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REVIEW OF FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) GENETIC COMPLEXITY AND MIGRATION

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ABSTRACT

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) is a significant economic pest in the western hemisphere, causing substantial losses in corn, sorghum, forage, and turf grasses. Although fall armyworm does not survive severe winters, it infests most of the central and eastern United States and Canada because of annual migrations from overwintering sites in Florida and Texas. A detailed description of these movements is a prerequisite for identifying the factors that determine the timing and direction of migration and for developing models that can predict the severity of infestations at the migratory destinations. Complicating this effort is genetic heterogeneity within the species, which increases phenotypic variability. Particularly important are 2 "host strains", defined by a preferential association with either large grasses (designated corn-strain), such as corn and sorghum, or smaller grasses (designated rice-strain), such as rice and bermudagrass. This paper reviews recent studies examining the genetic complexity of fall armyworm populations, including characteristics of the 2 strains and the possibility of subgroups within strains. The use of this information to monitor short and long distance movements is discussed.

Key Words: *Spodoptera frugiperda*, migration, haplotype, cytochrome oxidase I

RESUMEN

El gusano cogollero, *Spodoptera frugiperda* (J. E. Smith) es una plaga económicamente significativa en el hemisferio occidental, que causa perdidas substanciales en maíz, sorgo, forraje y céspedes. Aunque el gusano cogollero no sobrevive los inviernos severos, siempre infesta la mayor parte de las regiones central y este de los Estados Unidos y Canadá por la eigraciones anuales de los sitios de invernación en los estados de Florida y Texas. Una descripción detallada de estos movimientos es un prerrequisito para identificar los factores que determinan el tiempo y la dirección de la migración y para desarrollar modelos que pueden predecir la severidad de las infestaciones en las destinaciones donde emigra. Complicando este esfuerzo es la heterogeneidad genética que existe en la especie, la cual aumenta la variabilidad fenotípica. Particularmente importante son 2 "cepas de hospedero", definidas por su asociación preferencial con pastos grandes (designada la cepa de maíz), tales como el maíz y sorgo, o pastos pequeños (designados como la sepa de arroz), tales como el arroz y pasto bermuda. En este articulo se revisa los estudios recientes que examinan la complejidad genética de poblaciones del gusano cogollero, incluyendo las características de 2 cepas y la posibilidad de subgrupos entre las cepas. Se discute el uso de esta información para el monitoreo de su movimiento por a distancias cortas y largas.

The Two Host Strains

Molecular markers remain the most accurate indicators of strain identity (McMichael & Prowell 1999; Prowell et al. 2004) and the most convenient of these are mitochondrial haplotypes that can be assayed by polymerase chain reaction (PCR) amplification methods (Levy et al. 2002; Meagher & Gallo-Meagher 2003; Nagoshi et al. 2006b). Strain-specific polymorphisms within the mitochondrial Cytochrome Oxidase I (COI) gene consistently divide fall armyworm populations into 2 haplotype groups. The demonstration that these delineate the host strains is based primarily on the observation that the haplotypes are asymmetrically distributed among plant hosts in the field, with the corn-strain haplotype typically representing about 80% of the larvae isolated from corn and the rice-strain haplotype in over 95% of the larvae collected from pasture or turf grasses (Pashley 1989; Prowell 1998). Initial descriptions of fall armyworm assumed a genetically homogeneous population capable of large variations in such behaviors as plant host choice. This was shown to be overly simplistic by the demonstration of 2 morphologically identical host strains as originally indicated by comparisons of electrophoretic protein variants from samples collected from large grasses (designated corn-strain), such as corn and sorghum, or smaller grasses (designated rice-strain), such as rice and bermudagrass (Pashley et al. 1985; Pashley 1986; Pashley et al.

1987a Pashley 1988b). There are several reports describing differential effects of plant hosts on the viability and development of the 2 strains (Pashley 1986; Pashley 1988b; Whitford et al. 1992; Pashley 1993; Pashley et al. 1995; Meagher et al. 2004), as well as different levels of sensitivities to a variety of pesticides (McCord & Yu 1987; Yu 1991; Veenstra et al. 1995; Adamczyk et al. 1997; Yu 1999). There has been recent interest in examining *Bacillus thuringiensis* Berliner (Bt) susceptibility in fall armyworm, although in many cases the strain identity of the lines being tested was unclear (Adamczyk et al. 1997; Lynch et al. 1999; Adamczyk et al. 2001; Dequech et al. 2005; Polanczyk & Alves 2005; Monnerat et al. 2006; Williams et al. 2006; Chilcutt et al. 2007). Despite these studies, a behavioral or physiological bioassay capable of reliably distinguishing between strains has yet to be described.

Studies of fall armyworm populations from Brazil indicate that subpopulations with the same host preferences as the rice-strain and corn-strain are present in South America (Busato et al. 2004; Busato et al. 2005; Nagoshi et al. 2007b; Machado et al. 2008), and that these can be detected by the same strain-specific mitochondrial markers used to distinguish North American strains (Nagoshi et al. 2007b). This supports a relatively ancient divergence of the 2 strains (Lewter et al. 2006), and further suggests that the factors driving divergence is present throughout most of the western hemisphere.

Evidence of a Hybrid Subpopulation

The persistence of genetic and physiological differences between the host strains strongly suggests limitations to hybridization between strains. Supporting this hypothesis was the observation of directional interstrain mating biases. In crosses between corn-strain females to rice-strain males, no spermatophores were transferred to the females, while the reciprocal cross produced normal levels of fertility (Pashley & Martin 1987). The hybrid females produced by interstrain crosses could only successfully mate with their hybrid brothers. In comparison, the hybrid males could mate with females of either strain with near normal fertility. Similar directional mating bias was observed in field studies using multilocus genetic analysis where 2 or more genetic markers were used to identify strains, and discrepancies in identity were assumed to result from interstrain hybridization. In one set of studies, combinations of strain-biased markers from esterase allozymes, mitochondrial DNA (mtDNA), and AFLPs were use to identify samples discordant for at least one marker (Prowell et al. 2004). A discordance frequency of 16% was observed with a slight majority (54%) displaying a mitochondrial cytotype consistent with a rice-strain female to corn-strain male mating.

A second study compared mtDNA with a tandem-repeat sequence called *FR* (for *F*all armyworm *R*ice strain), which was reported to be localized to the sex-chromosomes and present in large clusters only in the rice-strain genome of the Mississippi populations tested (Lu et al. 1994). A PCR-based method for detecting *FR* sequences was developed that allowed rapid analysis of single individuals (Nagoshi & Meagher 2003). In a multiyear sampling of field collected samples from several regions we confirmed the rice-strain biased distribution of FR. Over 70% of the mt^R population sampled in Brazil in 2005 were FR^+ compared to 14% of the mt^C group (Nagoshi et al. 2008), while about 40% mt^R specimens from Texas (2006-7) and Florida (2003-7) were FR^+ compared to about 10% of the mt^C population (Nagoshi & Meagher 2003; Nagoshi et al. 2008). Such geographical and temporal consistency strongly supports the existence of mating or selection biases that are preventing a more homogeneous distribution of *FR* between the 2 strains.

There was an unexpectedly high proportion of mt^R $FR0$ samples, which in Florida and Texas represented the majority of the mt^R population. It is possible that this "discordant" class results from interstrain matings between rice-strain females and corn-strain males, an explanation supported by the observation that this genotype displayed a different plant host distribution pattern than either parental strain (Nagoshi et al. 2006a). If this pattern is a result of interstrain mating then it suggests a strong bias for rice-strain females mating with corn-strain males relative to the reciprocal pairing (Pashley & Martin 1987), as the reciprocal "hybrid" configuration, mt^C FR^+, is relatively rare (Nagoshi & Meagher 2003; Nagoshi et al. 2008).

The observation that the putative hybrids may behave differently from the parents is potentially important because it identifies an additional group besides the host strains whose behavior must be considered for a complete understanding of fall armyworm population dynamics. Prowell et al. (2004) also observed that the majority of the hybrids with the rice-strain mitochondrial cytotype (but other corn-strain markers) were found in a corn habitat, though they interpreted this as possibly resulting from increased opportunities for interstrain mating in corn habitats. While we cannot distinguish between these explanations, we note that the behavioral and physiological differences reported for the 2 strains would suggest that interstrain hybridization should have significant phenotypic consequences.

The possibility of genetic subpopulations in addition to the 2 strains could explain discrepancies observed between the published reports on fall armyworm behavior. In particular, 2 laboratories were unable to find directional differences in interstrain mating in controlled crosses (Whitford

et al. 1988; Quisenberry 1991). Instead normal fertility were observed in all crosses between strains and when using hybrids. One possibility is that mating behavior is a labile trait, perhaps sensitive to artificial rearing and testing conditions (Pashley 1993; Prowell et al. 2004). Alternatively, it may be that the fall armyworm population is more genetically complex than that described by the 2 strains. There may be a range of genotypes that exhibit different mating behaviors and strain specificities such that independently derived colonies of the same strain may not be equivalent.

Genome-wide Examination of Genetic Heterogeneity

There have been several studies with genome-wide methods to study genetic variation in fall armyworm populations. These include the RAPD (Random Amplification of Polymorphic DNA), RFLP (Restriction Fragment Length Polymorphism) and AFLP (Amplified Fragment Length Polymorphism) techniques (Lu et al. 1992; McMichael & Prowell 1999; Busato et al. 2004; Prowell et al. 2004; Busato et al. 2005; Martinelli et al. 2006; Clark et al. 2007). Attempts to identify genetic markers that can distinguish between populations from geographically distant regions have given mixed results. A survey of fall armyworm from maize and cotton plants in Brazil with RAPD identified some clustering of genotypes according to geographical origin, with only limited gene flow evident between sites. However, AFLP surveys that sampled populations from such distantly separated locations as those in Argentina, Brazil, Mexico, Puerto Rico, and Iowa failed to find evidence of clusters associated with geography (Clark et al. 2007; Martinelli et al. 2007). The overall results suggest that fall armyworm populations are genetically heterogeneous with interbreeding occurring generally throughout the western hemisphere (Clark et al. 2007). If so, then identifying genetic markers that can accurately and consistently identify the geographical origin of a population will be difficult by these methods.

These molecular studies bring into question how the host strains maintain their integrity in the face of substantial within-strain genetic variation and evidence of significant interstrain hybridization. One proposed explanation was based on the observations that strain-specific genetic markers represented a small minority of the detected polymorphisms, with the majority of these either mapping to the sex-chromosomes or, in the case of the mitochondrial haplotypes, displaying a sex-restricted inheritance pattern (Prowell 1998). If the sex chromosomes contain the strain-specifying genes then these may exhibit limited gene flow compared to the more profligate mixing of the rest of the genome. There is evidence for sex-chromosome biased speciation in Lepidoptera in

general and fall armyworm specifically (Sperling 1994; Prowell 1998). Therefore, techniques that use autosomal markers to examine population structure may not be successful in identifying fall armyworm strains.

Several studies identified phylogenetic groupings consistent with strain designations (Lu et al. 1992; McMichael & Prowell 1999; Busato et al. 2004; Prowell et al. 2004), with some indications that interstrain hybridization could be detected (McMichael & Prowell 1999). However, an AFLP survey comparing populations from the U.S., Central America, and South America failed to find clusters associated with plant host even in comparisons between samples collected from bermudagrass and maize, where strain differences would have been expected (Clark et al. 2007). This could indicate variability in strain host use, as has occasionally been observed with rice-strain predominating on corn (Nagoshi & Meagher 2004; Prowell et al. 2004), or the use of AFLP markers that were not specific to the strains. The latter is a distinct possibility given the substantial genetic heterogeneity observed in fall armyworm populations (Clark et al. 2007), even when sampling inbred laboratory lines (Lu et al. 1992).

Local Population Movements Between Corn and Cotton Habitats

The most simple and direct method to identify the strain infesting a plant is to analyze larvae for strain identity. But this is problematic for plant hosts that are secondary or sporadic targets of infestations where finding larvae is difficult and any such collections tend to be biased for unusual "outbreak" events when infestation levels are abnormally high. These may not be representative of the typical behavior of the species. Another issue is that larval surveys may not be predictive of adult numbers if there are substantial strain differences in fitness during pre-adult stages (Fitt 1989), a major problem when trying to estimate the contribution of a particular plant host to the overall fall armyworm population.

A useful method for estimating plant host usage was developed for the study of *Helicoverpa zea* (Boddie), which like fall armyworm is a pest of corn and cotton (Gould et al. 2002). The stable carbon isotope ratio ($^{13}C/^{12}C$) in adult wings, commonly designated as $\delta^{13}C$, was used to determine whether the specimen arose from a C_3 (i.e., cotton) or C_4 (i.e., corn) plant host. Studies in Lepidoptera have found that while adult behavior can influence the isotope ratio, the primary determinant is the larval diet (Ponsard et al. 2004). Gould et al. (2002) was able to show that corn can serve as a refuge for *H. zea* infesting Louisiana Bt cotton and used the observed seasonal changes in the proportions of C_3 and C_4 moths to infer patterns of plant host use and migratory behavior.

This strategy was used to identify of the strain of fall armyworm most likely to infest cotton in the U.S. Preliminary studies comparing protein polymorphisms showed that larvae collected from cotton in Ecuador were more similar to the corn-strain than the rice-strain (Pashley 1986), and genetic examination of Brazilian fall armyworm populations showed substantial gene flow between larvae isolated from corn and cotton fields (Martinelli et al. 2006). While both imply that the corn-strain infests both corn and cotton, it is not clear whether this observation applies to U.S. fall armyworm, the contribution of cotton to the overall population, or if the rice-strain might also be a significant cotton pest.

To address these issues, fall armyworms were collected by pheromone trapping in cotton fields within the Mississippi delta region during 2004 and 2005 and tested both for their carbon isotope ratios and strain identity (Nagoshi et al. 2007c). The prediction was that the fall armyworm subpopulation arising from cotton would display a higher proportion with a C_3 signature in a pattern corresponding to the availability of cotton at susceptible development stages. Fall armyworm can feed on squares, blooms, and bolls and has an approximately 37-d developmental cycle on cotton (Pitre & Hogg 1983). Assuming that infestation began in mid-Jun when approximately half the crop was squaring, the first adults arising from cotton should be present by late summer, with numbers increasing into the fall, and declining after harvesting. The corn-strain best displayed the expected pattern. After being largely absent during the early cotton growing season, the C_3 corn-strain population increased rapidly in the Aug to Oct period (Fig. 1). During these collections, the proportion of corn-strain developing from C_3 plants was at its highest levels, reaching averages of 17% in 2004 and 39% in 2005 that were significantly higher than the preceding and subsequent periods. These results are all consistent with the corn-strain, but not the rice-strain, infesting and successfully developing on cotton (Nagoshi et al. 2007c). The predominance of adults with the C4 signature early in the growing season further indicates that the infesting population originally developed on a C4 host, most likely corn since it is a preferred host of the corn-strain and large plantings were present within a few miles of the test site.

Long-range Migration Patterns

Historical studies. Various attempts have been made to describe the annual migrations of fall armyworm in North America. The only regions in the U.S. in which the insect is consistently know to survive the winter are southern Florida and southern Texas (Luginbill 1928). One of the early descriptions of migration from these overwinter-
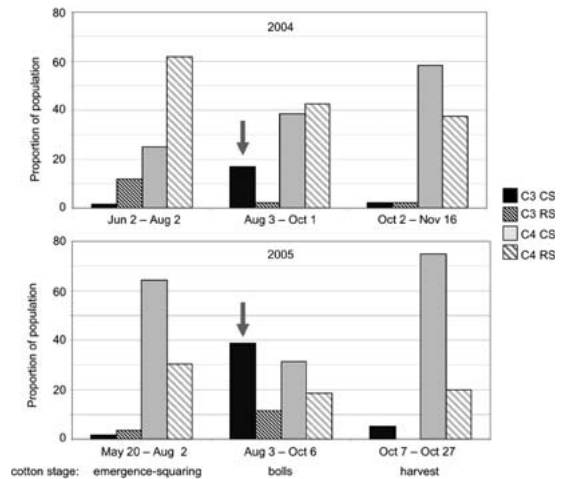

Fig. 1. Proportion of field-collected fall armyworm of a given strain and ^{13}C value in the Mississippi delta region during the 2004 and 2005 growing seasons. (n) represents the total number of samples tested during each time period. Data from Nagoshi et al. (2007c).

ing areas came from observations of the timing of fall armyworm appearance in selected locations (Luginbill 1928). Populations in southern Texas appear to move northward into Oklahoma and northeasterly following the coastal plain and into the Mississippi river valley. The southern Florida populations were believed to migrate to northern Florida typically by early May and into north-central Georgia by Jun, continuing east of the Appalachians into South Carolina by Jul. Fall armyworm first appears in central Tennessee by mid-Jul, in southeastern Kansas in late Jul, and in the Ohio Valley and Maryland during Aug and Sep (Luginbill 1928).

Synoptic meteorological analysis was used to calculate atmospheric trajectories that seemed to generally corroborate observations of fall armyworm at migratory destinations (Rose et al. 1975; Westbrook & Sparks 1986; Mitchell et al. 1991). When coordinated with pheromone trap captures, it was evident that favorable wind currents were conducive to the spread of fall armyworm into uninfested areas (Mitchell et al. 1991). These types of studies also provided evidence for a reverse (south to north) migration in the fall (Pair et al. 1987; Mitchell et al. 1991). However, the resolution of the trap data was not sufficient to identify the source of the migrant populations.

Pheromone trap methods in combination with larval collections were used in an extensive survey of southeastern states during 2 "off-years" in which widespread fall armyworm outbreaks were not observed in any location (Pair et al. 1986). The strategy again was to use the sequential appearance of the insect in different locations to estimate migration movement. It was observed that

infestations occurred earlier and were more severe in the Florida panhandle and Baldwin Co., AL (located just west of Pensacola, FL) than in southern Georgia. This suggested to the authors a northwesterly movement from southern Florida, perhaps infesting the Mississippi Valley states, as well as a subsequent northeastern movement into Georgia and South Carolina (Pair et al. 1986).

Population movements could also be inferred by a comparison of disease or pesticide resistance of fall armyworm from different locations. Examination of resistance to carbaryl and methomyl suggested that in 1977, infestations of the eastern states could have originated in both Texas and Florida while infestations farther west were derived primarily from populations in Texas and Mexico (Young 1979). However, a different study comparing pesticide resistance suggested that the Texas population was isolated from fall armyworm in Georgia and Florida, and that Mississippi and Florida populations were similarly separated (Pitre 1988). A comparison of resistance to nuclear polyhedrosis virus suggested that fall armyworm from Brazil was at least partly isolated from those around the Gulf of Mexico, but that there was mixing of populations through Texas, Louisiana, Florida (Fuxa 1987). While not completely consistent, these studies suggest regional differences between fall armyworm populations that may derive from geographical isolation. However, a possible complicating factor is that fall armyworm host strains were not considered in these studies.

Taken together, the data provide a broad estimation of the direction of fall armyworm migration into the northern U.S., but not one sufficiently detailed to identify the specific destinations of migrants arising from the overwintering sites in Florida and Texas. A more direct way to achieve this objective is to identify genetic markers that can distinguish between migrants from Florida and Texas.

Molecular monitoring of migration. Molecular analysis of the mitochondrial COI gene identified 2 nucleotide sites that were polymorphic within the corn-strain. The polymorphisms generated 4 haplotype subgroups (labeled as CS-h1, CS-h2, CS-h3, and CS-h4) that together make up the entire corn-strain population examined (Nagoshi et al. 2007a). Surveys of Florida corn-strain populations from different geographical locations, seasons, or plant hosts consistently showed the pattern of CS-h4 > CS-h2 > CS-h1, with only a small number of the CS-h3 haplotype sporadically found. These results combined with the relative stability of the haplotype distribution pattern during the 4-year period from 2002 to 2006 strongly suggest a homogeneous corn-strain population that is in equilibrium in the state of Florida. This is not surprising given that the mobility of fall armyworm should facilitate the rapid mix-

ing of populations. A different haplotype pattern was observed in Brazil, based on surveys in the 2 nonadjacent states of Parana and Mato Grosso that lie along the southwestern border. The Brazil populations display a haplotype relationship of CS-h2 > CS-h1 > CS-h4, with no CS-h3 haplotype collected. The CS-h4 haplotype, the dominant subgroup in Florida, was found in less than 10% of the samples from either Brazilian state.

Most relevant to studies on North American migration was the observation that haplotype proportions in Texas fall armyworm from both pheromone trap and larval collections consistently displayed the pattern of CS-h2 > CS-h1 = CS-h4, with the CS-h3 haplotype detected sporadically and at low levels (Nagoshi et al. 2008). This haplotype profile appears to be in equilibrium based on captures at three different locations over a multiyear period, and is similar to that found in Brazil corn-strain populations. Because the primary difference between the profiles lies in the relative proportions of the CS-h2 and CS-h4 haplotypes, a ratio of the 2 haplotype proportions provides a simple metric to quickly distinguish between the profiles. Collections in Florida, Brazil, and Texas gave CS-h4/CS-h2 ratios of 2.4, 0.05, and 0.15, respectively. Pairwise comparisons of the data demonstrated a statistically significant difference between the CS-h4/CS-h2 ratios observed in Florida populations with those from Texas or Brazil, but no indication of a significant difference between Texas and Brazil (Nagoshi et al. 2007b) (Fig. 2).

If the migration behavior of the corn-strain haplotypes is the same, and there is no reason to expect otherwise, then it should be possible to determine the origin of migrant populations by comparing their haplotype profiles with those in Florida and Texas. As a proof of concept, we tested corn-strain populations in Georgia, Alabama, Louisiana, and Mississippi, states that lie adjacent to Texas or Florida and along an east-west
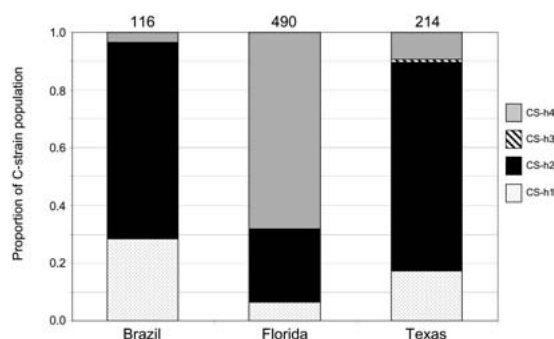

Fig. 2. Proportions of the corn strain haplotypes present in samples collected from different locations in Florida. Numbers above bars indicate number of samples tested. Data from Nagoshi et al. (2007b).

line from the Atlantic Ocean to the Gulf of Mexico (Nagoshi et al. 2008). The results indicated that the most eastern of the states, Georgia, was infested by corn-strain populations that were indistinguishable in haplotype distribution from those overwintering in southern Florida. Corn-strain populations in Louisiana, Mississippi, and Alabama were statistically indistinguishable to populations sampled in central and southern Texas. This distribution pattern suggests a migratory pattern similar to that described by Luginbill (1928), in which the fall armyworm overwintering in Texas migrate north and eastward through Lousiana, Mississippi, and into Alabama, while Florida populations move northward into Georgia (Fig. 3).

It has been suggested that there is a return migration of fall armyworm in the autumn during which the populations in the northern states move southward to repopulate the overwintering sites (Pair et al. 1987; Mitchell et al. 1991). If there is substantial mixing of the overwintering populations among the migrants followed by a southern return, then we should see a gradual homogenization of the Florida and Texas populations with respect to haplotype proportions. Alternatively, the long-term persistence of the asymmetrical haplotype distribution would argue that return migrations either do not occur or that any genetic mixing is limited in scope. The alternative seems to be the case as the haplotype profiles of Florida from 2003-2006 and Texas from 2004-2007 has remained relatively constant.

SUMMARY

The highly mobile and genetically diverse fall armyworm presents many technical challenges for studies on migration and population dynamics. Traditional methods of field observations, trap captures, and synoptic weather analysis have generally supported but only marginally added to the early estimations of fall armyworm migration (Luginbill 1928). However, relatively recent advances in molecular techniques make possible a far more detailed analysis of fall armyworm movements that begins to take into account the presence of genetically define subpopulations. In the near future, we anticipate mapping the annual migration of the corn-strain population throughout North America from their overwintering sites in Texas and Florida, and extending this analysis to compare the historical movements of the Brazil and Florida subgroups of this strain in the Caribbean, South America, and Central America. As more genetic markers are uncovered it may be possible to perform analogous studies on the rice-strain and interstrain hybrid populations to develop a more complete description of the migratory behaviors of this important agricul-

Fig. 3. Locations of the corn-strain fall armyworm haplotype profiles in selected states in the southeastern U.S. Circles with diagonal lines display the Florida profile, clear circles indicate the Texas profile. Data from Nagoshi et al. (2008).

tural pest. We anticipate that the more detailed understanding of fall armyworm population movements will facilitate efforts to find more accurate ways to predict the timing and severity of infestations and to assess the feasibility of mitigating infestations at migratory destinations by population suppression in the overwintering sites.

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