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# Oviposition Choice of Two Fall Armyworm (Lepidoptera: Noctuidae) Host Strains

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**Abstract** Fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is a noctuid species that is composed of two morphologically identical sympatric host strains (corn and rice) that differ in their distribution among plant hosts. In an effort to explain observations of host fidelity in the field, ovipositional preference of the two strains on corn (*Zea mays* L.) or pasture grass (*Cynodon nlemfuensis* Vanderyst var. *nlemfuensis*) was determined using two greenhouse bioassays. In the first bioassay, corn strain females placed more eggmasses on the screen enclosure than on corn plants while grass plants contained an intermediate number of eggmasses. Rice strain females placed most of their eggmasses on grass plants. In the second bioassay, corn strain females placed an equal number of eggmasses on corn and grass plants in comparison to rice strain females which placed >3.5× more eggmasses on grass plants than on corn plants. Individual eggs as part of the eggmasses were also counted on plants and on the screen enclosure. Corn strain females equally placed eggs on the two host plants and on the screen enclosures, however rice strain females placed more eggs on grass plants compared to corn plants or the screen enclosure. This is the first report of consistent differential oviposition between corn and rice strain fall armyworm females.

**Keywords** Host strains · fall armyworm · ovipositional choice · host fidelity

## Introduction

Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) is an important migratory pest species that feeds on a variety of crops throughout the Nearctic and Neotropical Western Hemisphere (Luginbill 1928; Wiseman and Gourley 1982; Jamjanya and Quisenberry 1988; Todd et al. 1991; Marenco et al. 1992; Braman et al. 2004; Hall

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et al. 2005; Adamczyk et al. 2008; Farias et al. 2008). This species is composed of two morphologically identical sympatric host strains that can be distinguished by genetic markers (Levy et al. 2002; Nagoshi and Meagher 2003b; Nagoshi et al. 2006b). The most distinguishing characteristic of the strains is their differential distribution among plant hosts in field surveys (Nagoshi and Meagher 2004a; Prowell et al. 2004), with “corn strain” larvae preferentially found on maize (*Zea mays* L.), sorghum (*Sorghum* spp.), and cotton (*Gossypium hirsutum* L.) plants, and “rice strain” larvae associated with rice (*Oryza sativa* L.) and forage grasses (*Cynodon* spp. and other species) (Pashley et al. 1985, 1987 Pashley 1986; Nagoshi et al. 2007).

There appears to be substantial strain differences in host fidelity. In pasture habitats rice strain individuals are predominant, with <7% of larvae or adult males (from pheromone traps) showing the corn strain haplotype. This contrasts with 16%–35% of larvae with rice strain markers in corn or cotton fields (Prowell et al. 2004; Nagoshi et al. 2006a, 2007; Machado et al. 2008). At least some of this variability may be due to interstrain hybrids, which genetic marker studies show are a significant component of field populations and that tend to be more prevalent in corn strain habitats (Nagoshi 2010; Nagoshi and Meagher 2003a). These hybrids could represent situations where the rice strain mitochondrial haplotype is now associated with corn strain host preference (Nagoshi and Meagher 2003a; Nagoshi et al. 2008; Nagoshi 2010). Pheromone trapping studies in agricultural habitats routinely attract males of both strains, indicating a sympatric distribution and ample opportunities for interstrain mating (Meagher and Nagoshi 2004; Nagoshi and Meagher 2004b). Despite this complication, the asymmetric distribution of the two strains is consistently observed, indicating strong pressure to maintain strain divergence with selective plant host preference a potentially important component. Host choice can produce pre-mating isolation between sympatric populations (Via et al. 2000), and host specialization has been observed in Lepidoptera to drive assortative mating (Emelianov et al. 2001, 2003; Malausa et al. 2005).

The basis for the strain-specific differences in plant host distribution is not known. There are two likely explanations, either there is differential larval survival on different plant hosts or females exhibit host-specificity in their ovipositional substrate. A number of feeding studies have been performed looking for strain differences in the utilization of different plant types for nutrition and development (Pashley 1988; Whitford et al. 1988; Pashley et al. 1995; Meagher et al. 2004; Stuhl et al. 2008). The results vary considerably between studies and generally show that strain differences in growth and development are relatively minor and often inconsistent. Both strains are capable of efficiently utilizing the preferred host plant of the other, indicating that differential larval feeding is unlikely to be sufficient to explain observations of host fidelity in the field (Groot et al. 2010).

Ovipositional preference of fall armyworm host strains has been examined in two reports with inconclusive results. In a laboratory choice bioassay, corn strain females laid significantly more eggmasses on corn or sorghum than bermudagrass, while the same study with rice strain females showed a preference for bermudagrass in one trial and no difference in the second trial (Whitford et al. 1988). However, another study showed oviposition from females obtained as larvae from corn fields (suspected corn strain) to be varied, with statistically similar numbers of eggmasses found on wheat, corn, sorghum, bermudagrass and rye (Pitre et al. 1983). Other laboratory oviposition choice tests were reported to have failed because of a high frequency of egg deposition on artificial structures (Prowell et al. 2004). Taken together, these studies do not provide a clear indication of ovipositing preference for particular host plants.

We reinvestigated the possibility of strain-specific ovipositional behavior with two major modifications from previous studies. The first was to use colonies where each member of the founder population was molecularly analyzed for strain identity, thereby minimizing the possibility of cross-contamination by the other strain. The second was to accept egg deposition on non-plant surfaces as a valid result and incorporate that data into the analysis. Two different bioassays were tested that measured oviposition frequency either by number of eggmasses or individual eggs. The results are discussed in the context of past studies and in relation to field observations of strain distributions in different Florida habitats.

## Materials and Methods

### Generation of Strain-specific Colonies

Fall armyworm eggmasses and larvae were collected during 2003, 2004 and 2008 from multiple sites in Florida and one location in Mississippi, U.S.A. The corn strain colonies (CS-Hag03 and CS-DRU08) were collected as larvae from field corn at the University of Florida Dairy Research Unit, Hague, Alachua Co. The rice strain colonies were collected as larvae from forage grasses located at the University of Florida Range Cattle Research and Education Center, Ona, Hardee Co. (RS-Ona03 and RS-Ona04) and from a bermudagrass pasture in Washington Co., MS by J. Adamczyk (RS-MS04). After development on artificial diet (see below), single adult pair matings were performed in small oviposition cages according to the procedures of Stuhl et al. (2008). After oviposition, the parents were analyzed for strain identity using cytochrome oxidase I gene (COI) markers (Nagoshi et al. 2006b). Only progeny from parents of the appropriate strain were used to generate the laboratory colonies (Table 1).

Culture procedures followed Stuhl et al. (2008). Briefly, adults were placed in cylindrical screen cages (28 cm height, 21 cm diameter) and supplied with a 2% sugar-honey solution for nourishment. Paper towels (Sparkle™, Georgia-Pacific,

**Table 1** Geographic location and host plant where larvae were collected, number of pairs used to establish the colony, and filial generation of moths used for the oviposition bioassays

| Strain | Colony | Location/Date | Host plant | # Pairs | Generations |
|---|---|---|---|---|---|
| Corn | CS-Hag03 | Hague, FL, USA May 2003 | Field corn | 6 | 6–8 |
| | CS-DRU08 | Hague, FL, USA May 2008 | Field corn | 24 | 5–18 |
| Rice | RS-Ona03 | Ona, FL, USA May-August 2003 | Mixed pasture grass | 16 | 6–8 |
| | RS-Ona04[a] | Ona, FL, USA October 2003 | Mixed pasture grass | 5 | 8–62 |
| | RS-MS04 | Greenville, MS, USA August 2003 | Bermudagrass | 10 | 8–10 |

[a] RS-Ona04 colony was a combination of RS-Ona03 plus new material analyzed and added from October 2003 larval collections

Atlanta, Georgia, U.S.A.) were stretched at the tops of the cages as an oviposition substrate. Emerging neonates were placed in rearing tubs (Rubbermaid No. 4025, 9.1 l, Fairlawn, Ohio, U.S.A) that had plastic grids (29×17.5 cm) on the bottom. Corn and forage grass host plants grown under greenhouse-growing conditions may provide an inconsistent level of nutritional quality (Jamjanya et al. 1990), therefore larvae were raised on a pinto bean artificial diet according to the procedures of Guy et al. (1985). After about 23 days, pupae were removed from the tubs, sexed, and emerged adults were placed in the screen cages. Larvae and adults were reared in incubators or large rearing units at ≈23°C, 70% RH, and 14:10 photoperiod.

### Oviposition Bioassays

Eight pairs of adults of either host strain (CS-Hag03 and RS-Ona03; <72 h old) were released in a screen enclosure placed inside a Conviron® plant growth chamber. Each strain was tested separately. The enclosure measuring 178×76×120 cm was constructed of 1.9 cm PVC pipe and nylon window screen. Five corn ('Truckers Favorite') and five forage grass plants (stargrass, *Cynodon nlemfuensis* Vanderyst var. *nlemfuensis* 'Florona') in 550 ml pots were randomly placed within the enclosure. An effort was made to provide equal surface areas between the two plant species but leaf area was not measured. 'Florona' stargrass is a long-lived, persistent perennial grass similar to bermudagrass types that was observed growing in Ona in 1973 (Mislevy et al. 1993). Previous research showed this grass to be an excellent host for fall armyworm (Meagher et al. 2007). Plants were fertilized weekly with Miracle-Gro® 15-30-15 plant food; no pesticides or fungicides were applied. Plant age during testing was approximately three weeks. The chamber was set at 23.9±2°C, ~80% RH with a 14:10 photoperiod. Two plastic soufflé cups (Solo, P100) with a saturated cotton ball containing a 10% honey-sugar solution were placed inside the enclosure for moth nourishment. Females were allowed to freely oviposit within the enclosure. The numbers of eggmasses were counted on each host plant after a period of 72 h. The inner surface of the enclosure was also inspected as a possible surface for oviposition. Eggmasses collected were labeled according to host plant, and number of eggmasses counted. Six replicates utilizing each of corn strain and rice strain were performed.

The second oviposition choice experiments were conducted in a greenhouse during June through October using plastic swimming pools as an enclosure (Meagher et al. 2004). Temperatures ranged from 20°C to 30°C and relative humidity was >70% during the trials. 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) with an inside and top layer of gray window screen was curled and placed in the sand along the inside edge of the pool. Four corn and four 'Florona' plants each were placed randomly in a circle inside the unit. The corn strain colony used was CS-DRU08, while the rice strain colonies included RS-MS04 (4 replications) and RS-Ona04 (7 replications). Ten male and female moths (<5 d old) from one colony were placed along with a 10%-sugar solution feeding station in the center of the enclosure. Moths could either oviposit on the plants or on the enclosed window screen. Plants and screen were sampled 72 h later for eggmasses and the number of eggs in each eggmass was counted. This trial was replicated 9 times for corn strain moths and 11 times for rice strain moths.

## Statistics

Data were transformed using a square root ($y+0.5$) transformation for the eggmass numbers and log10 ($y+1$) transformation for the egg numbers. Means were separated using the Contrasts statement in PROC MIXED (SAS Institute 2009; Littell et al. 1996).

# Results

## Number of Eggmasses

Corn plants provided both leaves and stems for oviposition sites, whereas eggmasses were located on the middle and end sections of grass plant leaves. Eggmasses were found on the top section of the screen cage, and were rarely found on the inner surface of the pots holding plants or on the small plastic soufflé cups used for the honey-sugar solution. In the cage bioassay, corn strain females laid more eggmasses (66) than rice strain females (52) ($F=7.9$; df=1, 25; $P=0.0094$), and there was a host strain × oviposition substrate interaction ($F=24.5$; df=1, 25; $P<0.0001$). However, the number of eggmasses per female was similar between strains (1.375 eggmasses per corn strain female and 1.083 eggmasses per rice strain female; $F=1.9$; df=1, 5; $P=0.2297$) over the 72 h test period. More eggmasses from corn strain females were laid on the screen enclosure (35) than on corn plants (11) ($F=5.9$; df=2, 10; $P=0.0208$) (Fig. 1a). Grass plants contained an intermediate number of eggmasses (20). In contrast, rice strain females displayed a strong preference for grass plants, with 50 of the 52 eggmasses found on these plants ($F=48.8$; df=2, 10; $P<0.0001$). Corn plants and the screen cage had only 1 eggmass each present in the 6 trials (Fig. 1a).

In the pool bioassay, eggmasses oviposited on the screen enclosure often appeared to be tightly laid together or overlapping, making the accurate estimation of eggmass number on this surface impossible. On plant surfaces alone, corn strain females oviposited a total of 149 eggmasses which was comparable to 146 eggmasses for rice strain females ($F=0.38$; df=1, 29; $P=0.5421$). This averaged to 1.66 eggmasses per corn strain female and 1.33 eggmasses per rice strain female ($F=0.54$; df=1, 8; $P=0.4827$). There was a significant interaction between host strain and plant ($F=10.6$; df=1, 29; $P=0.0029$). The same strain differences in eggmass location seen in the cage bioassay were observed in the pool bioassay. Corn strain females oviposited 83 eggmasses on corn compared to 66 on grass, which was not significantly different ($F=0.79$; df=1, 8; $P=0.3993$) (Fig. 1b). However, rice strain females oviposited almost four times more eggmasses on grass plants (114) than on corn plants (32) ($F=16.6$; df=1, 10; $P=0.0022$) (Fig. 1b).

## Number of Eggs

In order to include the ovipositional events on the screen surface in the pool bioassays, individual egg counts were performed on all structures. The 90 corn strain females laid more eggs (20,944) than the 110 rice strain females (18,226) ($F=4.3$; df=1, 43; $P=0.0451$). However, when calculated as the number of eggs laid per

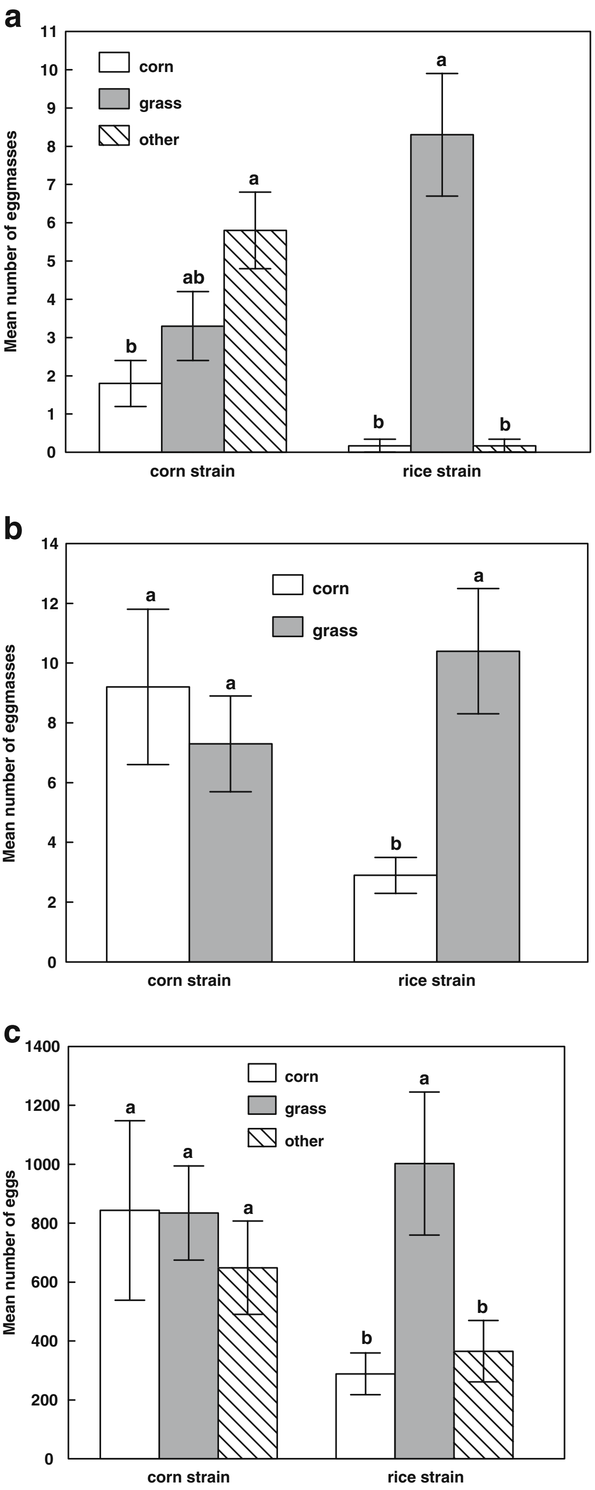

**Fig. 1** **a** Mean number of eggmasses (± SE) oviposited by corn or rice strain fall armyworm females on corn plants, grass plants, or the screen enclosure (other) in the cage bioassay ($n$=6). **b** Mean number of eggmasses (± SE) oviposited by corn ($n$=9) or rice strain females ($n$=11) on corn or grass plants in the pool bioassay. **c** Mean number of eggs (± SE) oviposited by corn or rice strain females on corn plants, grass plants, or the screen enclosure (other) in the pool bioassay. Columns within each strain followed by the same letter are not significantly different ($P>0.05$)

female the difference was not significant (corn strain 233.3±39.5 eggs per female; rice strain 165.2±36.1; $F=2.0$; df=1, 7; $P=0.1982$), indicating the large variation in the ovipositional frequency per individual female. There was no significant host strain by plant interaction ($F=2.0$; df=2, 43; $P=0.1488$).

Corn strain females oviposited numerically higher numbers of eggs on corn plants (7,590), but this was not significantly different than the number of eggs on grass (7,513) or on the screen (5,841) ($F=0.38$; df=2, 16; $P=0.6920$) (Fig. 1c). In comparison, rice strain females oviposited significantly more eggs on grass plants (11,031) than on corn plants (3,176) or on the screen (4,019) ($F=4.7$; df=2, 20; $P=0.0213$). Both strains produced equivalent-sized eggmasses on the two plant types. Corn strain eggmasses averaged 93.0±12.7 eggs per mass on corn plants versus 126.7±13.5 eggs per mass on grass plants ($F=3.7$; df=1, 8; $P=0.0924$). Similarly, rice strain eggmasses averaged 109.3±34.3 eggs and 108.3±24.2 eggs, respectively ($F=0.09$; df=1, 10; $P=0.7714$).

## Discussion

Upon arriving at their migratory destination, the two fall armyworm strains become distributed asymmetrically with respect to plant hosts. This is the predominant characteristic distinguishing the two strains and suggests an important role in driving divergence, perhaps by enhancing assortative mating through the isolation of subpopulations into different habitats as has been described for other Lepidoptera (Emelianov et al. 2001, 2003; Malausa et al. 2005).

The objective of this study was to develop a bioassay for ovipositional host choice and assess its role in directing fall armyworm habitat distribution patterns. In the only published comparison of ovipositional behavior differences between strains (Whitford et al. 1988), the colonies used in the analysis were established from larvae collected from corn (for the corn strain) or bermudagrass (for the rice strain), and tested for strain identity (in this case by comparison of electrophoretic alleles) nine generations later (Pashley et al. 1987). While this procedure confirms the predominant strain composition of each colony, it still allows for the possibility of significant contamination if the founder populations were heterogeneous. This is a particular concern for the corn strain colony since field surveys consistently find about 20% of larvae collected from corn carry rice strain genetic markers (e.g., Prowell et al. 2004), a level of contamination that could produce problematic phenotypic variability but may not be detected by a comparison of electrophoretic allele frequencies. To deal with this issue, the colonies in this study were derived from founder populations where each individual was tested for the appropriate strain-specific mitochondrial haplotype. We anticipated that better characterization of the founder populations will reduce the strain heterogeneity of the derived colonies and thereby improve the consistency of the bioassay results.

This appears to be the case as a comparison of multiple independently-generated colonies in two different bioassay configurations gave consistent results. Tests using three rice strain colonies each demonstrated that when given the choice between corn plant, forage grass, or artificial surface, rice strain females showed a strong statistically significant bias toward grass as an ovipositional substrate. Whitford et al.

(1988) reported a similar result in a four-choice test between corn, bermudagrass, centipedegrass, and sorghum (oviposition on the cage surface was not recorded), with rice strain females preferring the bermudagrass. However, this result could not be repeated in a second trial. The current findings confirm that rice strain females display ovipositional preferences that are sufficiently robust to be consistently observed in the laboratory using standard choice protocols.

A different dynamic was observed for the corn strain, which required the recording of egg deposition events on non-plant surfaces. Ovipositional events as measured by eggmasses or number of eggs occurred at least as frequently on the cage surface as on the plants and no significant differences were observed between corn and forage grass usage. This suggests that if ovipositional specificity is present in the corn strain, as suggested in an earlier study (Whitford et al. 1988), it may be more variable or sensitive to experimental conditions and/or colony age than that exhibited by the rice strain. The high frequency of oviposition events on the cage surface is a characteristic of the corn strain and has previously been reported for other corn strain lines (Prowell et al. 2004). This is in accord with field observations of fall armyworm eggs being frequently found on artificial substrates (Luginbill 1928; Thomson and All 1982, 1984), and oviposition preference for non-host structures or poor host plants has been associated with several species (Thompson 1988; Berdegué et al. 1998; Ladner and Altizer 2005; Sadek et al. 2010). One explanation is that the placement of eggs at elevations higher than the host plant, which is reported to be the case with most eggmasses found on artificial surfaces (Claycomb 1954), facilitates the dispersal of neonates. Since fall armyworm larvae are cannibalistic (Chapman et al. 1999a, b, 2000), the advantages of rapid and early dispersal are significant, while their broad host range and mobility facilitates finding a suitable (if not optimal) host plant (Luginbill 1928; grazer lifestyle of Thompson 1988). In addition, the enemy-free state hypothesis proposes that females will tend to place eggs in locations that provide protection against egg parasitoids and predators (Thompson 1988). Since oviposition on plants can induce plant-based mechanisms that attract insect parasitoids (Hilker and Meiners 2006; Fatouros et al. 2008) or otherwise facilitate parasitization (Romeis et al. 1998; Sadek et al. 2010), there may be selection advantages to oviposition on non-plant structures that are in the vicinity of appropriate plant hosts.

Given these considerations and the nature of their preferred habitats, the differential ovipositional behaviors of the two strains can be easily rationalized. In a survey of southern Florida fall armyworm populations (Meagher and Nagoshi 2004), the rice strain was found to predominate in naturalized wetland and pasture habitats where plant diversity and variations in plant quality are high. Under such conditions there might be substantial advantages for the direct placement of eggs on hosts suitable for larval development even at the cost of higher cannibalization and parasitization. In contrast, the corn strain was in the majority in areas associated with corn, cotton, and vegetable agriculture, habitats where the plant hosts are frequently found in large, dense monocultures. In these situations the maternal targeting of eggs to a specific plant may be less important than the placement of eggs to facilitate dispersion or reduce parasitization.

While ovipositional behavior likely contributes to differences in the distribution of the two strains it doesn't appear to be a complete explanation. Field surveys consistently show that rice strain larvae are more likely than corn strain to be found on plant hosts associated with the opposing strain (Prowell et al. 2004; Nagoshi et al. 2006a, 2007; Machado et al. 2008), a finding inconsistent with the stronger ovipositional host specificity displayed by the rice strain females in this study. This might reflect the higher genetic complexity (McMichael and Prowell 1999; Nagoshi et al. 2007; Nagoshi 2010) and frequency of interstrain mating (Nagoshi and Meagher 2003a; Nagoshi et al. 2006a) displayed by the rice strain, either of which could generate phenotypic variability with respect to plant host choice. We also cannot preclude the possibility that strain differences in larval mortality in the different habitats significantly contributes to the observed strain distribution patterns.

In summary, this study demonstrates that strain differences in ovipositional behavior exist for fall armyworm populations and can be observed in a relatively simple laboratory bioassay that provide a behavioral method for determining the strain identity of a laboratory colony to augment the genetic markers. Comparisons with the findings from earlier studies demonstrate the importance of using genetic markers to identify the strain of the test populations and the need to consider significant the tendency of the corn strain to place eggs on artificial substrates even when appropriate plant hosts are available. The results indicate that strain-specific ovipositional behaviors can contribute to but do not fully explain the distributions of the two strains in Florida habitats.

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