LARVAL DEVELOPMENT OF FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) ON DIFFERENT COVER CROP PLANTS

R. L. MEAGHER, R. N. NAGOSHI, C. STUHL[1] AND E. R. MITCHELL[2]
Center for Medical, Agricultural and Veterinary Entomology, Agricultural Research Service
U.S. Department of Agriculture, Gainesville, FL 32608

[1]University of Florida, Entomology and Nematology Department, P. O. Box 110620, Gainesville, FL 32611-0620

[2]Deceased

ABSTRACT

A series of laboratory and field experiments were conducted to compare larval development, feeding behavior, and ovipositional preference of fall armyworm (*Spodoptera frugiperda*) on a standard host plant, a standard cover crop plant, and two candidate cover crop plants. The results indicate that larvae from different rearing cultures and host strains developed comparably on corn and sorghum-sudangrass, but generally developed poorly on cowpeas and sunnhemp. Larval and ovipositional experiments also suggested a preference for either corn or sorghum-sudangrass. Field plantings of cowpeas and sunnhemp in two locations were ignored by fall armyworm in favor of corn. These studies suggest that cowpeas and sunnhemp have the potential to reduce stepping stone nursery populations of fall armyworm by lengthening developmental time and increasing larval mortality.

Key Words: *Spodoptera frugiperda*, Cowpeas, Sunnhemp.

RESUMEN

Una serie de experimentos de laboratorio y de campo fueron realizados para comparar el desarrollo de las larvas, el comportamiento de alimentación, y la preferencia de la oviposición del gusano cogollero (*Spodoptera frugiperda*) en una planta hospedera típica, una planta de cobertura típica, y dos plantas candidatas para ser usadas en cobertura. Los resultados indicaron que las larvas de diferentes crias y cepas de hospederos desarrollaron similarmente en maíz y sorgo-pasto de sudan, pero en general desarrollaron pobremente en caupí y en "sunn-hemp" (*Crotalaria juncea*). Los experimentos sobre las larvas y la oviposición también sugerieron que hay una preferencia para maíz o sorgo-pasto de sudan. Las siembras de campo con caupí y *Crotalaria* en dos localidades fueron ignoradas por el gusano cogollero en favor de maíz. Estos estudios sugerieron que la caupí y *Crotalaria* tienen un potencial para reducir las poblaciones del gusano cogollero en los viveros de piedra escalonados por alargar el tiempo de desarrollo y al aumentar la mortalidad de las larvas.

Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) is a polyphagous, migratory insect that moves northward each season from overwintering areas in southern Florida (Luginbill 1928; Mitchell 1979; Pair et al. 1986; Westbrook & Sparks 1986; Mitchell et al. 1991) and southern Texas/northern Mexico (Luginbill 1928; Raulston et al. 1986; Pair et al. 1991). Populations from the overwintering areas in southern Florida move into secondary source areas or "stepping-stone nurseries" located in northern Florida and southern Georgia in April and May, and it is believed that populations from these areas can increase and add to the numbers of moths moving northward (Mitchell 1979; Pair & Westbrook 1995).

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 and sorghum (corn strain) and the other strain was identified from populations feeding on rice and forage grasses (rice strain). The two strains can be distinguished by strain-specific allozyme variants and genetic markers (Lu et al. 1994, Lu & Adang 1996; McMichael & Prowell 1999).

Corn (*Zea mays* L.) and other host plants, including vegetables and cover crops, may allow fall armyworm populations of both strains to increase during spring in the stepping stone nurseries. In northeastern Florida, over 12,000 ha of vegetable crops, primarily potatoes (*Solanum tuberosum* L.) and cabbage (*Brassica oleracea* L. var. *capitata*) are grown during January to May in three counties (St. John's, Flagler, and Putnam) (Aerts & Nesheim 2000; Larson Vasquez & Nesheim 2000). After vegetable harvest, cover crops such as sorghum-sudangrass (*Sorghum bicolor* (L.) Moench, a sorghum/sudan hybrid) generally are planted. Sorghum-sudangrass is a warm-season annual grass hybrid that is used in Florida as a green manure cover crop following harvest of winter vegetables (Chambliss 2002). These plants are used to produce biomass, contribute nitrogen to the soil, increase soil organic matter, and prevent soil erosion (Chambliss et al. 2003; Rich et al. 2003). Benefits of cover crops in regards to biomass production, nitrogen yield, and crop yield have been shown for both large vegetable production systems (Creamer & Baldwin 2000) and small subsistence farming systems (Jeranyama et al. 2000).

In northern and southern Florida large populations of fall armyworm can develop in fields planted to sorghum-sudangrass (ERM, unpublished data; Pair & Westbrook 1995). Therefore, alternative cover crops that are poorer host plants for fall armyworm may reduce migrating populations. This research was conducted to compare population development and feeding behavior of fall armyworm host strains on a standard host plant (corn), a standard cover crop plant (sorghum-sudangrass) (SSG), and two candidate cover crop plants (iron-clay cowpeas and sunnhemp). Cowpeas [*Vigna unguiculata* (L.) Walpers spp. *unguiculata*] is a warm-season annual legume that alone or mixed with SSG can be used as a rotation or cover crop with vegetables (Miller et al. 1989). Sunnhemp (*Crotalaria juncea* L.) is a warm-season legume that is used as a cover crop in alternation with vegetable crops (Duke 1981; Li et al. 2000; Rich et al. 2003).

Materials and Methods

Larval Feeding Experiments

Larvae for this experiment were from two sources. 'Tifton' larvae were from a laboratory culture reared on artificial diet and shown to carry the mitochondrial marker of corn strain (Meagher & Gallo-Meagher 2003; Nagoshi & Meagher 2003). This culture originated from individuals received from Dr. James Carpenter, USDA-ARS, Tifton, GA and was reared on a pinto bean artificial diet according to the procedures of Guy et al. (1985). 'Ona' larvae were from a culture of individuals collected in July 2002 from the Range Cattle Research and Education Center, Ona, FL. This culture was reared on grasses (bermudagrass, *Cynodon dactylon* (L.) Pers. and stargrass, *C. nlemfuensis* Vanderyst var. *nlemfuensis* 'Florona') and has the rice strain mitochondrial marker (Nagoshi & Meagher 2003).

Plants were grown in 3.8-l pots in a greenhouse at ambient temperature, and were fertilized weekly with Miracle-Gro® 15-30-15 plant food. No pesticides were applied to the plants. New growth leaves were selected from plants aged ca. 3 wk. old for cowpeas, SSG, and corn, and 6 wk. old for sunnhemp. Plant foliage was placed on filter paper discs (Whatman®, 90 mm) moistened with ca. 1 ml deionized water in a 9-cm diameter polystyrene petri dish (Thomas Scientific, catalog #3488-B32). One neonate larva was placed on plant foliage, and the petri dishes were placed in an incubator at 23.9 ± 2° with a 14:10 photoperiod. The filter paper in each petri dish was moistened daily with ca. 1 ml of deionized water for the first 10 days. Larvae were supplied with a continuous amount of fresh plant material until time of pupation. Larval weights were measured at 10 days. Development time (in days) from neonate to pupa, pupal weight, and sex were recorded at pupation. For each host plant, 15-30 larvae were arranged in three replications on different dates, and mortality on each host plant was recorded. Analysis of variance of log10-transformed data (PROC MIXED, Contrasts, Littell et al. 1996) was used to examine variation among plants.

Larval Choice Experiments

The larval choice experiments were designed to evaluate the feeding preference of larvae on leaf sections of four host plants. Rice strain larvae from the Ona culture were used along with corn strain larvae collected from a population near Hague, FL. This culture was reared on greenhouse-grown corn and was in culture for < four generations. Plant culturing and leaf selection was similar to that used for the larval feeding experiment, except that leaves were trimmed to a uniform size (ca. 2 × 5 cm).

Four separate experiments were completed. First, a four-choice experiment compared sections from the four host plants. One section of each plant was randomly placed on filter paper discs moistened with ca. 3 ml deionized water and sections were placed ca. 2 cm from the center along the outer edge of the petri dish. Twenty neonate larvae from Ona or Hague cultures were placed in the center of each petri dish, which were then placed in an incubator at 23.9 ± 2° with a 14:10 photoperiod. Counts were made after 24 h by observing the number of larvae on or under each leaf section. The second experiment was a two-choice test comparing corn to each of the other plants using Ona larvae.

Results from the first two experiments led us to test two possible explanations for the reduced plant host specificity of the rice strain culture. The third experiment examined whether the feeding experience of the parents influenced the plant host preference of the next generation. Rice strain larvae that completed development on each host plant were mated and resulting progeny were tested against all four plants. The fourth experiment was a four-choice test that used the progeny of larvae that selected each host plant in Experiment 1. Therefore, larvae that selected corn, cowpeas, SSG, or sunnhemp were reared on that plant and their progeny used in the bioassay.

All experiments contained 10 replications. Analysis of variance of square root-transformed data (PROC MIXED, Contrasts, Littell et al. 1996) was used to examine variation among plants.

Oviposition Choice Experiments

In addition to larval preference, the differential distribution of fall armyworm on different plant types could result from selective ovipositional behavior by adult females. Oviposition choice experiments were conducted in a greenhouse using plastic swimming pools as a cage. The bioassay consisted of a plastic swimming pool (109.2 cm d × 12 cm h) containing 22.7 kg of commercially available sand. Hardware cloth (1.27 cm l, 25.4 cm h) was curled and placed in the sand along the inside edge of the pool. Gray window screen was placed on top of the hardware cloth, and a second inverted swimming pool was placed on top of the screen to form a 'sandwich'.

All tests used our Gainesville laboratory culture reared on artificial diet and shown to carry the mitochondrial marker of corn strain (Meagher & Gallo-Meagher 2003). Greenhouse-grown plants (same size and age as plants used above) were placed outside for 3 d before being used. One plant of each host was placed randomly in a circle inside the unit. Ten male and female moths (<5 d old) were placed along with a 10% honey-sugar solution feeding station in the center of the unit. The screen and top pool were placed on top of the hardware cloth enclosing the moths. In this way, moths could not oviposit on the smooth surface of the top or bottom pools. Plants were sampled 48 h later for eggmasses. Experiment 1 was completed June–August 2001 and used 10 separate cages (replications); experiment 2 was completed in October 2001 and used 8 replications. All data were transformed by a square root (y + 0.5) transformation and means were separated with the Contrasts statement in PROC MIXED (Littell et al. 1996).

Field Experiments

Corn, cowpeas, SSG, and sunnhemp were planted in four randomized complete blocks at a field site in Gainesville on 19 June 2001 and at the University of Florida Vegetable Research Station, Hastings on 8 July 2001. Each plot was four rows wide by 30.5 m long. An additional treatment of green manure (SSG, incorporated into the soil 60 d after planting) was added to the Hastings test. Standard agronomic practices were used except no insecticides were applied. All plots were sampled beginning in late July and ending in early October for evidence of plant damage and the presence of larvae. Plants were sampled for larvae by checking a randomly selected one-meter row at each observation point. Analysis of variance of square root-transformed data (PROC MIXED, Contrasts, Littell et al. 1996) was used to examine variation among treatments.

RESULTS

Larval Feeding

Differences between Tifton (corn strain) and Ona (rice strain) cultures were found for larval weight, pupal weight, larval development time, and survival, and there was a significant interaction between culture and host plant ($P < 0.0001$) (Table 1). Therefore results from each culture were statistically analyzed separately. For the Tifton culture, the largest larvae were found on corn, where the average weight was higher than that of larvae cultured on SSG or cowpeas ($P < 0.001$). Larvae grown on sunnhemp were significantly smaller, averaging approximately 21% of

TABLE 1. LARVAL WEIGHT, PUPAL WEIGHT, LARVAL DEVELOPMENT TIME, AND SURVIVAL OF TIFTON (CORN STRAIN) AND ONA (RICE STRAIN) FALL ARMYWORM LARVAE FED DIFFERENT HOST PLANTS. MEANS WITH THE SAME UPPERCASE (BETWEEN CULTURES) OR LOWERCASE (AMONG PLANTS WITHIN A CULTURE) LETTER ARE NOT SIGNIFICANTLY DIFFERENT, $P > 0.05$.

Culture	Plant	Larval wt. (mg)	Pupal wt. (mg)	Development time (days)	% Survival
Tifton		50.4 ± 4.1 B	182.4 ± 4.2 A	20.9 ± 0.3 B	62.2 ± 0.07 B
	corn	83.5 ± 8.8 a	160.3 ± 6.8 b	19.1 ± 0.5 a	62.2 ± 0.12 b
	SSG	51.2 ± 6.5 b	209.6 ± 5.7 a	19.7 ± 0.3 a	95.6 ± 0.04 a
	cowpeas	34.5 ± 5.0 bc	151.9 ± 8.9 b	23.3 ± 0.6 b	51.1 ± 0.06 b
	sunnhemp	18.0 ± 3.9 c	190.6 ± 7.4 a	23.4 ± 0.5 b	40.0 ± 0.04 b
Ona		109.0 ± 6.5 A	158.8 ± 2.2 B	18.1 ± 0.3 A	77.2 ± 0.05 A
	corn	122.2 ± 6.1 b	166.8 ± 3.0 a	15.6 ± 0.2 b	91.1 ± 0.02 a
	SSG	209.6 ± 12.9 a	176.2 ± 3.1 a	14.3 ± 0.2 a	86.7 ± 0 ab
	cowpeas	62.5 ± 6.4 c	151.0 ± 4.7 b	20.5 ± 0.5 c	67.8 ± 0.04 b
	sunnhemp	41.9 ± 4.6 c	140.6 ± 4.1 c	22.1 ± 0.4 d	63.3 ± 0.13 b

the weight from those on corn (Table 1). A somewhat different result was observed with pupal weights. The heaviest pupae were those developing on SSG and sunnhemp, with those from corn and cowpeas being about 20-25% smaller. Larvae feeding on cowpeas and sunnhemp took longer to develop than those on corn and SSG, and had lower survival than those on SSG.

The rice strain was similar to the corn strain in that the smallest larvae, longest development time, and highest mortality were associated with development on cowpeas and sunnhemp (Table 1). There was unusually high early larval growth on SSG, with an average weight about 70% greater than found on corn. However this early growth on SSG did not lead to an exceptionally high pupal weight.

Larval Choice

Larvae from the more recently derived corn strain culture (Hague) selected corn over SSG and were rarely found on cowpeas ($P < 0.0001$, Table 2). No larvae were found on sunnhemp. In comparison, rice strain larvae from the Ona culture displayed an equal preference for corn and SSG compared to sunnhemp and cowpeas (Table 2). The two-choice bioassays with rice strain larvae comparing corn with the other plants showed only a difference between corn and cowpeas (Table 3).

Ona larvae whose parents were reared on the different host plants were generally found more on corn and SSG and less on cowpeas, no matter what the host plant was of the parents (Table 4). The exception was larvae from SSG-reared parents, which showed equal preference for all plants. Ona larvae whose parents selected different host plants were generally found more on corn or SSG and less on cowpeas (Table 5). Larvae from parents that selected sunnhemp were an exception, choosing that plant at a similar frequency as corn or SSG.

TABLE 2. NEONATE FALL ARMYWORM LARVAE FROM HAGUE OR ONA CULTURES TESTED IN CHOICE BIOASSAYS COMPARING FOUR HOST PLANTS. MEANS (AMONG PLANTS WITHIN A CULTURE) WITH THE SAME LETTER ARE NOT SIGNIFICANTLY DIFFERENT, $P > 0.05$.

Culture	Plant	Larvae per section
Hague	corn	14.6 ±1.3 a
	SSG	4.9 ± 1.3 b
	sunnhemp	0 ± 0 c
	cowpeas	0.2 ± 0.1 c
Ona	corn	8.3 ± 0.8 a
	SSG	6.3 ± 0.8 a
	sunnhemp	2.6 ± 0.8 b
	cowpeas	1.8 ± 0.7 b

TABLE 3. TWO-CHOICE BIOASSAYS OF ONA FALL ARMYWORM NEONATES COMPARING CORN TO SSG, SUNNHEMP, OR COWPEAS. MEANS IN EACH COMPARISON WITH THE SAME LETTER ARE NOT SIGNIFICANTLY DIFFERENT, $P > 0.05$.

Plant	Larvae per section
Corn	3.2 ± 0.7 a
SSG	4.2 ± 1.9 a
Corn	8.6 ± 0.8 a
Sunnhemp	5.2 ± 1.0 a
Corn	11.6 ± 1.5 a
Cowpeas	2.6 ± 0.5 b

Oviposition Choice

The first study performed during the summer resulted in few eggmasses and no significant difference among plants (Fig. 1). Oviposition during October was higher, with more eggmasses found on corn and SSG plants and fewer on cowpeas or sunnhemp. These results indicate that at least under greenhouse conditions and during the autumn season, females can show a preference for corn and SSG over the other plants.

Field Experiment

In Hastings, larval populations were found primarily on corn plants (12.9 ± 2.6 larvae per 1 m-row) compared to SSG (2.1 ± 0.5) or SSG with

TABLE 4. FOUR-CHOICE BIOASSAYS WITH ONA FALL ARMYWORM NEONATES WHOSE PARENTS WERE REARED ON CORN, SSG, SUNNHEMP OR COWPEAS. MEANS (WITHIN A GROUPING) WITH THE SAME LETTER ARE NOT SIGNIFICANTLY DIFFERENT, $P > 0.05$.

Plant parents reared on	Plant	Larvae per section
corn	corn	4.6 ± 1.0 a
	SSG	6.9 ± 1.3 a
	sunnhemp	3.6 ± 0.8 b
	cowpeas	2.8 ± 0.5 b
SSG	corn	5.9 ± 1.1 a
	SSG	5.2 ± 0.9 a
	sunnhemp	3.7 ± 0.8 a
	cowpeas	3.4 ± 1.4 a
sunnhemp	corn	8.0 ± 0.8 a
	SSG	7.8 ± 1.1 a
	sunnhemp	1.4 ± 0.5 b
	cowpeas	1.6 ± 0.6 b
cowpeas	corn	6.7 ± 1.5 a
	SSG	5.4 ± 0.9 a
	sunnhemp	3.6 ± 0.6 ab
	cowpeas	1.8 ± 0.7 b

TABLE 5. FOUR-CHOICE BIOASSAYS WITH F_1 ONA FALL ARMYWORM NEONATES WHOSE PARENTS SELECTED CORN, SSG, SUNNHEMP OR COWPEAS IN FIRST TEST. MEANS (WITHIN A GROUPING) WITH THE SAME LETTER ARE NOT SIGNIFICANTLY DIFFERENT, $P > 0.05$.

Plant parents selected	Plant	Larvae per section
corn	corn	5.4 ± 0.5 a
	SSG	5.4 ± 0.6 a
	sunnhemp	6.6 ± 0.9 a
	cowpeas	0.9 ± 0.3 b
SSG	corn	7.1 ± 1.0 a
	SSG	3.8 ± 0.8 b
	sunnhemp	5.7 ± 0.8 ab
	cowpeas	1.9 ± 0.4 c
sunnhemp	corn	4.7 ± 1.0 ab
	SSG	6.2 ± 0.6 a
	sunnhemp	5.0 ± 0.8 ab
	cowpeas	3.1 ± 0.6 b
cowpeas	corn	6.7 ± 0.6 a
	SSG	5.5 ± 0.8 ab
	sunnhemp	3.2 ± 0.7 bc
	cowpeas	2.8 ± 0.7 c

green manure (1.9 ± 0.5) (Fig. 2). No fall armyworm larvae were found on cowpeas or sunnhemp. The Gainesville plots provided the same information, as more larvae were collected on corn (26.0 ± 3.8) compared to SSG (3.5 ± 1.0). Very few larvae were collected on sunnhemp (0.17 ± 0.1) or cowpeas (0.08 ± 0.06). It was surprising that few larvae were found on SSG, but the results suggest that when both corn and SSG are present in the same area, fall armyworm will show a strong bias to the former.

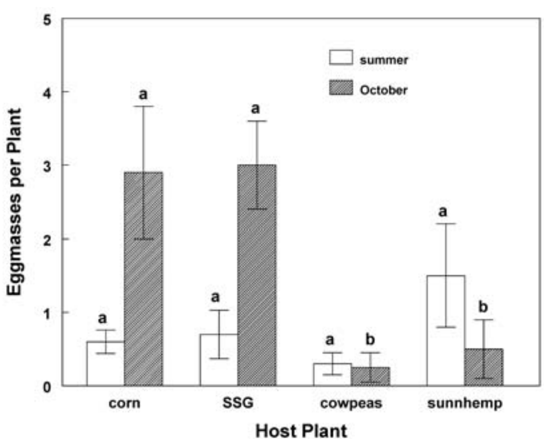

Fig. 1. Adult moths tested in swimming pool bioassays comparing oviposition on four host plants in summer and October experiments. For each test, columns with the same letter are not significantly different, $P > 0.05$.

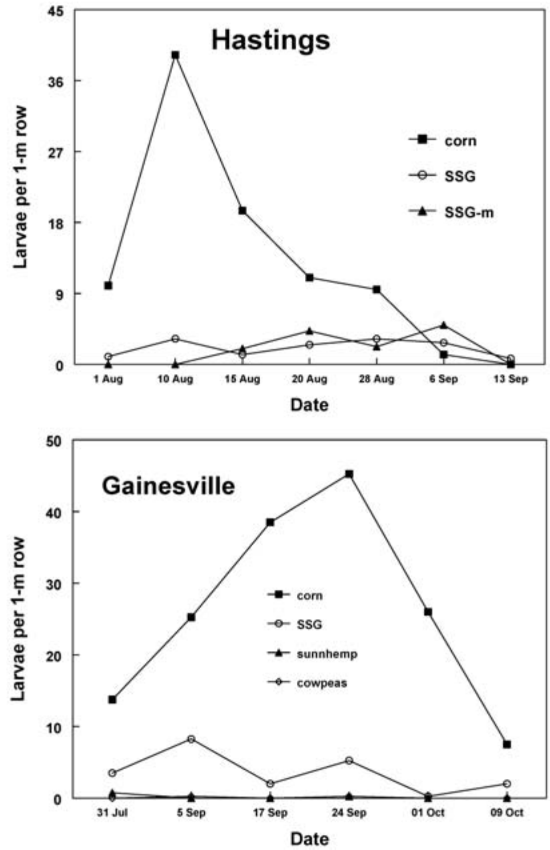

Fig. 2. Number of fall armyworm larvae collected from 1-m row of host plant in experiments conducted at Hastings and Gainesville, FL, 2001.

DISCUSSION

Previous studies have compared the development of the two host strains on different food sources, most notably corn and turf grass (Pashley 1988; Whitford et al. 1988; Pashley et al. 1995; Veenstra et al. 1995). These showed several strain-specific differences with respect to larval and pupal weights, consumption rates, development times, and mortality. It was surprising that only 62.2% of the Tifton larvae feeding on corn survived to the pupal stage. Although the Tifton culture shows the mitochondrial marker for corn strain, it was a laboratory culture that historically developed on meridic diet and may have exhibited feeding behavior effects of colonization (Mason 1987).

In general, rice strain larvae were larger and the development period shorter than the corn strain on all four host plants. This differs from previous reports indicating that when grown on corn, corn strain larvae were larger (Pashley et al. 1995). Apparently substantial variation can occur with different cultures and experimental conditions. Despite these potential difficulties, our larval feeding studies consistently indicated that the two strains find cowpeas and sunnhemp to be a less favorable food source than corn or SSG.

Results from the larval choice experiments suggest strain differences in the preference of larvae to particular plant hosts. While both strains were attracted to corn, the corn strain preference appeared to be stronger and more specific. The result with corn strain larvae is consistent with a previous study that showed that larvae demonstrated a strong preference for corn over turf grass (Pashley et al. 1995).

For rice strain larvae, parental feeding on corn or SSG did not lead to increased bias of their progeny for these plants. Similarly, the larvae from parents raised on cowpeas or sunnhemp showed no increased preference to these plants. These results indicate that parental feeding history does not significantly influence the feeding preference of the progeny. Experiment 4 tested whether the variation in the rice strain culture was due to genetic polymorphisms, e.g., the presence of subpopulations with heritable biases to different plants. If this were the case, then larvae from parents that selected a particular host should be predisposed to the same bias, resulting in an increased proportion of that generation choosing the same plant. Results showed no clear evidence of strong heritability for plant preference. Therefore, it appears that the reduced specificity of rice strain larvae to corn compared to the corn strain represents an innate strain-specific difference.

Fall armyworm oviposition has been described on corn (Thomson & All 1983) and cotton (Ali et al. 1989), with differential preferences reported both within and among crops (Combs & Valerio 1980; Pitre et al. 1983). Only one previous study examined oviposition preference between host strains, with results showing a strong preference for corn strain moths to oviposit on corn and rice strain moths to oviposit on bermudagrass (Whitford et al. 1988). Recent research suggests that tactile cues may be more important than plant volatiles (Rojas et al. 2003), consistent with observations of egg masses on many non-plant objects such as vinyl flags (Thomson & All 1982), plastic bucket traps, and vehicle mirrors (RLM, unpublished). Our results indicate that a seasonal and/or environmental context must be taken into account when interpreting ovipositional studies.

A previous study described fall armyworm infestation in a forage sorghum field in southern Florida (Pair & Westbrook 1995). With 64% of the 200-ha field infested, the authors calculated hypothetically that the field could have produced 320 million adults/ha if 50% of the larvae survived to adulthood. The amount of SSG grown in Florida is not known, but almost 122,000 ha of vegetables were planted in 2002 (Anonymous 2003). If 50% of the vegetable land is planted to a SSG cover crop, over 19 trillion adult moths are potentially produced (320 million adults per ha × 61,000 ha). Therefore, large numbers of moths are potentially produced that could migrate to northerly areas or remain in local areas to later infest future crops.

Our experiments suggest that cowpeas and sunnhemp have the potential to reduce these populations of fall armyworm by lengthening developmental time and increasing larval mortality. Furthermore, these alternative cover crops are much less attractive to fall armyworm larvae and adults, and so may limit the concentration of this pest when corn is unavailable. Reducing the endogenous fall armyworm population in cover crops could both mitigate the level and delay the timing of infestation during the subsequent corn-growing season while simultaneously interfering with migration. While a potentially effective and economical means of cultural control, substantial additional research is needed to determine the influence of cover crops on the population dynamics of fall armyworm and thereby the potential effect of changes in cover crop choice. In particular, we need to determine the extent to which different cover crops serve as refuges for fall armyworm populations throughout the year and in particular during periods when corn is unavailable.

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