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## BEHAVIOR AND DISTRIBUTION OF THE TWO FALL ARMYWORM HOST STRAINS IN FLORIDA

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### ABSTRACT

Fall armyworm is a significant agricultural pest in the United States, affecting most notably sweet corn and turf grass. While infesting much of North America, fall armyworms invading the eastern United States arise from annual migrations of populations wintering in southern Florida. It has long been noted that this seasonal geographical localization represents an opportunity for controlling this pest prior to its annual migration. However, such efforts have been hindered by the presence of two genetically distinct but morphologically identical strains that differ physiologically and behaviorally. The biology of the host strains is poorly understood and this lack of knowledge precludes accurate predictions of fall armyworm population behavior in the field. This paper reviews recent studies examining strain behavior and discusses the potential relevance of these results to the development of effective regional management strategies that can be used proactively to mitigate the economic impact of this pest.

Key Words: *Spodoptera frugiperda*, area wide management, corn, turf grass.

### RESUMEN

El gusano cogollero es una plaga significativa para la agricultura de los Estados Unidos, que afecta mas notablemente el maíz dulce y pastos. Mientras que infestan la mayor parte de America del Norte, los gusanos cogolleros que invaden el este de los Estados Unidos provienen de las emigraciones anuales de poblaciones que pasan el invierno en el sur de Florida. Por un largo tiempo se ha notado que esta localización geográfica por estaciones climáticas representa una oportunidad para controlar esta plaga antes de la emigración anual. Sin embargo, estos esfuerzos han sido paralizados por la presencia de dos cepas genéticamente distintas pero morfológicamente idénticas con una fisiología y un comportamiento diferentes. La biología de las cepas con respecto hospederos es pobremente conocida y es esta falta de conocimiento la que impide la predicción precisa del comportamiento de la población del gusano cogollero en el campo. Este artículo revisa los estudios recientes que han estudiado el comportamiento de las cepas y discute el potencial pertinente de estos resultados al desarrollo de estrategias de manejo regionales efectivos que pueden ser usados pro-activamente para mitigar el impacto económico de esta plaga.

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) is a periodic and significant economic pest in most of the continental United States, capable of causing substantial losses in maize, sorghum, forage grasses, turf grasses, rice, cotton, and peanut production (Luginbill 1928; Sparks 1979). Because fall armyworm do not survive conditions of prolonged freezing, most of the infestations in the continental U.S. derive from annual migrations of populations that over winter in southern Florida and southern Texas (Barfield et al. 1980). This localization of winter populations theoretically provides an opportunity to dramatically reduce the migratory population, as previously noted in a quote from E. F. Knipling: "The fall armyworm could serve as a model species for developing the concept of managing highly mobile pests by an organized attack on populations at a strategic time and place for the purpose of protecting crops in other and perhaps much

larger areas at some later time in the seasonal cycle" (Knipling 1980). Unfortunately, the biological information necessary to develop an area-wide management strategy for this pest has been slow in coming, in large part because two morphologically identical but physiologically distinct host strains have complicated efforts to understand and predict fall armyworm behavior in the field. This paper reviews recent studies describing new methods of strain identification that greatly enhance our capacity to investigate and understand fall armyworm population biology. Preliminary results suggest that at least one strain, whose primary target is corn, might be particularly amenable to a regional management program.

### Characteristics of the Two Host Strains

The existence of two strains was originally postulated after comparisons of electrophoretic pro-

tein variants from the wild identified genetically distinct subpopulations that were preferentially associated with either large grasses (designated corn-strain), such as corn and sorghum, or smaller grasses (designated rice-strain), such as rice and bermudagrass (Pashley 1986; Pashley 1988a; Pashley et al. 1985; Pashley et al. 1987a). This host plant specificity reflects nutritional adaptation, as rice-strain larvae feeding on corn displayed a slower rate of weight gain, longer developmental time, lower pupal weight, and reduced survival than when reared on bermudagrass (Pashley 1988b; Pashley et al. 1995; Veenstra et al. 1995). Whitford et al. (1988) also reported reductions in larval and pupal weight but did not observe differences in developmental time or survival. The effect on larval growth rate correlated with higher levels of mixed-function oxidase (an enzyme family involved in detoxification pathways) in the corn-strain. In contrast, the same set of studies showed that rearing corn-strain larvae on rice or bermudagrass had no consistent negative effect on larval development or fitness.

However, the observed nutritional variations are unlikely to completely account for the plant host bias exhibited by the strains. In behavioral preference tests, first instars of both strains strongly preferred corn to turf grass (Pashley et al. 1995; unpublished data). In addition, although both strains developed equally when reared on rice or turf grass, corn-strain larvae were rarely found on these plants in the field, present in only 3% of larvae collected from wild grass (McMichael & Prowell 1999). In contrast, and despite their adaptation to rice and bermudagrass, rice-strain larvae made up as much as 16% of the samples collected from corn plants. These results suggest that habitat specificity in strain distribution is probably due to adult behavior, the most obvious candidate being ovipositional host choice. However, because inconsistent results were obtained in the one major study testing this possibility, the biological basis for the plant host bias exhibited by the two strains remains unexplained (Whitford et al. 1988).

An important consideration for the management of this pest is that differences were found in the response of the two strains to chemical and biological agents. Rice-strain larvae were more susceptible than the corn-strain to several insecticides, including diazinon and carbaryl, while the reverse was true for carbofuran (Adamczyk et al. 1997; Pashley et al. 1987b). Similarly, the rice-strain was more susceptible than the corn-strain to transgenic *Bacillus thuringiensis* Berliner (Bt) cotton (Adamczyk et al. 1997). In addition, some bermudagrass cultivars bred for fall armyworm resistance showed differential effectiveness with respect to the two strains, with rice-strain larvae generally able to gain more weight and consume more plant material than their corn-strain counterparts (Jamjanya et al. 1990; Leuck et al. 1968;

Lynch et al. 1983; Pashley et al. 1987a; Quisenberry & Whitford 1988). Clearly strain-identity must be taken into consideration when evaluating the effectiveness of new insecticides and "resistant" plant cultivars.

#### DNA Markers of Strain Identity

The fall armyworm strains are morphologically identical, making an unambiguous determination of strain identity difficult and largely limited to molecular methods. Restriction Fragment Length Polymorphisms (RFLPs) were identified in genomic DNA and formed patterns that could be segregated into two distinct groups generally consistent with the rice-strain and corn-strain populations derived from allozyme comparisons (Lu et al. 1992). Similarly, dendrograms produced by amplified fragment-length polymorphism analysis revealed two assemblages that were over 90% consistent with strain assignments based on host plant (McMichael & Prowell 1999). The same two groups could be identified by comparing variations in mitochondrial DNA (mtDNA) sequences, which was modestly more accurate than allozyme analysis at distinguishing strains (Lu & Adang 1996; Pashley 1989). In particular, an *MspI* restriction enzyme polymorphism was identified that was diagnostic of strain identity and for which a PCR-based detection method was developed (Levy et al. 2002; Lu & Adang 1996). These techniques allowed detection of the strain-specific RFLP from individuals exposed to outdoor conditions for up to two weeks after death (Meagher & Gallo-Meagher 2003; Fig. 1a).

The potential usefulness of this methodology to assay populations was demonstrated by the examination of adult males captured in pheromone traps. Specimens from cornfields during the spring growing season were tested by PCR with 72% (21/29) shown to carry the corn-strain marker (*mtC*). This contrasted with 39% (15/39) when the same traps were tested a few weeks after harvest. We compared these findings to collections made during the same time periods from traps placed in a pasture habitat containing primarily small grass species. During the pre-harvest and post-harvest periods, over 90% (18/19 and 17/18, respectively) carried the rice-strain (*mtR*) marker. Therefore, the distribution of the *COI* polymorphism in adult males correlates with the expected behavior of fall armyworm strains with respect to the local plant population.

Another genetic marker for strain identity is *FR* (for Fall armyworm Rice strain), a tandem-repeat sequence present in large clusters only in the rice-strain genome (Lu et al. 1994). We developed a PCR-based method for detecting *FR* sequences that allowed analysis from single individuals (Nagoshi & Meagher 2003b). When *FR* clusters are present in the template DNA, PCR amplifica-

tion produces a "ladder" of fragments resulting from the synthesis of different multiples of the repeated sequence, a consequence of the tandem repeat organization that allows a variety of amplification alternatives (Fig. 1b). In comparison, amplification of genomic DNA from the corn-strain produces between 0-3 bands, indicating the absence of large clusters. Through a series of genetic crosses we unambiguously mapped *FR* clusters to the sex chromosomes (Nagoshi & Meagher 2003a). This was consistent with earlier reports of sexual dimorphism in the numbers of *FR* clusters present in the rice-strain, suggestive of an order of magnitude more copies on the Y than on the X chromosome (Lu et al. 1994).

#### Interstrain Mating Behaviour

The persistence of genetic and physiological differences between the host strains strongly suggests barriers to matings between strains. However, a comparison of strain-specific esterase allozymes and mtDNA polymorphisms suggested that interstrain hybridization was occurring in wild populations (Prowell 1998). Between 11-16%

of individuals carrying an allozyme marker of one strain had an mtDNA genotype of the other. One laboratory study indicated that this interbreeding may be limited in nature (Pashley & Martin 1987). When corn-strain females were mated to rice-strain males (C X R), no progeny were produced and no spermatophores were transferred. In contrast, the reciprocal mating of rice-strain females to corn-strain males (R X C) had fertility equal to control (within-strain) crosses. However, the hybrid R X C daughters produced failed to mate with males from either strain but were able to mate with their hybrid brothers, although with reduced fertility. In comparison, R X C hybrid males could fertilize females of either strain, although again fertility was somewhat reduced. These results suggest significant strain-specific mate selection, such that corn-strain females have a strong preference to males of the same strain or to hybrids, while rice-strain females are more promiscuous. However, this interpretation must be tempered by the failure of two subsequent studies to find similar directional and restricted interstrain mating behavior (Quisenberry 1991; Whitford et al. 1988). Instead, normal fertility was observed in both directions of interstrain crosses. We were also able to obtain fertile progeny from the mating of corn-strain females to rice-strain males in the laboratory, with no obvious differences in fecundity from within-strain crosses (unpublished results). The discrepancy between the mating experiments performed by different laboratories is unexplained, but suggests that laboratory culturing and conditions may easily confound strain-specific mate selection.

Support for the existence of an assortative mating mechanism came from field studies in which virgin females of each strain were used to attract and capture males in the wild. Males of both strains exhibited a (60-75%) preference to females of the same strain, suggesting that pheromone differences might have a role in mate choice (Pashley 1993; Pashley et al. 1992). However, a more substantial difference was observed in studies examining the temporal partitioning of nocturnal mating activities (Pashley et al. 1992). Corn-strain females began calling (releasing pheromone) earlier in the scotophase than the rice-strain. Even more significant was the observation that strain-specific matings occurred at opposite times of the night with little overlap. The corn-strain mated during the first two-thirds of the evening while the rice-strain mated in the last third. Hence assortative mating might reflect divergence in the timing of strain-specific mating activity, with additional contributions coming from differences in pheromone attraction.

To measure the degree to which interstrain matings occur in the wild, we made use of the fact that our two strain-specific genetic markers undergo different but predictable inheritance pat-

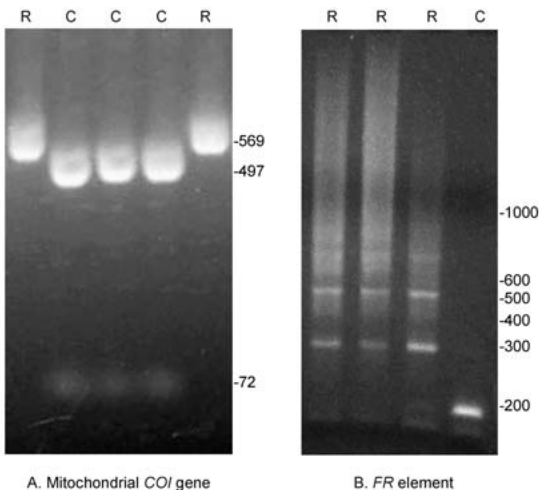


Fig. 1. Agarose gels displaying the diagnostic strain-specific DNA markers used to distinguish the host strains. Genomic DNA from individual adult males were individually amplified by PCR. (a). A portion of the mitochondrial *COI* gene was amplified. After digestion with *MspI*, a single band (569 bp) indicates the absence of the strain-specific *MspI* site, a characteristic of the rice-strain (*mt<sup>R</sup>*) (R). Two smaller bands (497 bp and 72 bp) are produced if the *MspI* site is present, indicating a corn-strain (*mt<sup>C</sup>*) (C) identity. (b). Three rice-strain individuals and one corn-strain individual were analyzed by PCR for the presence of *FR* clusters. PCR analysis produces a DNA ladder with an upper molecular weight smear in *FR<sup>R</sup>* specimens and 0-3 distinct bands in *FR<sup>C</sup>* samples. The gels were stained with ethidium bromide and photographed under ultraviolet illumination. Sizes are in base pairs.

terns. We designated the parental rice-strain marker configuration as  $mt^R FR^+$  and the corn-strain as  $mt^C FR^0$ . With interstrain crosses, the mitochondrial marker should display a strictly maternal inheritance pattern while  $FR$  will exhibit sex linkage. This was confirmed by genetic crosses performed in the laboratory in which each set of parents was sacrificed and tested for their molecular genotypes after mating and oviposition (Nagoshi & Meagher 2003a). As predicted the  $mt^C FR^+$  hybrid configuration was produced in males from a single cross between strains, while the reciprocal  $mt^R FR^0$  hybrid combination was produced in males in two generations (Fig. 2). Therefore, if interstrain matings are common in the wild and there are no substantial fitness differences between genotypes, a random sampling of field-collected males should show substantial numbers of all four combinations. In particular, the number of  $mt^C FR^+$  should approximate the number of  $mt^C FR^0$  males. In contrast, if mating within the parental strains is highly preferred or substantially more productive, then the parental marker configurations ( $mt^C FR^0$  and  $mt^R FR^+$ ) should predominate. After a random sampling of field collected males from several southern Florida locations, we found 56% (199/356) of  $mt^R$  individuals had the hybrid configuration ( $mt^R FR^0$ ), consistent with substantial R X C interstrain matings (Nagoshi & Meagher 2003a). In contrast, only 3% (4/144) of

$mt^C$  males were  $FR^+$ , the reciprocal hybrid pattern. These data strongly suggests that productive matings between corn-strain females and rice-strain males rarely occur in the wild, preventing the introduction of  $FR$  carrying X chromosomes into a corn-strain maternal background.

If the  $mt^R FR^0$  field population is derived from interstrain hybridization, then we might expect to see some deviation in plant host preference from their “pure strain”  $mt^R FR^+$  siblings. To examine this possibility, we compared the proportion of  $mt^R FR^0$  individuals in the rice-strain pool collected from different habitats (Nagoshi & Meagher 2003a). A “primarily corn habitat” was arbitrarily defined as one where in which over 70% of the fall armyworm collected were  $mt^C$ , indicating that the plants in this time and area were attractive primarily to the corn-strain. Similarly, traps containing over 70%  $mt^R$  males were defined as “primarily grass habitats.” The remainder formed the “mixed habitat” category. We found that the proportion of  $FR^0$  males within the rice-strain pool increased to 83% (15/18) of the total rice-strain population trapped in corn habitats, compared to 61% (39/64) in areas biased to the rice-strain and 51% (23/45) in mixed habitats. Although the differences are only of borderline statistical significance, the trend is consistent with  $mt^R FR^0$  males being less specific in their plant host preference than  $mt^R FR^+$  males.

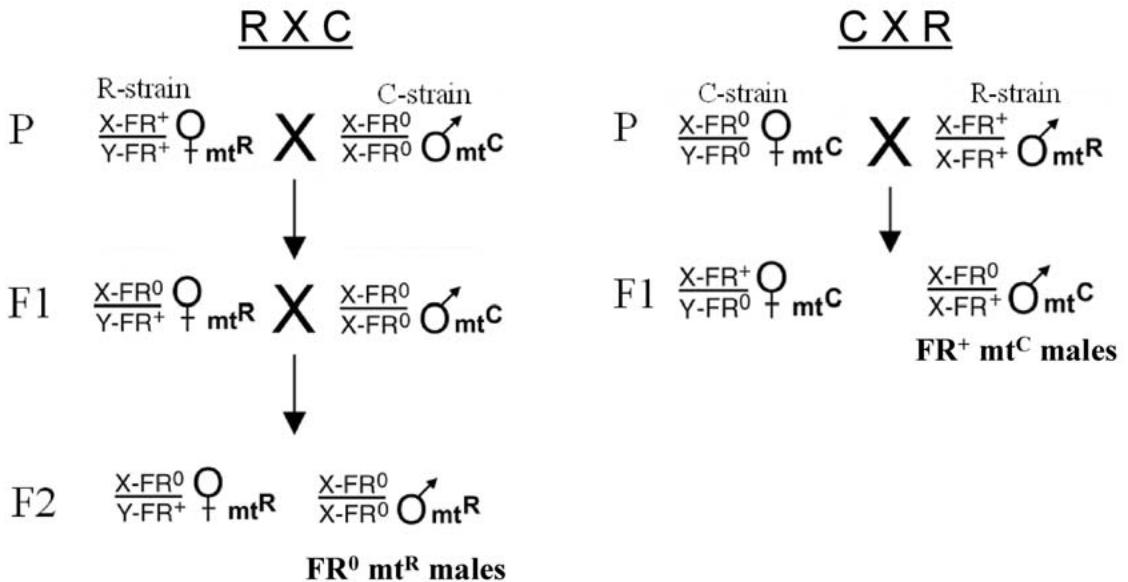


Fig. 2. Fall armyworm interstrain crosses designed to produce progeny with a hybrid marker configuration (Nagoshi & Meagher 2003b).  $FR$  clusters are on the sex chromosomes (X and Y) while the mitochondrial haplotype is maternally inherited. In Lepidopterans the female is the heterogametic sex. In the R X C mating, rice-strain females ( $mt^R FR^+$ ) are mated to corn-strain males ( $mt^C FR^0$ ). The hybrid female progeny are backcrossed to corn-strain males. All the resulting  $F_2$  males will have the hybrid configuration ( $mt^R FR^0$ ). The C X R mating represents the reciprocal cross. All  $F_1$  males will be heterozygous for  $FR$  clusters and therefore identified as  $FR^+$  by PCR. All will also be  $mt^C$  because of their corn-strain mother.

### Undeveloped Areas do not Support High Fall Armyworm Populations

Critical to the development of an area-wide management strategy for fall armyworm is an understanding of the relative contributions of the various host plants to the overwintering and migrating populations of each strain (Knippling 1980). While several studies have examined sweet corn growing agricultural areas in Florida, other types of environments have not been examined in detail. To address this issue, we surveyed four different habitats that reflect some of the principal environments present in southern Florida (Meagher & Nagoshi 2004; Nagoshi & Meagher 2004). These are naturalized grassy wetlands and three types of developed areas: agricultural fields, managed turf grass (a sod farm and golf course), and urban.

We found that traps placed in geographically dispersed natural areas all showed very low capture rates throughout the year (Meagher & Nagoshi 2004). Over the 18-month test period the average for these traps was 0.4 captures/night/trap. Aside from unusually high numbers in two collections in February 2002, the average captures/night/trap never surpassed 5 for any two-week collection period (from March 2002 to July 2003). This occurred even though there was a high density and variety of short and tall grass species in the areas adjacent to these traps. Apparently these undeveloped habitats do not serve as high density refuges for fall armyworm at any time of the year, and are therefore unlikely to contribute substantially to the northward migrating populations in the spring or be a major source of

the reinfestation of Florida agricultural areas in the fall and winter.

In contrast, 5-10-fold higher adult captures occurred in traps in a turf grass sod farm (average 8 captures/night/trap), agricultural fields (average 17 captures/night/trap), and urban developments (average 5 captures/night/trap). These results suggest that several types of human activities can lead to increases in the local fall armyworm population. 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 populations. Alternatively, developed areas may differ in the type, density, or quality of plant growth. 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.

### The Corn-Strain is Primarily Found in Agricultural Areas

We used the strain-specific molecular markers combined with extensive pheromone trapping to examine the distribution of the strains in the different habitats (Meagher & Nagoshi 2004; Nagoshi & Meagher 2004). The rice-strain was found to be present in substantial proportions in all areas examined. This was particularly the case in the natural habitats and the sod farm, where over 90% of the captured males were of the rice-strain, though in the former the overall rate of capture was low (Fig. 3). In terms of numbers, the largest contributions came from agricultural areas and, not surprisingly, the turf grass-rich sod farm.

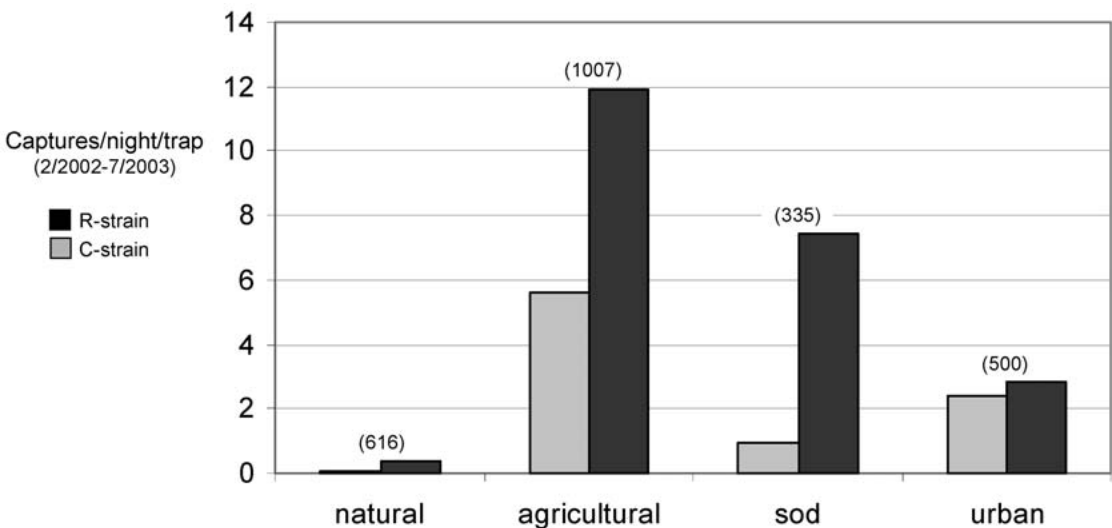


Fig. 3. Adult males captured per night in pheromone traps in four different habitats in southern Florida from February 2002 to July 2003. Fall armyworm numbers tested for strain identity at each habitat is in parenthesis. Data include those reported in Meagher & Nagoshi (2004) and Nagoshi & Meagher (2004).

By far the highest numbers of corn-strain captures occurred in the agricultural areas, where an average of nearly 6 corn-strain males was captured/night/trap, representing 32% of the total collection population at this site. Surprisingly, we also found a high proportion of the males trapped in urban areas were of the corn-strain, representing about half of the capture population. This was unexpected given that these sites did not have plant hosts in the vicinity known to be attractive to the corn-strain. However, the urban site averaged only a little over 2 corn-strain captures/night/trap, less than half of that observed in agricultural areas but still significantly (>95%) greater than observed in natural areas (Meagher & Nagoshi 2004). In comparison, although the overall fall armyworm population in the sod farm was relatively high (>8 captures/night/trap; Fig. 3), it contributed only modest amounts of corn-strain, averaging 1 capture/night/trap. Corn-strain captures in natural areas were inconsequential.

A critical question with respect to controlling fall armyworm infestation is to determine where the build up of strain populations occurs prior to the annual northward migration. This movement is at least in part dependent upon the timing of favorable weather patterns (Luginbill 1928; Mitchell et al. 1991); hence, a significant reduction in population numbers prior to the storm fronts could substantially reduce fall armyworm infestation in the eastern U.S. Population surveys in southern Florida cornfields typically show a rise in the overall fall armyworm population in the spring, followed by a rapid and prolonged decline during the summer months that presumably reflects the northward migration (Mitchell et al. 1991; Nagoshi & Meagher 2004; Pair et al. 1986). We conducted surveys of the four habitat types in the spring (February to May) of 2002 and 2003, just prior to the early summer migration period (Meagher & Nagoshi 2004). By far, the highest populations of corn-strain were found in the agricultural areas, displaying a 3-fold higher trap capture rate than the next highest (urban) site (Fig. 4a). Natural areas, the sod farm, and one season's data from a golf course indicated only minor contributions from these locales. In comparison, the rice-strain was found in substantial numbers in both agricultural and managed turf habitats, consistent with a broader host range (Fig. 4b). These results indicated that in the weeks prior to migration, the corn-strain population that will be the source of much of the corn damaging fall armyworm infestation in the eastern U.S. was mostly localized to the agricultural fields of southern Florida.

#### Comparisons of Seasonal Changes in Strain Populations

Because both strains are detected in regions where they are unlikely to survive the winter, it is expected that both migrate. However, given their

different habitat preferences it would not be surprising to find strain-specific variations in migration behavior. This possibility was first suggested by studies in Louisiana that found the corn-strain population, first detected in the spring, reached a peak in density in early to mid-summer coincident with the maturation of the local corn crop (Pashley et al. 1987b). In comparison, the rice-strain population did not show substantial numbers until late summer, a period when the corn-strain population was nearly absent (Pashley et al. 1992). These differences suggest that the timing and/or magnitude of migration may not be the same for both strains.

If there are habitat-dependent or strain-specific factors that initiate migration, then we might expect the two strains to differ in the timing of their northward movement, which presumably can be detected by the sudden decline in capture numbers in southern Florida traps. We tested this by the examination of fall armyworm populations in agricultural fields predominated by sweet corn and tomatoes and a sod farm associated with turf grass (Meagher & Nagoshi 2004; Nagoshi & Meagher 2004). These sites were chosen because their respective plant populations allow clear predictions about the strain that should be attracted. Our data indicated that the corn- and rice-strains showed the same July-October population trough, although there is some evidence that the rice-strain decline begins earlier than the corn-strain (Fig. 5, arrows). This was even the case in comparisons between the rice-strain population in the sod farm with corn-strain in the agricultural habitat, indicating this population pattern was not dependent on the timing of sweet corn planting and harvesting. Instead, the decline in population appears to be due to some more general environmental or biological condition. Previous studies have attributed similar changes in the fall armyworm population to variations in plant quality and quantity resulting from the wet-dry seasonal cycle characteristic of tropical areas (Pair et al. 1986). For example, in studies performed in Mexico, high capture rates tended to occur 60-90 days after rainfall peaks, while intervals of least capture most frequently occurred 60-90 days after periods of least rainfall (Raulston et al. 1986). Alternatively, sharp declines in capture numbers during the year may be related to extremes in the daily minimum temperature. We found in our study that fall armyworm captures for both strains were lowest when the daily minimum temperature rose above 20°C (July-October) or fell below 5°C (January; see Nagoshi & Meagher 2004). There is precedence for correlations between daily temperature and field capture numbers for other insects (Butler et al. 1999; Cammell & Knight 1992; Scott et al. 2000; Souza & Carvalho 2002). It may be that an important fall armyworm behavior, such as mating or

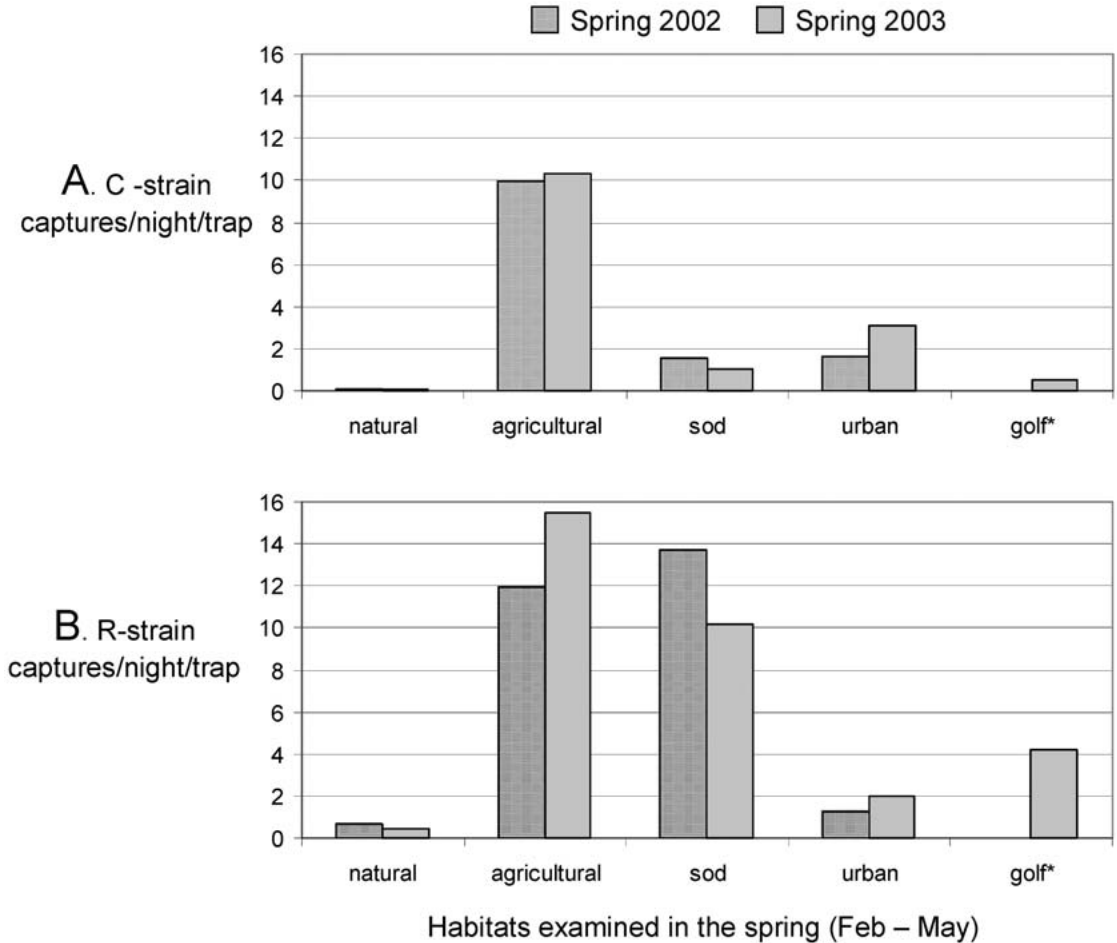


Fig. 4. Adult males captured per night in pheromone traps in four different habitats in southern Florida prior to the spring migration in 2002 and 2003 for corn-strain (a) and rice-strain (b) moths. Asterisk indicates only spring 2003 data available. Data include those reported in Meagher & Nagoshi (2004) and Nagoshi & Meagher (2004).

flight activity, is affected deleteriously by seasonal temperature extremes.

After the summer decline, fall armyworm populations begin increasing in the fall and winter in agricultural areas, coincident with the late year corn growing season. The timing of this increase was shown to correlate with weather and wind conditions conducive to southward migration, leading to the suggestion of a north-to-south return movement prior to the winter freeze (Mitchell et al. 1991; Pair et al. 1986; Pair et al. 1987). Our studies on strain distributions during this period led to the surprising observation that the fall population peak was due entirely to increases in rice-strain numbers (Nagoshi & Meagher 2004). Despite the presence of extensive sweet corn plantings in the agricultural trap areas from October to May, corn-strain numbers did not increase until February (Fig. 5, dashed line). The same pattern was observed in the fall of 2003 in

the same and in additional agricultural test sites (Nagoshi & Meagher 2004; unpublished results). Interestingly, the rice-strain population in the sod farm site showed a similar population dynamic, indicating that this behavior is not specific to the agricultural planting and harvest cycle. Apparently, the presence of its preferred host plant and environmental conditions conducive to expansion of the rice-strain population were not sufficient to stimulate corn-strain increases during the fall. The reason for this is unknown, but these observations suggest that if there is a return migration in the fall, it is rice-strain specific.

Alternatively, there may be environmental factors that specifically prevent the expansion of either a migrant or indigenous corn-strain population late in the year. An intriguing, but purely speculative, explanation would be the existence of a corn-strain specific pathogen or natural enemy whose numbers increase during the year,



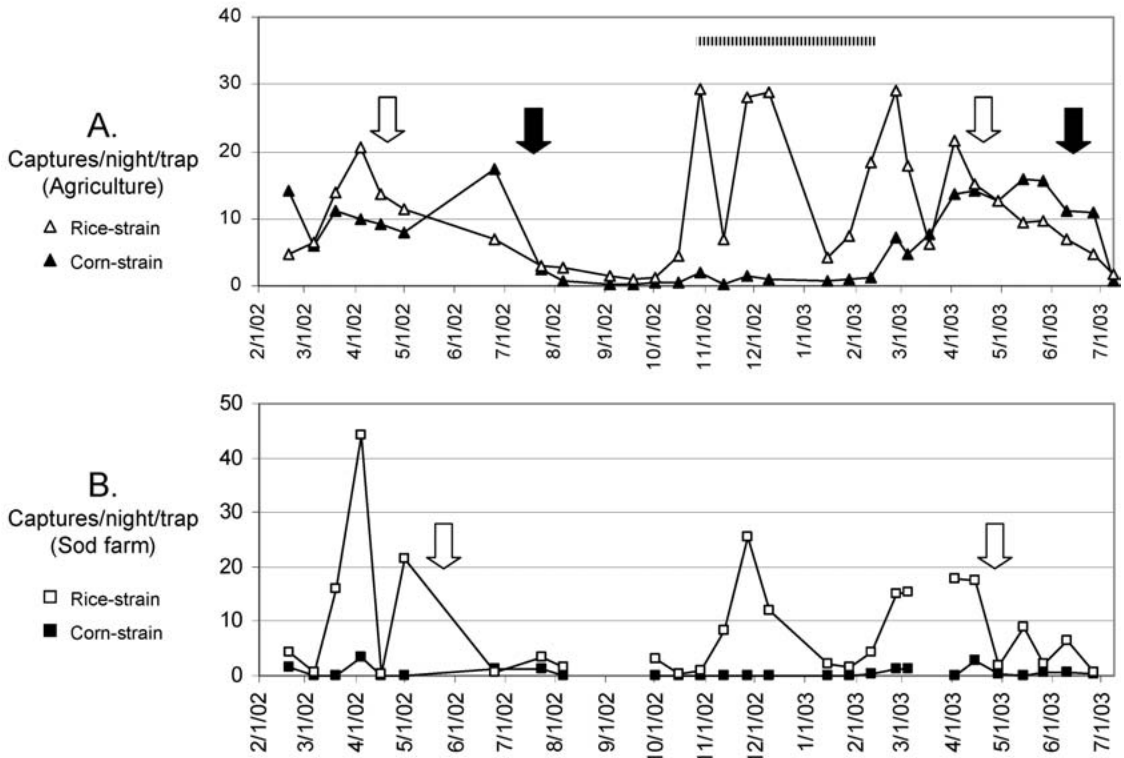


Fig. 5. Distribution of strains collected from pheromone traps in agricultural areas and a turf grass sod farm. The strain composition of each collection was determined by PCR and used to calculate the average number of each strain present per night per trap during each collection period. Arrows point to when the spring population begins to decline (open: rice-strain; filled: corn-strain). Dashed line indicates period of high fall armyworm numbers in the fall/winter associated with the rice-strain. Data include those reported in Nagoshi & Meagher (2004).

thereby suppressing reestablishment of a late season corn-strain, but not rice-strain, reinfestation. A crash in this putative population during the winter would then allow the corn-strain population peak observed every spring. It is clear that identifying the biological or environmental reasons for the relative absence of the corn-strain in the fall could have important ramifications for the development of strain-specific suppression methods.

#### Prospects for the Area-wide Control of Fall Armyworm Strains

Studies show that weather conditions prior to migration and changes in agricultural practices in southern Florida can mitigate significantly the duration and severity of fall armyworm damage in the eastern U.S. (Luginbill 1928; Westbrook & Sparks 1986). These observations suggest that changes in fall armyworm population dynamics in the overwintering area can significantly alter the magnitude of the northward migration. Unfortunately, the large amount of acreage, the broad host range and high mobility of the pest, the inter-spersion of urban development in the infested

areas, and the presence of many ecologically-sensitive habitats make area-wide suppression of fall armyworm in southern Florida difficult. Current technology does not provide an affordable or environmentally benign method for the complete suppression of fall armyworm populations under these conditions. However, our studies show that the corn-strain has a relatively limited seasonal and geographical distribution in southern Florida. It may, therefore, be economically feasible to focus efforts over a limited time and space just prior to the normal migration period, with the objective to substantially reduce the corn-strain migrant population or delay migration such that the most vulnerable portions of the more northern corn growing seasons are missed.

Studies on the seasonal and geographical distribution of fall armyworm strains also have uncovered possible seasonal or habitat-specific factors that seem very effective in controlling the corn-strain. Both strains are largely absent in naturalized areas despite the presence of grass species that should be attractive to the rice-strain and laboratory evidence that corn-strain larvae are fully capable of normal development on these

substrates. We also observed surprisingly low numbers of corn-strain males captured in pheromone traps in all habitats tested during the fall, a period of extensive agricultural activity and substantial increases in the rice-strain capture population. The absence of a corn-strain population peak under conditions favorable to the rice-strain, and when host plants normally attractive to the corn-strain are present, suggests the existence of unknown factors effective in suppressing population numbers.

Current and ongoing studies on the strains indicate that a regional management program designed to mitigate or delay fall armyworm migration might be feasible. Still needed are longer term and more detailed information on the geographical and seasonal distribution of the fall armyworm strains in southern Florida, in particular the timing of the spring and fall population increases with respect to seasonal and environmental factors. We also need a more extensive understanding of strain-specific biology, including the mechanisms of strain-specific mating and ovipositional choice, and the effects of interstrain hybridization on behavior and physiology (in particular fertility, migration, plant host choice, and susceptibility to chemical and biological agents). While substantial research remains, we believe that information and techniques are now available that can address these issues and lead to the development of an effective area-wide management strategy.

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