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Population dynamics and occurrence of *Spodoptera frugiperda* host strains in southern Florida

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Abstract. 1. The development of an area-wide management programme for the migratory pest fall armyworm [*Spodoptera frugiperda* (J. E. Smith)] requires knowledge of its preferred habitats throughout the year and a detailed description of seasonal changes in population numbers.

2. Molecular markers were used to determine the host strain (*corn* or *rice*) of male moths captured in sex pheromone-baited traps placed in different habitats in the overwintering areas of southern Florida.

3. The results indicated that rice strain moths were found in all traps and that this strain was the primary population observed in naturalised pasture and wetlands in southern Florida. In comparison, larger populations of both strains and a higher proportion of corn strain moths were observed in areas associated with golf courses, agriculture, or urban development. Corn strain adults were most prevalent during the spring and early summer.

4. These results represent the first geographical survey of fall armyworm host strain distribution in Florida and indicate that corn strain moths are limited in their habitat choice while rice strain moths have a substantially broader range. The localisation of the corn strain population to discrete areas at specific times of the year provides an opportunity to reduce or delay its northward migration.

Key words. Fall armyworm, host strains, population distribution.

Introduction

Spodoptera frugiperda (J. E. Smith), or the fall armyworm, is a migratory polyphagous pest of maize, sorghum, forage grasses for livestock, turf grasses, rice, cotton, and peanuts in eastern and central North America and South America (Luginbill, 1928; Sparks, 1979). Fall armyworm is composed of two sympatric and morphologically identical strains that are defined by their host plant preferences (Pashley *et al.*, 1985; Pashley, 1986). One strain was identified from populations feeding on corn, sorghum, and other *large* grasses (corn strain), and the other strain was identified from populations feeding on rice, Bermuda grass, and other *small* grasses (rice strain). The two strains can be distinguished by strain-specific allozyme variants and genetic markers (Pashley, 1989; Lu *et al.*, 1992; Lu *et al.*, 1994; Lu & Adang, 1996; McMichael & Prowell, 1999). A number of studies have identified strain-specific differences in several physiological and behavioural characteristics, including larval development on different plant sources (Pashley *et al.*, 1987a; Quisenberry & Whitford, 1988; Pashley *et al.*, 1995; Veenstra *et al.*, 1995), resistance to pesticides (Pashley *et al.*, 1987b), and mating behaviour (Pashley & Martin, 1987; Pashley *et al.*, 1992).

The fall armyworm is not known to diapause and so cannot survive the winters in areas with freezing temperatures. Therefore, the infestation of much of the U.S.A. occurs entirely from populations overwintering in southern Florida and southern Texas/northern Mexico (Luginbill, 1928; Mitchell, 1979; Sparks, 1979; Pair *et al.*, 1986). If the populations of the corn and/or rice strains can be controlled in the overwintering sites, it should be possible to substantially reduce or delay their northward migrations, mitigating agricultural damage. Such area-wide management requires knowledge of the population distribution of each strain in the major habitats within the overwintering region. Population surveys that have been performed in Florida

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have focused on sweet corn fields. These indicate an increase in fall armyworm numbers in spring, followed by a rapid and prolonged decline in numbers during the summer months (Pair *et al*., 1986; Mitchell *et al*., 1991). This decline corresponds to, and presumably reflects, the northward migration of this population into northern Florida and southern Georgia in April and May (Snow & Copeland, 1969; Greene *et al*., 1971), which continues into the northern states by July and August (Mitchell, 1979). Unfortunately, surveys of fall armyworm populations did not examine non-agricultural locales nor have they analysed the distribution of individual strains. Hence, it is not known whether and to what degree the natural habitats of southern Florida can serve as a refuge for fall armyworm populations.

To address this issue, the seasonal dynamics of fall armyworm host strain populations was examined in naturalised pasture and wetland environs, habitats common to southern Florida, and the results were compared with populations observed in developed areas. These studies utilised a combination of pheromone trapping and PCR techniques that were previously shown to be an efficient means of estimating the proportion of each strain present in a given location (Meagher & Gallo-Meagher, 2003). In principle, trap captures should reflect males from both the endogenous and transient populations, although studies with a related species, *Spodoptera littoralis* (Boisduval), suggest that locally derived specimens are predominantly collected (Campion *et al*., 1977).

Methods

Moth collection and trap sites

Standard plastic Universal moth traps (Unitraps) baited with commercial fall armyworm sex pheromone lures [(*Z*)-9-tetradecen-1-ol acetate (*Z*)-11-hexadecen-1-ol acetate and (*Z*)-7-dodecen-1-ol acetate; Scenturion® (Scenturion Inc., Clinton, Washington)] were placed in several different habitats in Lee, Collier, Broward, and Miami–Dade counties, Florida (Table 1). All traps contained insecticide strips (Hercon® Vaportape II containing 10% 2,2-dichlorovinyl dimethyl phosphate, Hercon Environmental Co., Emigsville, Pennsylvania) to kill moths. Traps were placed on 22 January 2002 and collections were made at approximately 2-week intervals until 22 July 2003. Trapped moths were separated from other species, counted, and a subset (10–15) selected randomly for PCR analysis. Previous research showed that PCR analysis could be completed on dead moths held in traps for up to 15 days (Meagher & Gallo-Meagher, 2003). Because of low trap captures, the data for traps 1 and 2, traps 8–10, and traps 17 and 18 were pooled. Specimens were stored at −20 °C after collection.

Traps located in natural (unmanaged grasses, trees, and wetlands), or pasture (natural or improved grasses used for livestock) habitats included traps 1 and 2, trap 7, traps 8–10, and traps 17 and 18 (Table 1). Traps 1 and 2 were located in southern Lee Co. and were adjacent to natural and improved pasture grasses, surrounded by natural areas. Trap 7 was along U.S. 41 near Collier-Seminole State Park and Big Cypress National Preserve. Traps 8–10 were located along U.S. 41, adjacent to the Tamiami Canal, with the Everglades Wildlife Management Area north and Everglades National Park south. Traps 17 and 18 were set in rest areas along Interstate 75 and were surrounded by the Everglades Wildlife Management Area.

Two traps were located near turf (managed grasses used for golf courses or lawns) or agricultural [seasonal managed vegetable crop plants including sweet corn (*Zea mays* L.), tomato (*Lycopersicon esculentum* Mill.), and snap beans (*Phaseolus vulgaris* L.)] habitats. Trap 6 was placed along U.S. 41 near a golf course with adjacent natural wetlands.

Table 1. Site location, description, and seasonal capture rate of fall armyworm moths in pheromone traps examined from February 2002 to July 2003, Florida.

Location description	Trap no.	County	Coordinates	Average months per night per trap (mean ± SE)
Natural	1 and 2	Lee	26°27.116′N, 81°43.467′W; 26°01.046′N, 81°37.667′W	0.88 ± 0.26
Natural	7	Collier	25°59.158′N, 81°34.113′W	1.56 ± 0.80
Natural	8–10	Miami–Dade	25°45.714′N, 80°42.615′W; 25°45.648′N, 80°37.524′W; 25°45.652′N, 80°33.635′W	0.55 ± 0.13
Natural	17 and 18	Broward	26°08.795′N, 80°34.602′W; 26°08.689′N, 80°37.658′W	1.26 ± 0.37
Golf/natural	6	Collier	26°01.046′N, 81°37.667′W	6.93 ± 1.13
Golf/corn	13	Miami–Dade	25°32.609′N, 80°28.690′W	8.81 ± 1.78
Urban	15 and 16	Miami–Dade	25°38.409′N, 80°17.523′W; 25°38.516′N, 80°17.931′W	5.00 ± 0.70

For logistical reasons this trap was only examined for a 10-month period from September 2002 to July 2003. Trap 13 was located along Highway 997 adjacent to agricultural fields and across the road from a golf course.

The two traps set in an urban setting (mixture of managed turf and natural areas) were placed at the United States Department of Agriculture–Agricultural Research Service (USDA–ARS) Subtropical Horticulture Research Station near Biscayne Bay. This 80-ha site contains a National Germplasm Repository of tropical fruits, sugarcane (interspecific hybrids of *Saccharum*) and *Tripsacum*, and is surrounded by suburban Miami. Traps 15 and 16 were set about 1 km apart.

DNA preparation

Individual moths were homogenised in 1 ml of homogenisation buffer (0.03 M Tris–HCl at pH 8.0, 0.1 M NaCl, 0.2 M sucrose, 0.01 M EDTA at pH 8.0, 0.5% Triton X-100) in a 5 ml Dounce homogeniser using either a hand pestle or a motorised mixer. To remove large debris, the homogenate was filtered through a 5-ml plastic syringe plugged with cheesecloth (pre-wet with distilled water) into a 1.5-ml microfuge tube. The Dounce homogeniser was washed with 800 µl of buffer, which was filtered and added to the homogenate. Cells and nuclei were pelleted by centrifugation at 12000 *g* for 10 min at 4 °C and the supernatant was removed by aspiration. The pellet was re-suspended in 600 µl nuclei buffer (0.01 M Tris-HCl at pH 8.0, 0.35 M NaCl, 0.1 M EDTA, and 1% N-lauryl sarcosine), and extracted with 400 µl phenol–chloroform (1:1). The supernatant was transferred to a new 1.5 ml tube, precipitated with 400 µl isopropanol for 1 h at room temperature, and centrifuged at 12000 *g* for 10 min. The DNA pellet was washed with 70% ethanol and dried. The pellet was re-suspended in 50 µl distilled water, followed by purification using DNA Clean and Concentrator-5 columns (Zymo Research, Orange, California) according to manufacturer's instructions. Each PCR reaction used 1 µl of the DNA preparation (between 0.1 and 0.5 µg).

PCR analysis

Genomic DNA was tested by PCR for the mitochondrial *COI* gene restriction fragment length polymorphism (RFLP) to confirm strain identity as described previously (Levy *et al.*, 2002; Nagoshi & Meagher, 2003). PCR amplification of genomic DNA was performed in a 50 µl reaction mix containing 5 µl 10X reaction buffer with $MgCl_2$ (Promega, Madison, Wisconsin), 1 µl 10 mM dNTP (New England Biolabs, Beverly, Massachusetts), 0.5 µl 20 µM primer mix, 1 µl DNA template, 0.5 µl Taq DNA polymerase (Promega). Amplification of the *COI* gene used primers *JM76* and *JM77* and began with an initial incubation at 94 °C (1 min), followed by 38 cycles of 94 °C (1 min), 56 °C (1 min), 72 °C (1 min), and a final segment of 72 °C for 5 min. Upon completion of the PCR, 0.5 µl of *Msp*I was added to each reaction and incubated at 37 °C for 1 h. Five microlitres of gel loading buffer was added to each sample, and 20 µl was loaded on a 1.5% agarose gel. The R-strain pattern is a 569 bp PCR band, while the C-strain fragment is cut by *Msp*I to produce two fragments of 497 and 72 bp. Primers were synthesised by DNAgency (Malvern, Pennsylvania). They included *JM76*, 5′-GAGCTGAATTAGG(G/A)ACTCCAGG-3′, and *JM77*, 5′-ATCACCTCC(A/T)CCTG-CAGGATC-3′, which span the mitochondrial cytochrome oxidase C subunit I gene (*COI*) (Levy *et al.*, 2002). Typically, about 70–90% of the DNA preps gave useable PCR information.

Results

Four natural sites represented by traps 1 and 2, trap 7, traps 8–10, and traps 17 and 18, had low numbers of moths captured over the testing period, with an overall average below two moths per night per trap (Table 1). Relatively high captures were observed in February 2002 for trap 7 and traps 17 and 18; however, in all other sample periods, the capture rate never exceeded six moths per night (Fig. 1). The overall mean number of moths per night per trap for these traps was 0.96 ± 0.17. Random sampling of 690 moths established that the great majority was of the rice strain, which represented 95.3 (183/192), 95.7 (156/163), and 88.0% (205/233) of moths collected for traps 1 and 2, traps 8–10, and traps 17 and 18 respectively. The highest proportion of corn strain was found in trap 7 (22/102, 21.6%), the bulk of which was captured on 15 April 2003; however, trap 7 captures during this period averaged less than 2 moths per night per trap, suggesting that the endogenous fall armyworm population in this area was minimal.

Substantially higher capture numbers were obtained in managed areas where the overall capture rate ranged from five to nine moths per night per trap (managed $= 6.4 \pm 0.66$ vs. natural $= 0.96 \pm 0.17$, $P < 0.0001$) (Table 1). Moths captured in trap 6 exceeded 10 moths per night during October–November, April, and June (Fig. 2). The examination of strain distribution during these peaks indicated that the rice strain predominated between October 2002 and February 2003, representing 91.5% (43/47) of the captured population. In comparison, during the following spring (February–June 2003) the corn strain proportion increased to 24.4% (21/86) and was a majority in June 2003 (13/22) when the spring capture rate peaked at 16 moths per night per trap.

Trap 13 was also located near a golf course but in addition was adjacent to an agricultural field. During the spring and fall of 2002 and 2003, sweet corn was planted less than 100 m from the trap, leading to an expectation of high capture numbers with a strong bias in the direction of the corn strain. Surprisingly however, capture numbers from February to October 2002 were very low, never rising above five moths per night per trap (Fig. 2). This changed dramatically from October 2002 to July 2003, where the average capture rate was 15 moths per night per trap with peaks as

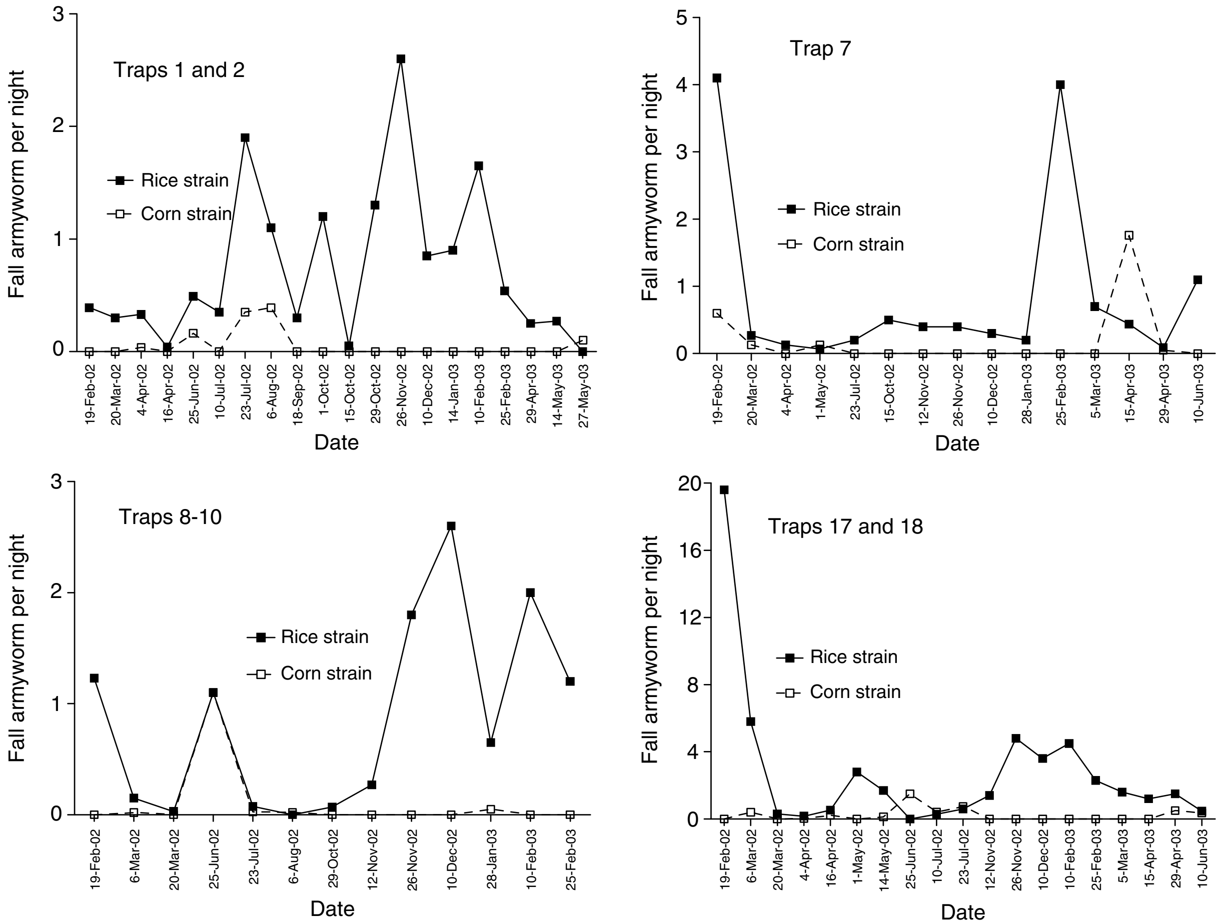

Fig. 1. Rice and corn strain male fall armyworm moths per night collected in four sex pheromone-baited trap combinations in natural or pasture habitats. Each data point represents total males captured divided by the number of evenings in the capture period, multiplied by the proportion of the sample determined to be rice or corn strain.

high as 43 moths per night per trap. The highest proportion of corn strain moths were observed during spring and early summer months. The February to early June/late July period contained 29.1% (16/55) in 2002 and 41.7% (40/96) corn strain moths in 2003. In comparison, during the periods of highest capture rate that occurred between October 2002 and February 2003, only 4.4% (3/69) of the captured moths were of the corn strain.

Substantial fall armyworm captures were consistently observed in traps located in an urban habitat (Fig. 3). Traps 15 and 16 were placed in a small park surrounded by suburban dwellings. Capture numbers fluctuated throughout the year with an average of 7.2 ± 1.2 moths per night for trap 15 and 2.8 ± 0.5 moths per night for trap 16. Highest capture rates were observed during the spring and summer months with as many as 28 moths per night obtained for trap 15. On average, these traps were associated with the highest percentage of corn strain moths, with 41.1 and 49.5% for traps 15 and 16 respectively. The corn strain was particularly prevalent during the spring and summer months. Corn strain moths represented 32.7% (17/52) of captures during 19 February to 14 May 2002 and 66.3% (61/92) during 2 April to 22 July 2003 in trap 15. The proportion of corn strain moths in trap 16 were higher during this same period, accounting for 73.5% (25/34) and 74.0% (37/50) of the moths captured respectively. The proportions of corn strain moths were low in each trap during the fall and winter months. Corn strain moths in trap 15 represented 21.0% (13/62) and 32.9% (25/76) of the moths captured during 23 July to 15 October 2002 and 29 October 2002 to 5 March 2003 respectively. In trap 16, corn strain moths represented 35.7% (25/70) and 22.5% (9/40) during 6 August to 12 November 2002 and 26 November 2002 to 18 March 2003 respectively.

Discussion

The overwintering areas of southern Florida and southern Texas comprise the source areas for populations attacking crops in the U.S.A. (Luginbill, 1928; Mitchell, 1979; Raulston *et al.*, 1986; Pair *et al.*, 1991). In the south-eastern

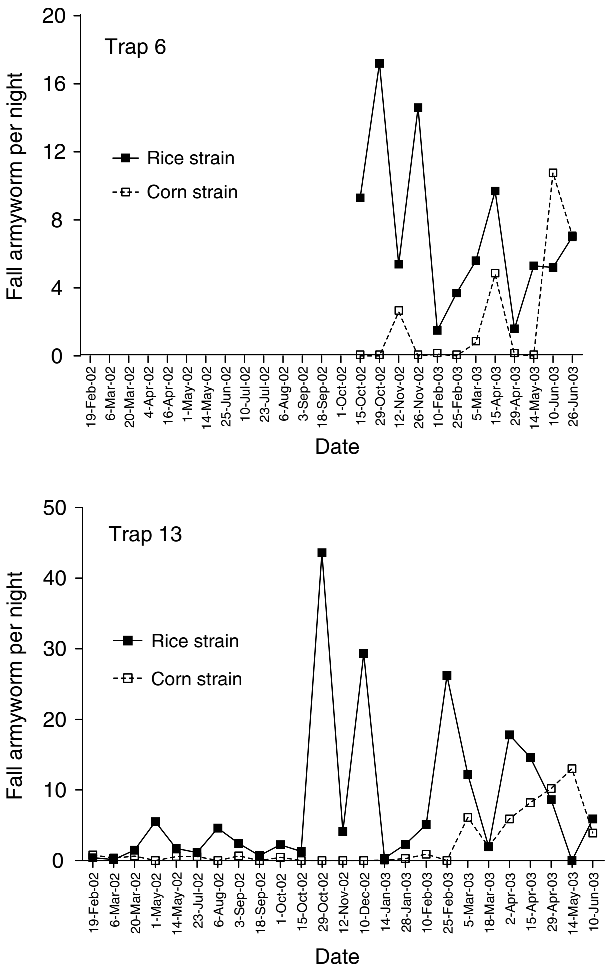

Fig. 2. Rice and corn strain male fall armyworm moths per night collected in two sex pheromone-baited traps in turf and agricultural habitats. Each data point represents total males captured divided by the number of evenings in the capture period, multiplied by the proportion of the sample determined to be rice or corn strain.

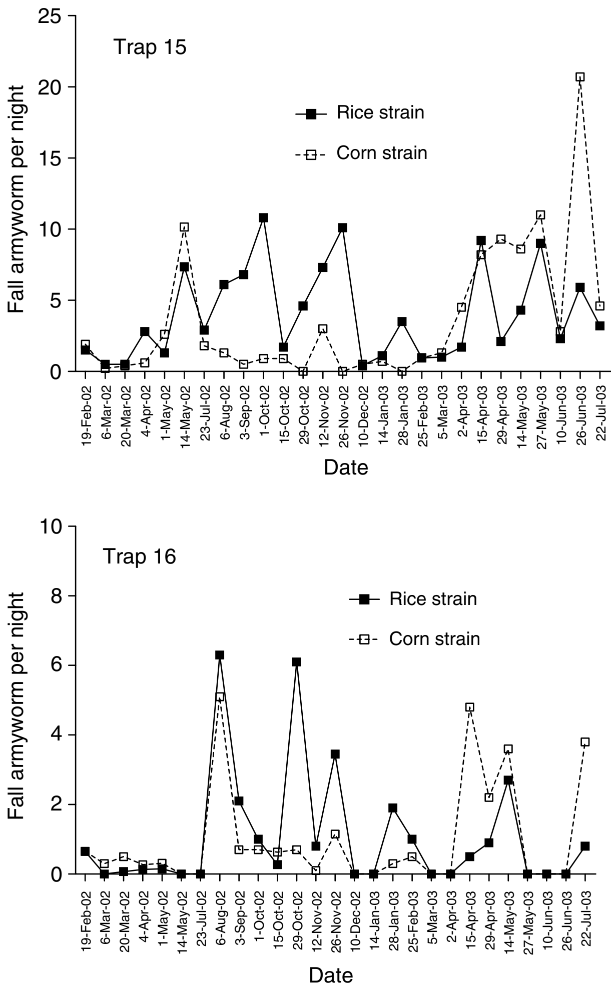

Fig. 3. Rice and corn strain male fall armyworm moths per night collected in two sex pheromone-baited traps in an urban habitat. Each data point represents total males captured divided by the number of evenings in the capture period, multiplied by the proportion of the sample determined to be rice or corn strain.

U.S.A., transport of moths has been correlated with favourable weather conditions from southern Florida in March and April (Westbrook & Sparks, 1986; Pair & Westbrook, 1995). Previous surveys of fall armyworm populations in southern Florida and tropical America focused on agricultural regions and showed a bimodal pattern of pheromone trap capture rates, with peak numbers occurring typically during the spring and fall seasons (Silvain & Hing, 1985; Pair *et al.*, 1986; Raulston *et al.*, 1986; Mitchell *et al.*, 1991).

It was the search for source areas of migrant populations that led to the discovery of fall armyworm host strains. Populations from the Caribbean west along the Gulf Coast to Mexico were analysed for genetic differences and the largest difference was due to a population collected from rice in Puerto Rico (Pashley *et al.*, 1985; Pashley, 1986). Research conducted on samples collected in the overwintering areas in Florida showed that late instar larvae collected from corn in Hendry Co. were identified as corn strain in 1983 and 1984 (Pashley *et al.*, 1985). In separate studies, both corn and rice strain populations were identified from southern Florida, although no information regarding location or collection habitat were provided (Pashley, 1988; Pashley *et al.*, 1992). The results in the work reported here is the first large-scale analysis of southern Florida host strain populations for this migratory pest.

Pheromone trapping combined with PCR analysis provided an efficient and sensitive method for surveying the geographical and temporal distributions of adult fall armyworm. Results demonstrated that this population dynamic is habitat-specific, since traps placed in geographically dispersed natural areas all showed very low capture rates throughout the year. This was the case even for the rice strain population despite the fact that the pasture and wetlands contained a variety of short and tall grass species. The apparently low numbers of adult fall armyworms in these natural pasture and wetland areas strongly suggest that they cannot serve as refuges for fall armyworm populations when preferred plant hosts (e.g. sweet corn and sugarcane) are scarce, nor do these habitats support significant populations when moth numbers in adjacent agricultural areas are high. Therefore, these habitats are unlikely to contribute tangibly to the northward migrating populations in the spring or be a major source of the re-infestation of Florida agricultural areas in the fall and winter.

In contrast, substantially higher adult populations were periodically indicated by trap captures in sites associated with golf courses (traps 6 and 13), sweet corn agriculture (trap 13), or urban development (traps 15 and 16). These results suggest that the apparent resistance of natural habitats to high concentrations of fall armyworm infestation is much reduced by the intrusion of human development. It may be that unmanaged habitats are supportive of natural enemies that effectively control fall armyworm infestation or that the higher diversity of plant types in some way inhibits the establishment of high moth populations. In any case, identifying the environmental factors that make certain habitats unattractive to fall armyworm could have important benefits to the development of new control methods for this important agricultural pest.

Also affected by habitat is the distribution of the host strains. In the natural habitats, the rice strain predominates in all the traps. In comparison, the developed sites show periods when the corn strain is present in substantial numbers. This is particularly true for the spring and summer months when the corn strain is the predominant population captured. While this was not surprising for trap 13, which was located adjacent to the corn field, it was unexpected for the collection sites at the golf course (trap 6) and urban area (traps 15 and 16) where known plant hosts of the corn strain were not present in great abundance. The reason for these increases in the corn strain capture frequency is unknown, but the observations suggest that the corn strain can be supported and even thrives in non-agricultural areas. If correct, then strain differences in geographical distribution and habitat choice may reflect not only plant host preference, but also strain-specific variations in susceptibility to environmental and/or biotic factors.

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