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Authors: Murúa, Gabriela, Molina-Ochoa, Jaime, and Coviella, Carlos

Source: Florida Entomologist, 89(2): 175-182

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/0015-4040(2006)89[175:PDOTFA]2.0.CO;2

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POPULATION DYNAMICS OF THE FALL ARMYWORM, SPODOPTERA FRUGIPERDA (LEPIDOPTERA: NOCTUIDAE) AND ITS PARASITOIDS IN NORTHWESTERN ARGENTINA

GABRIELA MURÚA¹, JAIME MOLINA-OCHOA² AND CARLOS COVIELLA³ ¹Estación Experimental Agroindustrial Obispo Colombres, William Cross 3150, Las Talitas 4101 Tucumán, Argentina

²Universidad de Colima, Facultad de Ciencias Biológicas y Agropecuarias Km. 40, autopista Colima-Manzanillo, Tecomán, Colima 28100, México

³Universidad Nacional de Luján, Laboratorio de Ecología, cruce rutas 5 y 7, CC 221, 6700 Luján, Argentina

ABSTRACT

In order to know the population dynamics of the fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith), and its parasitoids in northwestern Argentina, larvae were weekly collected at two different agrological regions (Tafi Viejo, and Vipos) over four years. The relationship between larval and parasitoid populations, climatologic factors, percent of infested plants, parasitoid relative importance index, abundance of the parasitoids, and percent parasitism were estimated. FAW attacked cornfields when the plants achieved V1 and V2 stages. Temperature and rainfall were the climatologic factors that significantly affected pest density, and temperature affected the parasitoid abundance as well. The FAW parasitoids collected were *Campoletis grioti* (Blanchard), *Chelonus insularis* (Cresson), *Ophion* sp. and *Archytas* spp. (possibly marmoratus and/or incertus). The average parasitism percentage was 39.4% and 15% in T. Viejo and Vipos, respectively. Parasitoid abundance in both regions was similar, but diversity was different possibly relating to the native surrounding vegetation in Vipos. This is the first report of population dynamics of the fall armyworm and its parasitoids in northwestern Argentina.

Key Words: $Spodoptera \ frugiperda$, parasitoid complex, population fluctuation, performance, corn

RESUMEN

Para conocer la dinámica poblacional del gusano cogollero del maíz (GC), Spodoptera frugiperda (J. E. Smith) y la de sus parasitoides en el Noroeste argentino, se colectaron larvas semanalmente en dos regiones agrológicas (Tafí Viejo y Vipos) durante cuatro años. Se determinó la relación entre la fluctuación poblacional de la plaga y la de sus parasitoides con los factores climáticos. Se estimó el porcentaje de plantas dañadas, el índice de importancia relativa, la abundancia de los parasitoides, y el porcentaje de parasitismo. El GC ataca los cultivos de maíz ni bien son implantados, cuando las plantas alcanzan las etapas fenológicas V1 y V2. La temperatura y la precipitación fueron los factores climatológicos que afectaron significativamente la abundancia de la plaga. La abundancia de los parasitoides también fue afectada por la temperatura. Los parasitoides colectados fueron Campoletis grioti (Blanchard), Chelonus insularis (Cresson), Ophion sp., and Archytas spp. (posiblemente marmoratus y/o incertus). Los porcentajes de parasitismo fueron 39.4% y 15% en T. Viejo y Vipos, respectivamente. La abundancia de los parasitoides en las dos zonas estudiadas fue similar, pero la diversidad fue diferente posiblemente relacionada a la vegetación circundante en Vipos. Este es el primer estudio sobre la dinámica poblacional del GC y la de sus parasitoides en el Noroeste argentino.

Translation provided by the authors.

INTRODUCTION

Insects are a dominant component of agricultural ecosystems, and they impact crop yields in many ways. Several species are pests of row and horticultural crops, reducing yields by the transmission of diseases or by direct damage. Other insects are natural enemies of pest species, and can be used as biological control agents for reducing pest organisms. Insects are considered indicators of biodiversity, providing a means of determining the effects of agricultural practices on whole communities or on abundance and dynamics of individual species (LaSalle 1993). Understanding the factors that influence the distribution and abundance of an insect is a fundamental issue of insect ecology and is a practical concern with insects that cause economic damage (Baskauf 2003). Insect population dynamics have fundamentally different characteristics depending on the strength and form of exogenous (density-independent) vs. endogenous (density-dependent) forces. Many factors affect population abundance such as competition, natural enemies, and resources, but the relative contribution of exogenous and endogenous effects remains an open question for nearly all biological populations (Ylioja et al. 1999).

The fall armyworm (FAW), *Spodoptera fru-giperda* (J. E. Smith) was recognized as a destructive pest of many agricultural crops more than 200 years ago (Luginbill 1928). It is an important economic pest of corn, rice, sorghum, peanut, alfalfa, cotton, Sudan grass, soybean, tobacco, oat, wheat, sugarbeet, and diverse pasture grasses such as Bermuda grass, Johnson grass, and others (Sparks 1979; Andrews 1980; Capinera 1999), and it is widely distributed in America. Its distribution extends eastward into the Caribbean, southward to northern Argentina and northern Chile, and northward through Central America, Mexico, the United States, and southern Canada (Andrews 1980).

Because the FAW has a wide distribution, it is subjected to much climatic diversity, namely, temperature, moisture, and soil type. The environmental factors influencing development and survival, as well as genotype, agricultural practices, crop phenology, and plant maturity may contribute to the dynamics of the system in a given locale (Harrison 1984a; Pair et al. 1986; Barfield & Ashley 1987; Simmons 1992; Riggin et al. 1993).

The FAW is the most important corn pest, causing yield losses fluctuating from 17% to 72% in northeastern Argentina (Perdiguero et al. 1967). However, studies related with the population dynamics of FAW in Argentina, and how environmental factors affect this phenomenon were not previously reported in Argentina. Reports related to the relationship between date and damage by FAW in commercial corn in northwestern Argentina have been published by Willink et al. (1993a, b), and Sosa (2002a, b).

FAW has a diverse complex of natural enemies in the Americas and the Caribbean basin (Ashley 1979; Ashley et al. 1982; Molina-Ochoa et al. 2003). In Argentina at least thirteen species of hymenopteran parasitoids and eight dipteran parasitoids are known to attack FAW (Vera et al. 1995; Virla et al. 1999; Murúa et al. 2003; Murúa & Virla, 2004). However, there is a lack of information on the natural distribution of FAW and its parasitoids in northwestern Argentina, as well as the influence of environmental factors on their dynamics. We report the population dynamics of FAW, its parasitoids, and the influence of environmental factors on the dynamics in the northwestern region of Argentina.

MATERIALS AND METHODS

Sampling Sites

Two agrological regions (Zuccardi & Fadda 1985) of northwestern Argentina were systematically sampled for FAW larvae during the cropgrowing part of the year over a period of four years. The two regions were located in the province of Tucumán. The first region was Tafí Viejo (Department of Tafí Viejo), located between the coordinates 26° 44' S, 65° 14' W, and 609 m altitude. This region is part of the Chaco Pampeana Plain, and it is characterized by good availability of soil moisture during the year. The cornfield used for monitoring was seven ha in size and planted with the regional corn variety Leales 23.

The second region was Vipos (Department of Trancas) located at $26^{\circ} 28'$ S, $65^{\circ} 18'$ W, and 786 m altitude, in the Intermontana of Tapia-Trancas basin. This region is characterized by soil moisture availability only during the rainy part of the year (December-January), and irrigation is usually required. The cornfield sampled at Vipos was ca. 40 ha, and was also planted with the corn variety Leales 23. Other commercial crops grown in the area included corn, soybean, pumpkins, and vegetables. All commercial fields routinely applied insecticides.

Both regions exhibit agrological differences in their hydrological conditions such as rainfall and evapotranspiration. These differences determine the planting date for each region. Corn can be planted during late October at Tafí Viejo, while the planting date at Vipos occurs from late December to early January.

Sampling for FAW larvae was conducted weekly at Tafí Viejo from October 1999 to January 2000 (Year 1), from October to December in 2000 (Year 2), from October to December 2001 (Year 3), and November 2002 to January 2003 (Year 4). In Vipos, the larvae were sampled from January to March in 2000 (Year 1), from October to December in 2000 (Year 2), from October to December 2001 (Year 3), and from January to March in 2003 (Year 4). Insecticides were not applied in any of the fields sampled in this study.

Larval Sampling

FAW larvae were sampled beginning approximately 10-12 d after the date corn plants exhibited two ligulate leaves, and continued until the beginning of the reproductive stage (R1) (Ritchie et al. 1992). The sampling period lasted about five to seven weeks. Fifty corn plants were randomly sampled at each sampling date, and divided in five groups of ten plants. The plants were checked for the presence of FAW eggs, larvae, and/or adults following the methodologies used by Willink et al. (1993a,b), García Roa et al. (1999), and Fernández (2002). The number of corn infested plants was recorded in order to determine the percentage of infested plants (Harrison 1984b).

FAW larvae collected from cornfields were placed in glass vials (12 cm long \times 1.5 cm diameter) containing a piece of fresh corn leaf, and were kept in a chamber under controlled conditions at $25 \pm 2^{\circ}$ C, 70-75% RH, and 14L:10D photoperiod. FAW larvae were then transferred to similar tubes containing 1 cm³ of artificial diet (Osores et al. 1982). The diet vials containing FAW larvae were maintained in the laboratory until the parasitoids had emerged, or until FAW adult emergence (Riggin et al. 1993).

Parasitoid Identification

Parasitoids were recorded and identified by several specialists. Tachinids were identified by Lic. Susana Avalos (Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, Argentina), and *Campoletis grioti* (Blanchard) by Dra. Carolina Berta (Fundación Miguel Lillo, Departamento de Zoología, Entomología, San Miguel de Tucumán, Argentina). The remaining parasitoids were compared to specimens previously identified by Dr. Luis De Santis (Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina).

Population Variables

The Percent of infested plants (% IP) (Harrison 1984b, Urbaneja García 2000, Diez 2001) was calculated by the following equation:

% IP = $\frac{\text{Infested plants}}{\text{total plants}} \times 100$

The relative importance index (RII) of the parasitoid species allows for an estimation of the species not only considering its abundance but also its occurrence or frequency. In this way, species poorly represented in individual numbers but frequently recovered over a long period can be balanced with numerous species with sporadic occurrence (Remes-Lenicov & Virla 1993; Rueda 1999; Diez 2001). It was calculated by the following formula:

$$\label{eq:PRII} \begin{split} & \text{PRII} = \frac{\text{No. of individuals of the species }^{\text{``I''}} \times \frac{\text{No. of samples species }^{\text{``I''}} \text{occurred}}{\text{Total No. different species}} \times \frac{100}{\text{Total No. of samples}} \end{split}$$

Frequency (F) is the percent of individuals of certain species in relation to total individuals of all species (Canal Daza 1993; Molina-Ochoa et al. 2001; Molina-Ochoa et al. 2004), and was calculated by using the following formula: $F = No. individuals of species "i" \times 100$ No. total collected individuals

Percent of parasitism (%P) was calculated according to Van Driesche (1983); Pair et al. (1986), and Crisóstomo-Legaspi et al. (2001), as follows:.

 $%P = No. total parasitized individuals \times 100$ No. total individual observed

Statistical Analysis

Percent data were angularly transformed and subjected to analysis with the software Statistics © 5.5 (2000). In order to determine differences between and among FAW and parasitoid collections from the same region and those from different regions, student *t* tests were performed.

Regression analyses also were performed to determine the relationship between FAW populations and parasitoid abundance with temperature and rainfall (Diez 2001; Schliserman 2001) by a stepwise approach. For the analyses, the mean of low and high temperatures and mean rainfall during the sampling week, and the mean of low and high temperatures and rainfall recorded in the two weeks previous to the sampling date, were used. From these data it was possible to estimate the week in which the environmental factors most affected the FAW populations, and the abundance of FAW parasitoids.

RESULTS AND DISCUSIÓN

The percent of infested plants (%IP) by FAW larvae was higher at Vipos (≅20%) than at Tafí Viejo (5.5%) (t = 0.0001, P < 0.001, df = 75). The annual percentage of infested plants at Tafí Viejo was highest during 2001 (9%), while at Vipos the highest record was during 2000 (71.3%). The %IP during the four year study in Tafí Viejo were 5.8%, 0.1%, 8.9%, and 8.9%. However in Vipos the %IP were 71.3%, 19.7%, 21.3%, and 18.4%. The total percent of infested plants (%TIP) in Tafí Viejo, and Vipos were 5.5, and 30%, respectively. ANOVA revealed significant differences in the number of infested plants among years during the 4-year study in both areas (T. Viejo: F =106.38; P < 0.001; df = 72, and Vipos: F = 91.46;P < 0.001, df = 74). The results obtained at Tafí Viejo (early planting) and Vipos (late planting) agreed with those previously reported by Willink et al. (1991) for the Tucumán region, and Sosa (2002a) for the North of Santa Fé province. Earlier plantings had lower levels of FAW infestation and damage, a response similar to that reported by Mitchell (1978), and Harrison (1984b) on corn infested by corn earworm and fall armyworm, respectively.

FAW Collection

About 2400 corn plants were examined in Tafí Viejo, and 132 FAW larvae were collected and 52 parasitoids were recovered. The mean number of FAW larvae per 10 plants was 0.58, 0.013, 0.89, and 0.88 during years 1, 2, 3, and 4, respectively. Larvae were collected as early as late September because of the early planting date. FAW larvae were not found in the first phenological stages (one to three ligulate leaves, V1-V3). One larva was recorded in year 2 during the late crop-growing season, when the plants had seven to eight leaves (V7-V8). Overall, years 1 and 3 produced higher densities of FAW larvae during the vegetative stages V3 to V6, similar to what was found by Hernández-Mendoza (1989) in Colima, México. In contrast, higher larval densities were recorded in years 2 and 4 at the end of the vegetative period.

In Vipos, 2750 plants were examined, 540 larvae were collected, and 82 parasitoids were obtained. The mean number of FAW larvae per 10 plants was 2.59, 2.17, 1.25, and 1.83 during years 1, 2, 3, and 4, respectively. During years 1 and 2, higher larval numbers were recorded in the V1-V3 stages. Larval populations were consistent throughout the vegetative plant phase for the other years. Overall, larval densities diminished with the age of the cornfield, achieving the lowest numbers during the beginning of the corn's reproductive stages. Comparing FAW population fluctuations in both locations during this 4-year study, FAW at Vipos exhibited significantly higher larval numbers (t = 1.99, P < 0.001, df = 72).

FAW and Corn Phenology

FAW infestations displayed a plant age-dependent response at both localities during the 4-year study. Reduced mean larval numbers were related to plant age and development. Mitchell et al. (1974), and Beserra et al. (2002) found that the distribution of FAW larvae and eggs varied according to the phenological stage of the corn. During the early plant stages (V1-V3), first and second instars were predominant, and about one to six larvae per plant were found. During V4 and V6, only one larva was usually recovered per plant. Carvalho & Silveira (1971) found that small and medium larvae would coexist, but the number of larvae per plant decreased as larval size increased. Larval cannibalism, larval mortality from disease or predators, and larval age are possible factors that influence distribution.

FAW and Climatic Factors

In Tafí Viejo a temperature-dependent response was obtained with respect to FAW population abundance $[Y = -1.34 + 1.29 \log Max 2T^{\circ}$ (mean high temperatures recorded in the week previous to the sampling plus mean high temperatures recorded in the second week previous to the sampling) - 0.29 log rainfall 2 (mean rainfall recorded in the week previous to the sampling plus mean rainfall recorded in the second week previous to the sampling)]; n = 30; P < 0.001; $\mathbb{R}^2 =$ 0.99). Barfield & Ashley (1987) reported that corn phenology and temperature affected larval development, food consumption, and adult female longevity and fecundity, and that developmental times were temperature-dependent and were modified by the stage of corn consumed. However, at Vipos an associated response was observed with rainfall $[Y = 3.89 + 0.5 \log rainfall 0 (mean$ rainfall during the sampling week) -0.18 log Max T°0 (means of high temperatures during the sampling week)]; n = 30; P < 0.01; $\mathbb{R}^2 = 0.219$). Silvain & Ti-A-Hing (1985) found that the highest populations of FAW moths and larvae were observed during the rainy seasons, and lowest during the dry seasons.

Insect phenology, density, and number of FAW generations are influenced by the climatic conditions in a given region. Climatologic differences between and among localities could explain the phenological differences, and climatologic conditions among years also could explain fluctuations in pest abundance in each area (Dent 1991; Diez 2001).

Parasitoid Species

Considering the diversity of parasitoids reported from the Tucumán area (Vera et al. 1995; Virla et al. 1999; Berta et al. 2000; Murúa et al. 2002; Murúa et al. 2003; Murúa & Virla 2003; Murúa & Virla 2004) few species were recovered in our study. Only two ichneumonids, Campoletis grioti (Blanchard) and Ophion sp., one braconid, Chelonus insularis (Cresson), and possibly one or two species of tachinids, Archytas marmoratus (Town.) and/or A. incertus (Macquart) were found. All species were collected at Vipos (Table 1), and only C. grioti was recovered at Tafí Viejo. Of all parasitoids collected at Vipos, Archytas spp. comprised 38.3%, C. grioti 35.8%, Ch. insularis 22.2%, and *Ophion* sp. 3.7%. Seasonally, *Ophion* sp. was collected when corn plants were V4, whereas Archytas spp. and C. grioti were collected at the end of the crop cycle. These results are in agreement with those by Virla et al. (1999) and Vera et al. (1995), who reported C. grioti and Ophion sp., respectively, attacking FAW larvae collected from corn in Argentina. Our results are also in agreement with Molinari & Avalos (1997), who showed that the dipteran parasites attacked the last instars of FAW in Argentina. No differences were determined in the abundance of parasitoids in both locations during the 4-year study (t = 1.36, P= 0.19, df = 38). We speculate that differences in early or late corn planting would not affect the abundance of FAW parasitoids.

Species	Frequency during year (%)				Relative Importance during year $(\%)$				
	1	2	3	4	1	2	3	4	Total
C. grioti	52.2	44.4	33.3	5.5	0.26	0.19	0.15	0.004	0.13
Ch. insularis	5.6	33.3	33.3	38.9	0.01	0.007	0.11	0.07	0.056
Ophion sp.	34.8	5.6	4.2	0.0	0.02	0.007	0.146	0.0	0.005
Dipteran spp.	25.0	44.4	29.2	57.9	0.1	0.2	0.1	0.2	0.14

TABLE 1. FREQUENCY AND RELATIVE IMPORTANCE OF THE FAW PARASITOID COMPLEX IN VIPOS DURING THE FOUR-YEAR STUDY.

Percent Parasitism

Campoletis grioti was the single parasitoid responsible for 39.4% parasitism at Tafí Viejo. In Vipos, overall percent parasitism during the 4-year study was 15%. The tachinid species, *C. grioti, Ch. insularis,* and *Ophion* sp. caused 5.7%, 5.4%, 3.3%, and 0.6% of total FAW parasitism, respectively. The highest record of annual parasitism was recorded during year 2 with 10.5% for *C. grioti* and the dipteran species, but during year 3, *C. grioti,* and *Ch. insularis* each caused 8.5% of parasitism (Table 2).

Kogan et al. (1999) mentioned that cultural practices developed in a plot can affect in a positive or negative way the natural enemy populations, increasing or inhibiting the parasitoid colonization in cultivated fields. These practices could also have direct or indirect effects, directly through environment alterations and indirectly affecting the host plant architecture, lack of food, or refuge. The lack of vegetation surrounding the sampling area in the cornfields at Tafí Viejo could be a reason for the low diversity found. This area was surrounded by lemon groves where insecticide applications are commonly applied. It is known that the presence of spontaneous vegetation associated with the crop results in higher numbers and diversity of natural enemies related to this vegetation (Altieri & Whitcomb 1980; Hoballah et al. 2004).

It is important to consider that *C. grioti* is a oligophagous parasitoid that attacks different hosts of several genera in the family Noctuidae. Another possible cause for low diversity is early planting in Tafí Viejo that reduces FAW infestation, and damage to cornfields (Willink et al. 1991). Conversely, in Vipos corn is planted later and the fields were surrounded by native vegetation without significant anthropogenic disturbances affecting potential parasitoid refuges. Higher diversity of parasitoids and higher rates of parasitism in Vipos also may be related to a

	Abundance and percent parasitism (%)									
Location	Tafí Viejo					Vipos				
Year	1	2	3	4	1	2	3	4		
NPS*	500	750	450	700	900	350	750	750		
FAWCL	29	1	40	62	233	76	94	137		
Species										
C. grioti	4	1	18	29	12	8	8	1		
	(13.8)	(100)	(45.0)	(46.8)	(5.2)	(10.5)	(8.5)	(0.7)		
Ch. Insularis	_	_	_	_	2	1	8	7		
					(0.8)	(1.3)	(8.5)	(5.1)		
Ophion sp.	_	_	_	_	1	1	1	_		
					(0.8)	(1.3)	(1.1)			
Dipteran spp.	_	_	_	_	5	8	7	11		
					(2.1)	(10.5)	(7.5)	(8.0)		
Total parasitoids collected (%)	4	1	18	29	20	18	24	19		
	(13.8)	(100)	(45.0)	(46.8)	(8.6)	(23.7)	(25.5)	(13.9)		

TABLE 2. ABUNDANCE AND PERCENT PARSITISM OF FAW PARASITOIDS OBTAINED IN TAFÍ VIEJO AND VIPOS DURING THE FOUR-YEAR STUDY.

 (\ast) Number of plants sampled, FAWCL = FAW collected larvae.

more diverse habitat with more forest, orchards, groves, and pastures near to cornfields (Molina-Ochoa et al. 2001; Hoballah et al. 2004). Overall, the percent parasitism measured in this study was similar to other studies. Berta et al. (2000) reported parasitism ranging between 5.26% and 50% in cornfields with and without insecticide application in the province of Tucumán, respectively. Luchini & Almeida (1980) listed FAW parasitoids occurring in Brazil and considered *C. grioti* the most important parasitoid causing about 95% parasitism.

Ashley (1986) and Andrews (1988) listed Ch. insularis occurring throughout North America highlighting its role as parasitoid of FAW by showing parasitism of 63% in southern Florida; however, Pantoja & Fuxa (1992), Molina-Ochoa et al. (2001), and Molina-Ochoa et al. (2004) reported lower levels of parasitism by Ch. insularis of about 5% in Puerto Rico and Mexico, respectively. This braconid has the broadest distribution in Latin America and South America (Molina-Ochoa et al. 2003). Lewis & Nordlund (1980) consider this parasitoid an excellent candidate for augmentative release because it can be introduced throughout its overwintering zone. It is capable of early-season colonization, and can be used in direct therapeutic releases on target crops.

The ichneumonid *Ophion* sp. caused the lowest level of FAW parasitism in Vipos, ranging between 0.8 and 1.3% during the 4-year study. Similar results have been reported by Molina-Ochoa et al. (2001). Gross & Pair (1991) state that *Ophion flavidus* (Brullé) parasitized 4th, 5th, and 6th instar FAW with equal success, but were minimally successful in completing development on late 6th instars. This parasitoid caused 19.5% of parasitism in June in southern Georgia. *Ophion* sp. has been reported previously in Argentina (Vera et al. 1995).

Dipteran parasites played an important role in Vipos in the 4-year study, providing high parasitization levels. *Archytas marmoratus* and /or *A. incertus* caused levels of parasitization between 2.1%, and 10.5%. The importance of these species in Argentina and other South American countries was emphasized by Molina-Ochoa et al. (2004) based on reports by Molinari & Avalos (1997) and Virla et al. (1999).

Parasitoids and Climatic Factors

Temperature was the most important climatic factor influencing parasitoid populations in both locations. Similar responses of other parasitoids have been reported by Diez (2001), and Schliserman (2001) for the Tucumán region, such as those attacking the fruit flies, *Ceratitis capitata* (Weid.), *Anastrepha fraterculus* (Weid.), and citrus leafminer, *Phyllocnistis citrella* (Stainton). The maximum temperature in Tafí Viejo was the most important factor $[Y = -1.55 + 1.3 \log Max 2T^{\circ}]$ (mean high temperatures recorded in the week previous to the sampling plus mean high temperatures recorded in the second week previous to the sampling) - 0.3 log rainfall 0 (mean rainfall during the sampling week)]; n = 38; P < 0.001, $R^2 = 0.99$) affecting the parasitoid population fluctuation.

In Vipos minimum temperature was important factor but no climatic factor was a significant variable describing parasitoid populations [Y = $2.62 + 0.387 \log T^{\circ}$ Min 0 (mean low temperatures during the sampling web) – 0.18 log rainfall 1(mean rainfall recorded in the week previous to the sampling)]; n = 30; P = 0.11; $R^2 = 0.085$). Factors, such as insecticides, farming and cultural practices, and other natural enemies, may be influencing parasitoid populations.

ACKNOWLEDGMENTS

The authors thank MSc. Patricia Diez (CRILAR-CONICET, Tucumán, Argentina) and Dr. John J. Hamm (USDA-ARS Crop Protection & Mangement Research Laboratory, P.O. Box 748, Tifton, GA 31793-0748, USA) for critical review of the manuscript. We thank Mr. Rubén Pedraza (Servicio meteorológico del INTA-EEA Famaillá-Tucumán, Argentina) and Ing. César Lamelas (Sección Agrometeorología EEAOC-Tucumán, Argentina) for meteorological data and advice.

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