of several species of Lepidoptera, including the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), in French Guiana (Remillet & Silvain 1988, Rogers et al. 1990). *N. guyanense* was later recovered from *S. frugiperda* throughout tropical and subtropical America (Simmons & Rogers 1990a). This nematode lives only on adult moths and is transmitted during host mating (Remillet & Silvain 1988, Rogers et al. 1990, Simmons & Rogers 1990b). In the United States, the fall armyworm has overlapping generations year-round in south Florida and in south Texas; it does not diapause, and usually does not survive the winter north of these border areas (Luginbill 1928, Snow & Copeland 1969). When the fall armyworm migrates northward in the United States during the spring and early summer, *N. guyanense* is carried with it (Simmons & Rogers 1991). As the season advances, prevalence and density of the transported nematodes increases and then decreases during the fall; however, overlapping host generations are necessary for continuous maintenance of this nematode (Simmons & Rogers 1991). Data on incidence and density of *N. guyanense* have been collected, but samples were generally only made within one month per location and collection dates were not synchronized among locations in a survey at 22 tropical and subtropical locations where the fall armyworm has overlapping generations year-round (Simmons & Rogers 1990a).

To obtain a thorough understanding of the seasonal chronology of *N. guyanense*, data were needed using coinciding collecting dates from locations where the hosts occur year-round. The objective of this study was to obtain information on the seasonal chronology of *N. guyanense* at locations where the fall armyworm (an economically important pest in the Americas) has year-round overlapping generations.

Materials and Methods

Moths of *S. frugiperda* were collected and handled as described by Simmons & Rogers (1991), except as noted below. From mid-September 1988 to mid-September 1989, specimens of adult male fall armyworms were collected at six locations in tropical and subtropical America: Hamilton, Bermuda; Belle Glade, Fla.; St. Georges, Grenada; Panama, Republic of Panama; Isabela, Puerto Rico; and Weslaco, Tex., as well as in Tifton, Ga. (Fig. 1). Additional collections were made at Fortuna and Vega Baja, Puerto Rico; these data were combined with data collected at Isabela, Puerto Rico. Fall armyworm moths can normally be found year-round at all of these locations, excluding Tifton. Tifton was selected for a comparison with the warmer locations.

There were 18 specific collection weeks: 19-23 September, 10-14 October, 31 October - 4 November, 21-25 November, 12-16 December, 2-6 January, 23-27 January, 13-17 February, 6-10 March, 27-31 March, 17-21 April, 8-12 May, 29 May - 2 June, 19-23 June, 10-14 July, 31 July - 4 August, 21-25 August, and 11-15 September, starting in 1988 and ending in 1989. The number of moths recovered for examination per sampling period from each location is shown in Table 1. Nematode counts were for adults and juveniles combined. Mean daily temperature, relative humidity, and rainfall data were averaged over 21 d preceding each sampling period. Vapor pressure deficiency was used as an index of humidity. Voucher specimens from each location were deposited with the USDA Nematode Collection, Beltsville, Md.

Data were analyzed using SAS (SAS Institute 1985) computations. Percentage infestation data were analyzed after arcsine transformation; log transformation, base 10, was used before analysis of the nematode population data. Means presented herein are for back-transformed data. Unless stated otherwise, $P < 0.05$ level of significance was used.

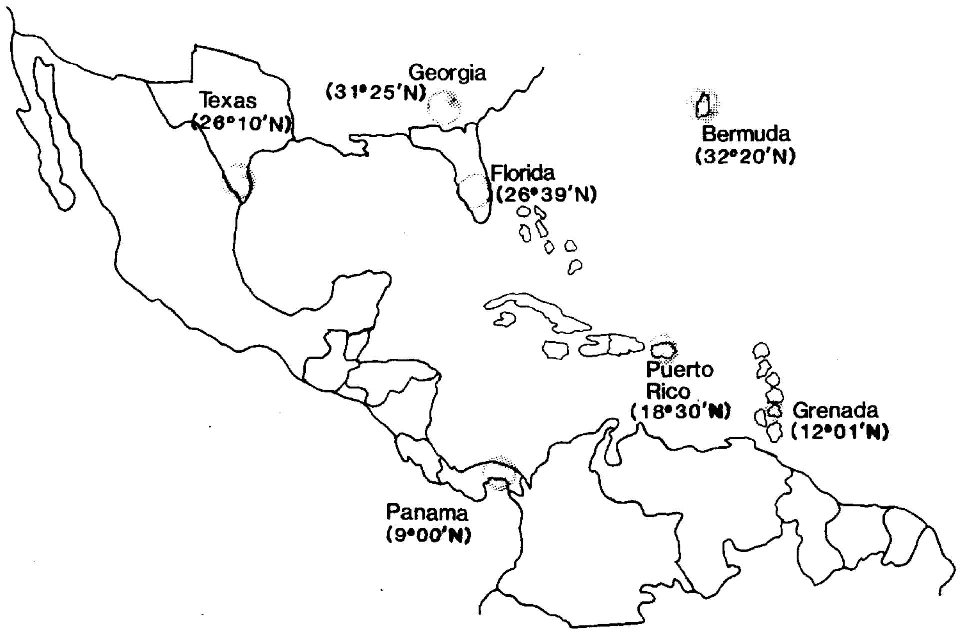

Fig. 1. Locations, with corresponding latitudes, where male *S. frugiperda* moths were sampled for *Noctuidonema* from mid-September 1988 to mid-September 1989.

Results and Discussion

Although our objective was to examine 50 male fall armyworm moths per sampling week per location, frequently, fewer than 50 moths or occasionally no moths were recovered. Also, the preservative fluid leaked from a few vials (maximum of 3 samples per location per week) during shipment, rendering collected specimens unsuitable for examination. Traps were checked as scheduled, but moths were recovered only during one period (mid-December) at Vega Baja and at 5 periods (mid-September to mid-December 1988) at Fortuna, Puerto Rico. Data of coinciding periods for the 3 locations in Puerto Rico were similar and were therefore combined. Each sample size in Table 1 between 1 and 47 may be interpreted as the relative number of moths collected during or near a designated sampling week. However, because of the limit of 50 moths for examination and because no attempt was made to collect moths during some weeks, the association between moth captures and moth populations is partially obscured. Snow et al. (1968) reported sharp peaks about every 4-5 weeks in number of fall armyworm moths captured in pheromone traps in St. Croix, U.S. Virgin Islands, and noted that although populations overlapped year-round, temperature did not influence the fluctuation in trapping data.

The overall percent parasitism of *S. frugiperda* by *N. guyanense* varied among locations, but averaged around 30% (Table 2). Two notable exceptions were 77% parasitism in Grenada and 1% in Texas. Nematode population density averaged about 30 nematodes per parasitized moth at each location (Table 2). However, the mean number of nematodes per parasitized moth was 13 in Georgia, 38 in Puerto Rico and 44 in Grenada.

Percent *S. frugiperda* parasitism and the number of nematodes per host in this study were similar to levels seen at 22 other tropical and subtropical locations during a brief collecting period during 1987/88 (Simmons & Rogers 1990a). There was a positive correlation between the number of nematodes per host and percentage of *S. frugiperda* parasitized ($P < 0.05$). Simmons & Rogers (1990a) also found such a relationship with

TABLE 1. NUMBER OF MALE *S. FRUGIPERDA* MOTHS EXAMINED FOR *NOCTUIDONEMA* DURING SPECIFIC WEEKS (FROM MID-SEPTEMBER 1988 TO MID-SEPTEMBER 1989) AT SELECTED TROPICAL AND SUBTROPICAL LOCATIONS.

	Number of moths examined per designated period																	
Location	Sept. 19-23	Oct. 10-14	O-N 31-4	Nov. 21-25	Dec. 12-16	Jan. 2-6	Jan. 23-27	Feb. 13-17	Mar. 6-10	Mar. 27-31	Apr. 17-21	May 8-12	M-J 29-2	June 19-23	July 10-14	J-A 31-4	Aug. 21-25	Sept. 11-15
Bermuda	50	50	50	48	50	49	49	50	48	49	50	25	50	—	49	49	49	48
Florida	27	50	49	50	100	0	0	0	50	50	49	—	50	50	50	47	50	10
Georgia	10	10	12	10	0	28	10	13	12	11	1	2	68	45	57	64	30	31
Grenada	—	—	37	6	75	4	9	76	5	42	50	28	10	3	6	7	0	49
Panama	22	6	0	0	0	0	0	0	0	0	0	16	14	50	50	0	0	50
Puerto Rico	61	73	55	52	28	6	0	50	4	1	15	0	50	0	0	0	50	46
Texas	0	20	49	42	0	42	43	2	0	0	0	46	40	50	1	43	20	15

Dash (—) indicates no attempt was made to collect moths.

TABLE 2. PREVALENCE AND NUMBER OF *NOCTUIDONEMA* ON MALE *S. FRUGIPERDA* MOTHS AT SELECTED TROPICAL AND SUBTROPICAL AMERICAN LOCATIONS FROM MID-SEPTEMBER 1988 TO MID-SEPTEMBER 1989 (±SEM).

Location	No. moths examined	Mean % parasitism	Mean no. nematodes per infested moth
Bermuda	813	24.0 ± 1.5	26.8 ± 3.5
Florida	682	38.0 ± 1.8	25.6 ± 3.1
Georgia	414	20.0 ± 2.0	13.1 ± 2.2
Grenada	407	77.4 ± 2.1	43.5 ± 3.8
Panama	208	34.6 ± 3.3	26.3 ± 5.7
Puerto Rico	471	46.6 ± 2.3	37.9 ± 4.6
Texas	413	1.2 ± 0.5	27.8 ± 2.5

field-collected moths in the tropical and subtropical Americas. The prevalence of *N. guyanense* infestation and number of nematodes per host were not consistent over time, although data were more variable at some locations than at others.

In Georgia, the number of nematodes per moth in the fall of 1988 declined to zero as the season progressed (Fig. 2). From 1 November 1988 to late May 1989, none of the collected moths in Georgia was parasitized (Fig. 2). Thereafter, there was an increase in both the prevalence and number of *N. guyanense* per host. The winter of 1988-89 was warmer than most winters in Georgia. Consequently, a few fall armyworm moths were collected throughout much of the winter, although some of those moths may have resulted from emigration from southern locations rather than from local emergence. Local moth populations, not overlapping during the winter months, could result in a long period of zero parasitism because an adult host is required for the nematode. Asynchrony of populations of parasitized and non-parasitized moths may also help explain the reduction in parasitism during the late fall. Nematode population and rate of parasitism peaked during late summer of 1989 in Georgia. Similarly, Simmons & Rogers (1991) reported a peak in nematode activity during mid-to-late-August in Georgia in 1988.

Populations of *N. guyanense* in locations extending from Bermuda to Puerto Rico in the Caribbean Basin, as well as Georgia, had low numbers in winter which became higher in spring and summer (Fig. 2). There was a reduction in Bermuda's populations during the winter; the effect was lessened southward from Florida to Puerto Rico, but not in Grenada. Also, as in Georgia, moths were collected throughout most of the year in south Texas. However, parasitized moths were only collected during two weeks in 1989, in late May/early June and in late August. The number of nematodes on *S. frugiperda* averaged 28 per infested moth during the restricted collecting period in Texas. There was much more nematode activity on *S. frugiperda* in Panama than in Texas. During the first sampling date in Panama, none of the collected moths was parasitized, and only one of 6 specimens during the next sampling period was parasitized. (Thereafter, data are missing for several sampling weeks.) However, parasitism of *S. frugiperda* in Panama declined from a high of about 85% in early-May 1989 to a low of about 20% in mid-September 1989. Simmons & Rogers (1990a) also reported higher parasitism and more nematodes on *S. frugiperda* at locations in the Caribbean Basin than at locations on the mainland of tropical and subtropical America (from Colombia, South America to southern Texas).

Across all locations, percent parasitism and the number of nematodes per moth were positively correlated ($P < 0.001$, $r^2 = 0.57$ and $P < 0.05$, $r^2 = 0.42$, respectively) with temperature, but less association occurred with mean vapor pressure deficiency. An analysis of data from each location suggests that temperature was correlated with pop-

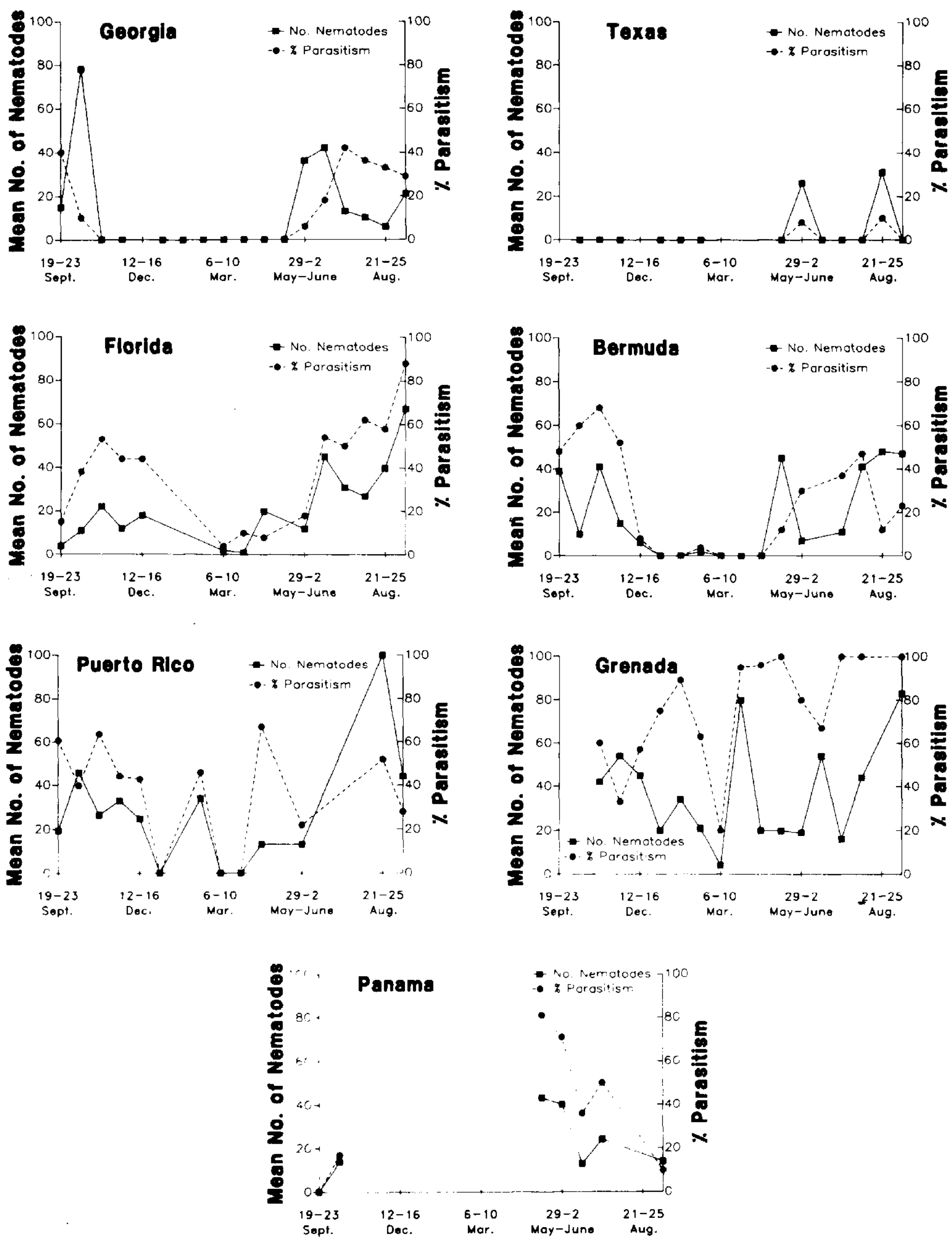

Fig. 2. Prevalence and mean number of *Noctuidonema* per infested *S. frugiperda* moth at sample locations from mid-September 1988 to mid-September 1989.

ulations more at some locations, e.g., Georgia, than at others, e.g., Puerto Rico (Table 3). In general, temperature appeared to be more closely related to nematode abundance than was humidity, although humidity data were only available for 4 locations. The importance of temperature was apparently more pronounced at higher latitudes (Georgia, Bermuda, and Florida) than lower latitudes (Puerto Rico, Grenada and Panama). Locations in lower latitudes were characterized by less extreme daily and seasonal temperature fluctuations as well as by warmer overall temperature. There was high fidelity

TABLE 3. CORRELATION OF PREVALENCE AND NUMBER OF *NOCTUIDONEMA* PER INFESTED *S. FRUGIPERDA* MOTH WITH MEAN TEMPERATURE, MEAN RELATIVE HUMIDITY, OR RAINFALL AT SELECTED TROPICAL AND SUBTROPICAL LOCATIONS IN 1988-1989.

	Temperature			Vapor Pressure Deficiency			Rainfall		
		Correlation coeff.[a]			Correlation coeff.[a]			Correlation coeff.[a]	
Location	Mean	% parasitism	No. of nematodes	Mean	% parasitism	No. of nematodes	Total (mm)	% parasitism	No. of nematodes
Bermuda	22.8	0.73***	0.75*	4.52	0.48†	0.19	1,291	0.50*	0.01
Florida	23.3	0.58*	0.65*	3.13	0.35	0.05	747	0.57*	0.60*
Georgia	19.7	0.83*	0.69†	4.48	0.47†	0.03	1,098	0.58*	0.35
Grenada	26.7	0.58*	0.16	7.52	0.53*	0.08	1,870	0.22	0.33
Panama	26.4	0.65	0.45	—	—	—	1,945	-0.78*	0.10
Puerto Rico	24.4	0.53†	0.44	—	—	—	1,508	0.22	0.34
Texas	25.6	0.28	ne	—	—	—	279	0.19	ne

[a]Correlation coefficients; †, significant at $P < 0.1$; *, significant at $P < 0.05$; *** significant at $P < 0.001$; ne = not estimable; — indicates missing data; number of nematodes are per parasitized moth.

between the nematode populations and temperature at the more northerly sites (Georgia, Bermuda, and Florida). For example, in Bermuda (Fig. 2), the decline in nematode population occurred with a decrease in temperature during the winter months, but as the temperature increased during the following spring, the number of nematodes and percent parasitism likewise increased. In the laboratory, Simmons & Rogers (1990b) substantiated that *N. guyanense* is adapted for a tropical environment; it does best at high temperature and high relative humidity. They found that a temperature of less than 20°C or low relative humidity (about 20%) were not favorable for either growth or survival of *N. guyanense*. Climatological effects on the nematode could not be adequately evaluated for the Texas location because parasitized moths were collected only on two dates.

Although we feel that temperature and humidity have large effects on *N. guyanense* populations, other factors undoubtedly affect its bionomics as well. For example, the age of the moths or moth migration may be involved. Over time, the population of *N. guyanense* on a host increases because of nematode development and reproduction (Simmons & Rogers 1990b). As the fall armyworm ages, its incidence of mating events increases, hence, increasing its probability of acquiring or disseminating nematodes. During periods of significant moth emergence, the majority of moths within a population would be virgin or would have mated only a few times. Consequently, moths collected from a newly-emerged population may have zero or a low rate of parasitism and harbor zero or a few nematodes. With overlapping generations, captured moths were of different ages on a given day. Thus, we also attribute some of the large variation in nematode populations among moths and among dates to age differentials among collected moths. Older moths were more likely to have been parasitized, and were more likely to harbor more nematodes, resulting from nematode reproduction, than were younger moths. We made no attempt to determine the relative age or mating status of the moths collected during this study. Nevertheless, observations indicated that moths which looked newly-emerged, i.e., with most of their scales still intact, were the least likely to have a high density of nematodes. Yet, at locations where parasitism was high throughout the year (e.g., Grenada), numerous fresh-looking moths also harbored nematodes. During the winter months in Georgia, when no nematodes were recovered, many captured moths appeared to be newly-emerged. Conversely, in Texas, where nematodes were recovered only from a few moths during the spring/summer months, both fresh-looking and worn moths were collected. Apparently, moth immigration was an important factor in reintroducing nematodes to Texas. Similarly, the parasitized moths which appeared in Georgia in late May were most likely immigrants (Pair & Sparks 1986, Pair et al. 1986).

Across all locations, percent parasitism but not number of nematodes was positively correlated ($P < 0.05$, $r^2 = 0.28$) with rainfall. However, the importance of rainfall was not consistently evident at each location (Table 3). Parasitism was negatively correlated with rainfall in Panama, which received more rainfall than any other location. On the other hand, nematode abundance was positively correlated with rainfall in Florida, and percent parasitism with rainfall in Bermuda, Georgia, and Florida. Numerous *N. guyanense* were found in the preservative fluid of the storage vials, but we do not know if significant numbers may be washed from the host by rainfall. Eggs and some nematodes are not as easily removed from the host because of their association with sticky material and concealment within the intersegmental folds of the abdomen (Marti et al. 1990).

In summary, *N. guyanense* population fluctuations during the year were correlated with variations in temperature and humidity, with other factors also likely being important. Hence, the seasonal chronology of *N. guyanense* may vary among locations. We found little association of humidity with nematode populations. Most locations were humid, and relative humidity fluctuations during the year were usually not dramatic; similarly, temperature varied little at the more tropical locations. We had hoped to compare humidity effects on *N. guyanense* from the more arid Texas location with the effects from more humid locations, but parasitism of *S. frugiperda* at the former location was too low. These field data, coupled with laboratory studies (e.g., Simmons & Rogers 1990b) provide vital basic information to help us understand the field biology of *N. guyanense* on *S. frugiperda* and other pest lepidopterans. However, much additional research, including the impact of *N. guyanense* on host survival, host migratory ability, etc., in the laboratory and field are needed to ascertain its utility as a natural enemy in pest management schemes.

ACKNOWLEDGMENT

The authors thank R. A. Franqui and H. Ruiz for collecting moths in Puerto Rico. The mention of a commercial or proprietary product does not constitute an endorsement of this product by the USDA.

REFERENCES CITED

HUNT, D. J. 1980. *Acugutturus parasiticus* n.g., n.sp., a remarkable aphelenchoid nematode from *Periplaneta americana* (L.), with proposal of Acugutturinae n. subf. Syst. Parasit. 1: 167-170.

LUGINBILL, P. 1928. The fall army worm. USDA Tech. Bull. 34: 1-92.

MARTI, O. G., C. E. ROGERS, J. F. SILVAIN, AND A. M. SIMMONS. 1990. Pathological effects of an ectoparasitic nematode *Noctuidonema guyanense* Remillet and Silvain (Nematoda: Aphelenchoididae) on adults of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith). Ann. Ent. Soc. Am. 83: 956-960.

PAIR, S. D., AND A. N. SPARKS. 1986. Evidence of annual long-distance migration by the fall armyworm, pp. 25-33 *in* A. N. Sparks (ed.), Long-range migration of moths of agronomic importance to the United States and Canada: specific examples of occurrence and synoptic weather patterns conducive to migration. USDA Misc. Publ. ARS-43. 104 pp.

PAIR, S. D., J. R. RAULSTON, A. N. SPARKS, AND J. K. WESTBROOK. 1986. Fall armyworm distribution and population dynamics in the southeast states. Florida Entomol. 69: 468-487.

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

ROGERS, C. E., O. G. MARTI, A. M. SIMMONS, AND J. F. SILVAIN. 1990. Host range of *Noctuidonema guyanense* (Nematoda: Aphelenchoididae): an ectoparasite of moths in French Guiana. Environ. Entomol. 19: 795-798.

SAS INSTITUTE. 1985. SAS user's guide: statistics. SAS Institute, Cary, North Carolina.

SIMMONS, A. M., AND C. E. ROGERS. 1990a. Distribution of an ectoparasitic nematode, *Noctuidonema guyanense*, on moths of the fall armyworm (Lepidoptera: Noctuidae) in tropical America. J. Entomol. Sci. 25: 510-518.

SIMMONS, A. M., AND C. E. ROGERS. 1990b. Temperature and humidity effects on *Noctuidonema* (Nematoda: Aphelenchoididae), an ectoparasite of adult *Spodoptera frugiperda* (Lepidoptera: Noctuidae), and transfer success during host mating. Ann Entomol. Soc. Am. 83: 1084-1087.

SIMMONS, A. M., AND C. E. ROGERS. 1991. Dispersal and seasonal occurrence of *Noctuidonema*, an ectoparasitic nematode of adult fall armyworm (Lepidoptera: Noctuidae), in the United States. J. Entomol. Sci. 26: 136-148.

SNOW, J. W., W. W. CANTELO, R. L. BURTON, AND S. D. HENSLEY. 1968. Populations of fall armyworm, corn earworm, and sugarcane borer on St. Croix, U. S. Virgin Islands. J. Econ. Entomol. 61: 1757-1760.

SNOW, J. W., AND W. W. COPELAND. 1969. Fall armyworm: use of virgin female traps to detect males and to determine seasonal distribution. USDA, Prod. Res. Rep. 110, 9.