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GENETIC VARIATION IN NEONATE BEHAVIOR OF FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE)

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ABSTRACT

Bioassays were developed to test plant selection of fall armyworm (*Spodoptera frugiperda* (J. E. Smith)) host strains to corn (*Zea mays* L.) and stargrass, a forage grass closely related to bermudagrass (*Cynodon nlemfuensis* Vanderyst var. *nlemfuensis*). Neonate larvae from 3 corn strain and 3 rice strain colonies preferentially selected corn over stargrass in petri dish choice tests. However, bioassays of whole plants and whole plant volatiles showed that selection of a particular host was not clear and there were no significant differences in plant choice. Two additional bioassays were conducted to determine if larvae would continue to disperse once they came in contact with a plant source. One colony was always biased towards corn regardless of which plant was encountered first. For 4 colonies, the attraction to corn was reduced such that when stargrass was first contacted, equal or greater numbers of larvae stayed and did not migrate to corn. Finally, the attraction to corn was lowest in 1 colony in which significantly more larvae moved away from corn even when it was presented first. Results of our study, along with behavioral and feeding trials from other studies, suggest that there is a consistent attraction of neonates to damaged corn regardless of "strain" designation, but substantial variability in the strength of that attraction if they come in contact with another plant host first. These differences among colonies most likely reflect genetic and phenotypic variation in wild populations. More information at http://www.ars.usda.gov/pandp/people/people.htm?personid=11809

Key Words: *Spodoptera frugiperda*, choice tests, larval behavioral traits, host plant selection

RESUMEN

Se desarrollaron bioensayos para probar la selección de plantas por cepas del gusano cogollero (*Spodoptera frugiperda* (J. E. Smith)) según su hospedero hacia el maíz (*Zea mays* L.), el pasto estrella, y un pasto de foraje cercano a "bermudagrass" (*Cynodon nlemfuensis* Vanderyst var. *nlemfuensis*). Las larvas recién nacidas de 3 colonias de la cepa de maíz y 3 colonias de la cepa de arroz preferían secciones de maíz sobre las secciones del pasto estrella en las pruebas de opciones realizadas en platos petri. Sin embargo, bioensayos de la planta entera y volátiles de toda la planta mostraron que la selección de un hospedero particular no fue clara y no hubo una diferencia significativa en la selección de plantas. Se realizaron dos bioensayos adicionales para determinar si las larvas continuarán su dispersión una vez que estén en contacto con la planta. Una colonia siempre tuvo como preferencia la selección del maíz sin importar cual de las plantas fueron encontradas inicialmente. Para 4 de las colonias, la atracción al maíz fue reducida de tal manera que cuando fueron puestas en contacto con el pasto estrella, un numero igual o mayor de las larvas se quedaron y no emigraron al maíz. Finalmente, la atracción al maíz fue la mas baja en 1 colonia donde un numero significativamente mayor de las larvas se apartaron del maíz aun después de ser presentado inicialmente. Los resultados de nuestro estudio, junto con las pruebas de comportamiento y alimentación hechas en otros estudios, sugieren que hay una atracción consistente de las larvas recién nacidas a maíz dañado sin importar la clase de la cepa, pero hay una variabilidad substancial en el grado de la atracción de las larvas si se ponen en contacto con otra planta inicialmente. Estas diferencias entre las colonias a lo mejor reflejan la variación genética y fenotípica en poblaciones de campo.

Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) is a polyphagous insect that migrates each season from overwintering areas in southern Florida and southern Texas to the eastern and central U.S. (Luginbill 1928; Mitchell 1979; Pair et al. 1986; Pair et al. 1991; Westbrook & Sparks 1986; Mitchell et al. 1991). This pest can cause injury and economic damage to many crops, including corn (Marenco et al. 1992) and pasture grasses (Martin et al. 1980). Fall armyworm is composed of two sympatric and morphologically identical strains that are defined by their host plant preferences (Nagoshi & Meagher 2004). One strain was identified from populations feed-

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ing on corn (*Zea mays* L.) and sorghum (*Sorghum* spp.) (corn strain) and the other strain was identified from populations feeding on rice (*Oryza sativa* L.) and forage grasses (*Cynodon* spp.) (rice strain) (Pashley et al. 1985; Pashley 1986). The 2 strains can be distinguished by genetic markers (Levy et al. 2002; Nagoshi & Meagher 2003a; Nagoshi & Meagher 2003b; Nagoshi et al. 2006).

Based on capture of adult males in pheromone traps, corn strain individuals were found primarily in agricultural areas, whereas rice strain individuals were found in agricultural, natural, and urban habitats (Meagher & Nagoshi 2004; Nagoshi & Meagher 2004). However, rice strain larvae were found in both corn and forage grasses but corn strain larvae were only found in corn (Meagher & Gallo-Meagher 2003; Nagoshi et al. 2006).

There have been several reports of behavioral and physiological differences between strains that could explain their asymmetrical distribution in the wild. For example, rice strain larvae feeding on corn were observed to display a slower rate of weight gain, longer developmental time, lower pupal weight, and reduced survival than when reared on bermudagrass (Pashley 1988; Pashley et al. 1995; Veenstra et al. 1995). However, in many cases these biological differences have been difficult to reproduce. For example, while Whitford et al. (1988) also reported reductions in larval and pupal weights when rice strain larvae were raised on corn, they did not observe differences in developmental time or survival. They similarly showed that rearing corn strain larvae on rice or bermudagrass had no consistent negative effect on larval development or fitness, a finding that we have also observed (Meagher et al. 2004; RLM unpublished data).

The inability to reproduce strain-specific behaviors under controlled laboratory settings has stymied attempts to dissect the mechanism of strain divergence and limited our overall understanding of fall armyworm biology. A better description of why this occurs could allow for better bioassays that would make possible the experimental identification of strain-specific characteristics. One explanation is that these observational disagreements are due to environmental influences, in particular the effects of artificial culturing practices on more complex behaviors (Quisenberry & Whitford 1988; Jamjanya et al. 1990). An alternative explanation is that there is substantial genetic variability even within strains such that individual isolates can exhibit substantial differences in physiology and behavior. To examine the latter possibility, we took advantage of an observation by Pashley et al. (1995) that ≈90% of neonate larvae of both strains preferred corn over bermudagrass in petri dish choice-tests. Simple modifications of this bioassay were made to test plant specificity and to compare the behaviors of several independently isolated colonies of both strains. The behavioral differences are described and their ramifications on our understanding of strain biology discussed.

Materials and Methods

Strain Isolation and Plant Growth

Fall armyworm egg masses and larvae were collected during 2003 and 2005 from multiple sites in Florida (field corn, University of Florida Dairy Research Unit, Hague, Alachua Co.; forage grasses, University of Florida Range Cattle Research and Education Center, Ona, Hardee Co.; and sweet corn, Miami-Dade Co.), and 1 location in Mississippi (Washington Co. by J. Adamczyk from bermudagrass). Single adult pair matings were performed in small oviposition cages which consisted of a cylindrical 473-mL plastic food container (Solo Cup Co., Urbana, IL) lined with a 7-cm × 7.6-cm coffee filter (Bunn, Springfield, IL). Holes (5 mm) were placed in the bottom of the containers to allow for airflow. Two holes (1.5 cm) were placed in the lid (Solo, ML8) so that braided cotton rolls (Richmond Dental, Charlotte, NC) could be inserted. The cage was inverted and placed over a 177-mL container (S306, Sweetheart Products Group, Owings Mills, MD), which held 2 plastic soufflé cups (Solo, P100), one with deionized water and the other with 10% honey/sugar solution. This system allowed for absorption of liquids for adult nourishment. Females were allowed to freely deposit eggs on the inner surface of the coffee filter. At least 20 pairs of F_1 moths were used to establish the colonies.

Upon death, male and female moths were analyzed separately for strain identification with mitochondrial markers (Levy et al. 2002; Meagher & Gallo-Meagher 2003). Eggs were collected daily, and labeled according to pair mating. Newly emerged larvae were reared on pinto bean diet (Guy et al. 1985) until strain identification was verified. Once strain association was confirmed with the 2003 colonies, F_2 larvae were placed either on a corn ('Truckers Favorite') or stargrass (*Cynodon nlemfuensis* Vanderyst var. *nlemfuensis* 'Florona') foliage diet according to their host strain (CS-Hag03 and RS-Ona03, respectively). In 2005, two more colonies of each strain were established according to the procedures above. However, larvae from these colonies (CS-Hag05, CS-JS05, RS-MS05, and RS-Ona05) were continuously reared on pinto bean diet.

Plants were grown in 550-mL pots in a greenhouse at ambient temperature (22-40°C) and were fertilized weekly with Miracle-Gro® (Marysville, OH) 15-30-15 plant food. Plant age during experimentation was approximately 3 weeks for both corn and 'Florona' stargrass. 'Florona' stargrass is a long-lived, persistent perennial grass,

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similar to types of bermudagrass, that was observed growing in Ona in 1973 (Mislevy et al. 1989; Mislevy et al. 1993). Previous research showed this grass to be an excellent host for fall armyworm (Meagher et al. 2007).

Choice Test Bioassays

Three separate bioassays were designed to compare preferences of neonate larvae of both host strains for either corn or stargrass. The first experiments were conducted in 9-cm diameter polystyrene petri dishes (Thomas Scientific, Swedesboro, NJ) as a choice arena to present cut leaf sections to neonates. New growth leaf sections were taken from each plant type, and trimmed along the top and sides to achieve a uniform size (5 cm × 1.5 cm). Since stargrass leaves are smaller than corn leaves, 2 leaf sections were used to obtain the same area as the corn leaves. One section of each plant host was placed on filter paper discs (9 cm; Thomas Scientific) moistened with 1 mL of deionized water. Sections were placed 2 cm from the center, along the outer edge of the petri dish. Twenty newly-hatched larvae (0-24 h) were placed in the center of each dish, and the lid put into place. Ten replicates were performed for each colony. Petri dishes were placed in an incubator at 23.9 ± 2ºC with a 14/10 day/night cycle, 80% RH. The number of larvae on or under each leaf section was counted 24 h after introduction. Three corn strain (CS-Hag03, CS-Hag05, and CS-JS05) and 3 rice strain (RS-Ona03, RS-Ona05, and RS-MS05) colonies were tested.

The second bioassay was conducted with a Y-tube olfactometer made of 2.5 cm-diameter clear Plexiglas tubing with a 58.0-cm body and 15.2-cm arms to test neonate responses to odors alone. Odor sources for the bioassay consisted of whole plants in 550-mL pots housed in a 3.8-L glass jar. Charcoal-filtered house air was passed over the plants in the jar and through an arm at 0.2 L/min. Airflow was pulled through the base of the Y-tube by a vacuum at 0.4 L/min.

Larval attraction to the volatiles of 1 corn plant or a small group of stargrass plants was tested by placing an eggmass at the midpoint in the body of the Y-tube. A black 9-cm filter paper disk (Thomas Scientific) was placed encircling the area outside of the tube above the eggmass to reduce light interference. Larvae were allowed free movement within the olfactometer. The number of larvae in each arm was counted after 24 h. There were 7 replicates each of corn (CS-Hag03) or rice strain (RS-Ona03) larvae; the position of the host plant was alternated for each replicate.

The third bioassay was made with a clear acrylic plastic cage (measuring 51 (L) × 25 (W) × 28 (H) cm with a testing area of 51 × 25 × 18 cm) to test neonate responses to whole plants rather than plant sections. Potted plants were placed in rectangular receptacles (15 × 7.5 cm) that were removable and allowed for the soil/plant interface to be level with the floor surface. The corn receptacle contained 4 plants and the stargrass receptacle contained between 15 and 20 plants. During testing, the cage was placed in an environmentally controlled room at 23.9 ± 2°C with a 14/10 day/night photoperiod and 80% RH. Eggmasses (CS-Hag03 and RS-Ona03) were placed in the center, and the number of neonate larvae on either the corn plants or stargrass plants was counted after 24 h. Plant location was alternated for each of the 5 replicates.

Passing-Over Tests

These tests were conducted to determine if larvae would continue to disperse once they came in contact with a plant source. Two bioassays were conducted. Sections of corn and stargrass leaf material were placed on filter paper discs (Thomas Scientific) moistened with ca. 1 mL deionized water and cut to fit the dimensions of a 14-cm diameter polystyrene petri dish (Thomas Scientific). The plant material first encountered (and potentially "passed-over") by the neonates was cut to dimensions large enough to span the diameter of the petri dish. Another more distally-located plant section was trimmed to a uniform size (5 cm × 1.5 cm) and placed 30 mm from the center, and 20 mm along the outer edge of the petri dish. As with the choice test petri dish bioassays, extra sections of stargrass were used to provide the same surface area as the corn. Twenty neonate larvae were placed in the dish opposite the leaf section. Petri dishes were placed in the incubator and the number of larvae on or under each leaf section was counted after 24 h. Since bioassays on larvae from the 2 initial host strain isolates provided interesting results (CS-Hag03 and RS-Ona-03), 2 more colonies of each strain were examined (CS-Hag05, CS-JS05, RS-Ona05, and RS-MS05). For each colony, there were 10 replicates passing over corn to stargrass and 10 replicates passing over stargrass to corn.

The second passing-over bioassay used the choice cage as described above, except it was modified to allow inflow and outflow of air over the odor sources. Charcoal-filtered house air was passed sequentially over the distal plant material and then over the proximal plant material before being presented to the larvae. Air was vented to the outside to prevent plant volatiles from re-entering the cage. Plants were arranged in the cage so that larvae would have to pass through one plant host to reach the other plant. Four corn plants and between 15-20 stargrass plants were used. Newly emerged larvae from an eggmass were placed in the downwind position from the first plant. For each strain (CS-Hag03 and RS-

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Ona03) examined, there were 5 replicates of larvae passing through corn to stargrass and 5 replicates of larvae passing through stargrass to corn. The number of larvae on each plant was counted after 24 h.

Statistics

Data were analyzed as binomial experiments where the null hypothesis was that corn and stargrass were chosen equally. Since larval numbers differed among replicates (r), the proportion of larvae (p = number of larvae selecting corn / total number of larvae) selecting corn was converted to z scores [$z = (p - 0.5) / \sqrt{(p * (1 - p) / \text{total}}$]. For each test, z scores for all r values were averaged and t-tests (t = z scores mean / SEM; r - 1 df) were calculated. When p was either 0 or 1.0, a conversion factor was used: for $p = 0$, $p = 0.375$ / (total number + 0.75); for $p = 1.0$, $p =$ (number selecting corn + 0.375) / (total number + 0.75); (Ott & Longnecker 2001).

Results

CS-Hag03 and RS-Ona03 Colonies

Initial experiments were performed with 1 corn strain and 1 rice strain colony generated in 2003 from Florida populations. In the petri dish bioassays, larvae were provided a choice between 2 equal-sized cut sections from corn or stargrass leaves. Larvae of both strains showed a strong preference for corn sections, with almost 80% of corn strain and over 92% of rice strain neonates selecting corn (Fig. 1). A different behavior was observed in olfactometer studies where larvae were exposed only to volatiles from whole plants. No statistically significant differences were observed (Fig. 1). Less than 1% of the larvae moved opposite of the airflow.

To reduce the artificiality of the bioassay, a choice test was designed where the larvae were exposed to and could make contact with whole plants. This required a larger assay chamber, but otherwise the overall design was similar to the petri dish experiment. Neonates of both strains rapidly moved to the plant material, but showed no significant preference to corn or stargrass (Fig. 1).

The choice cage passing-over bioassay was designed to introduce forced air flow thereby facilitating exposure to volatiles while also allowing contact with whole plants. In addition, the assay required that the larvae contact 1 plant type before reaching the second. This was to test whether neonates simply chose the first suitable food source encountered, or were able to detect and actively search for the preferred host. The results presented the first indication of colony-specific and perhaps strain-specific larval feeding behavior. Corn strain neonates were found at statistically equal proportions on corn and stargrass independent of which was encountered first (Fig. 2). In contrast, there was a general tendency for rice strain neonates to remain on the first plant contacted whether it was corn (69.6%) or stargrass (82.4%), although only the latter was statistically significant (Fig. 2).

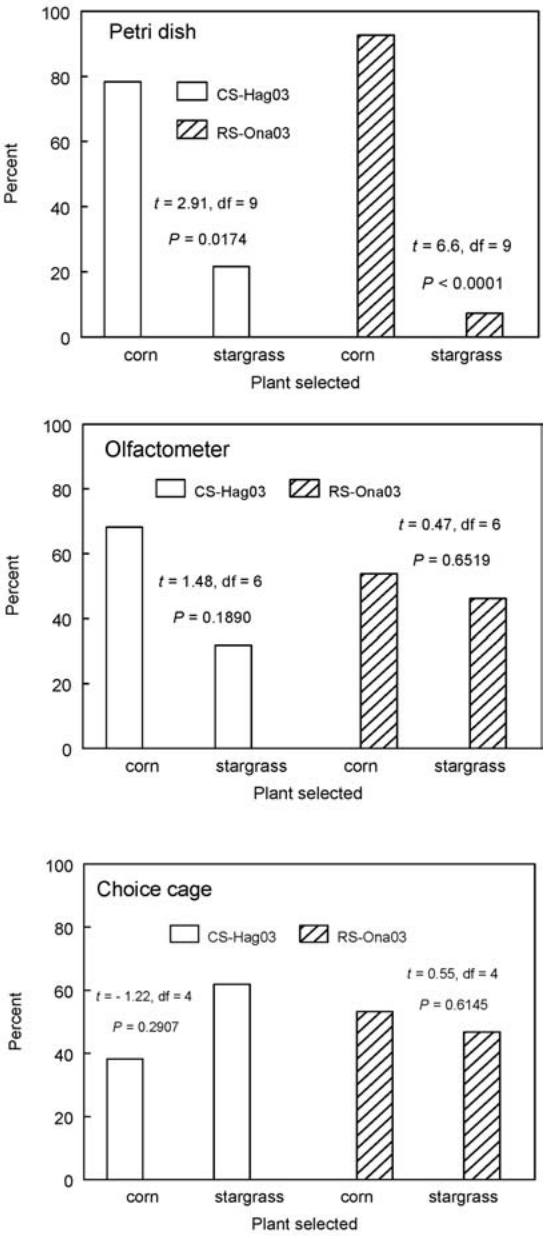


Fig. 1. Percentage of corn strain (CS-Hag03) or rice strain (RS-Ona03) larvae that chose either corn or stargrass in a petri dish, olfactometer, or choice cage bioassay.

Because the strongest plant host preferences were observed with leaf sections in petri dishes,

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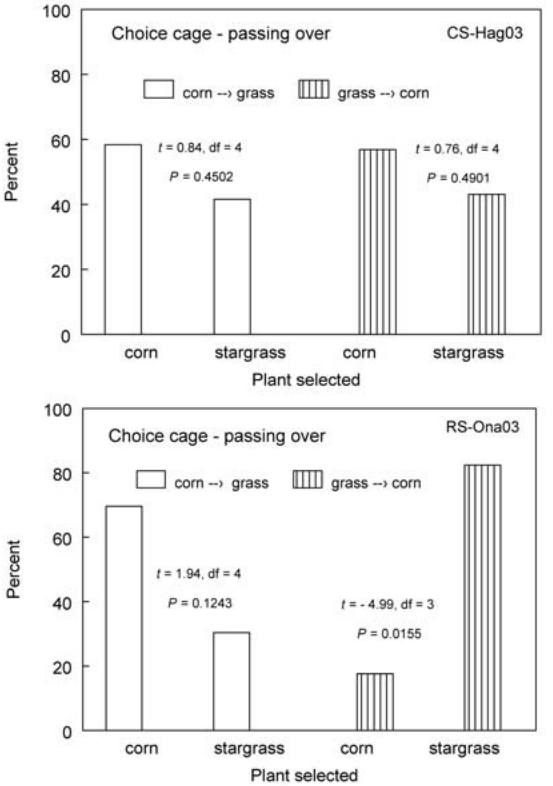


Fig. 2. Percentage of corn strain (CS-Hag03) or rice strain (RS-Ona03) larvae that chose either corn or stargrass in a choice cage passing-over bioassay. For each host strain, larvae encountered either corn (corn → grass) or stargrass (grass → corn) first and then dispersed to the second plant.

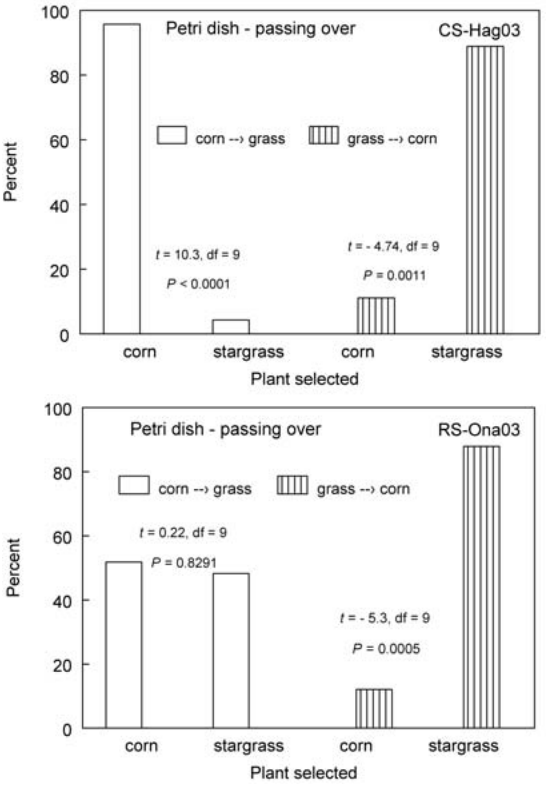


Fig. 3. Percentage of corn strain larvae (CS-Hag03) or rice strain larvae (RS-Ona03) that chose either corn or stargrass in a petri dish passing-over bioassay. Larvae encountered either corn (corn → grass) or stargrass (grass → corn) first and then dispersed to the second plant.

the passing-over tests were repeated with that simplified experimental design. The results identified 2 distinct behavioral patterns characteristic of the 2 colonies. Neonates from the CS-Hag03 colony tended to remain on the first plant material contacted regardless of plant type (Fig. 3). In contrast, rice strain neonates were influenced by host plant. In the configuration where the corn section was contacted before the stargrass material, the RS-Ona03 larvae distributed themselves equally on the 2 plant types. If stargrass was encountered first, over 90% of larvae remained on that section (Fig. 3).

CS-JS05, CS-Hag05, RS-MS05, and RS-Ona05 Colonies

Subsequent studies were performed with 4 colonies established in 2005 from populations in southern and central Florida and the Mississippi delta. In the petri dish choice bioassay, neonates from all 4 colonies displayed a significant bias to the corn material, consistent with that observed with the 2003 colonies (Fig. 4).

The passing-over experiments with plant sections in petri dishes identified 2 distinct behaviors, both different from that observed with the

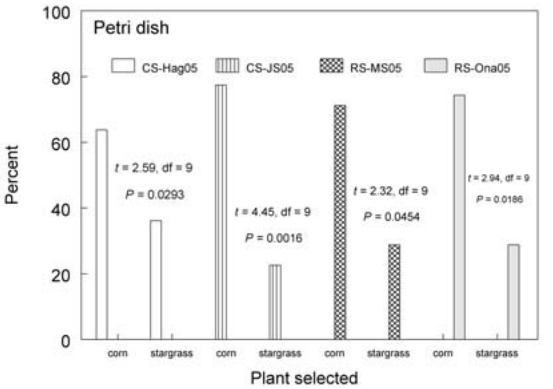


Fig. 4. Percentage of corn strain (CS-Hag05 and CS-JS05) or rice strain (RS-MS05 and RS-Ona05) larvae that chose either corn or stargrass in a petri dish bioassay.

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2003 colonies. Over 90% of the neonates from all 4 colonies remained on the corn section when it was contacted first (Fig. 5). In the reciprocal configuration, larvae from the CS-JS05, RS-MS05, and RS-Ona05 colonies distributed themselves equally on the 2 plant types (Fig. 5). In contrast, larvae from the CS-Hag05 colony always preferred the corn section (Fig. 5).

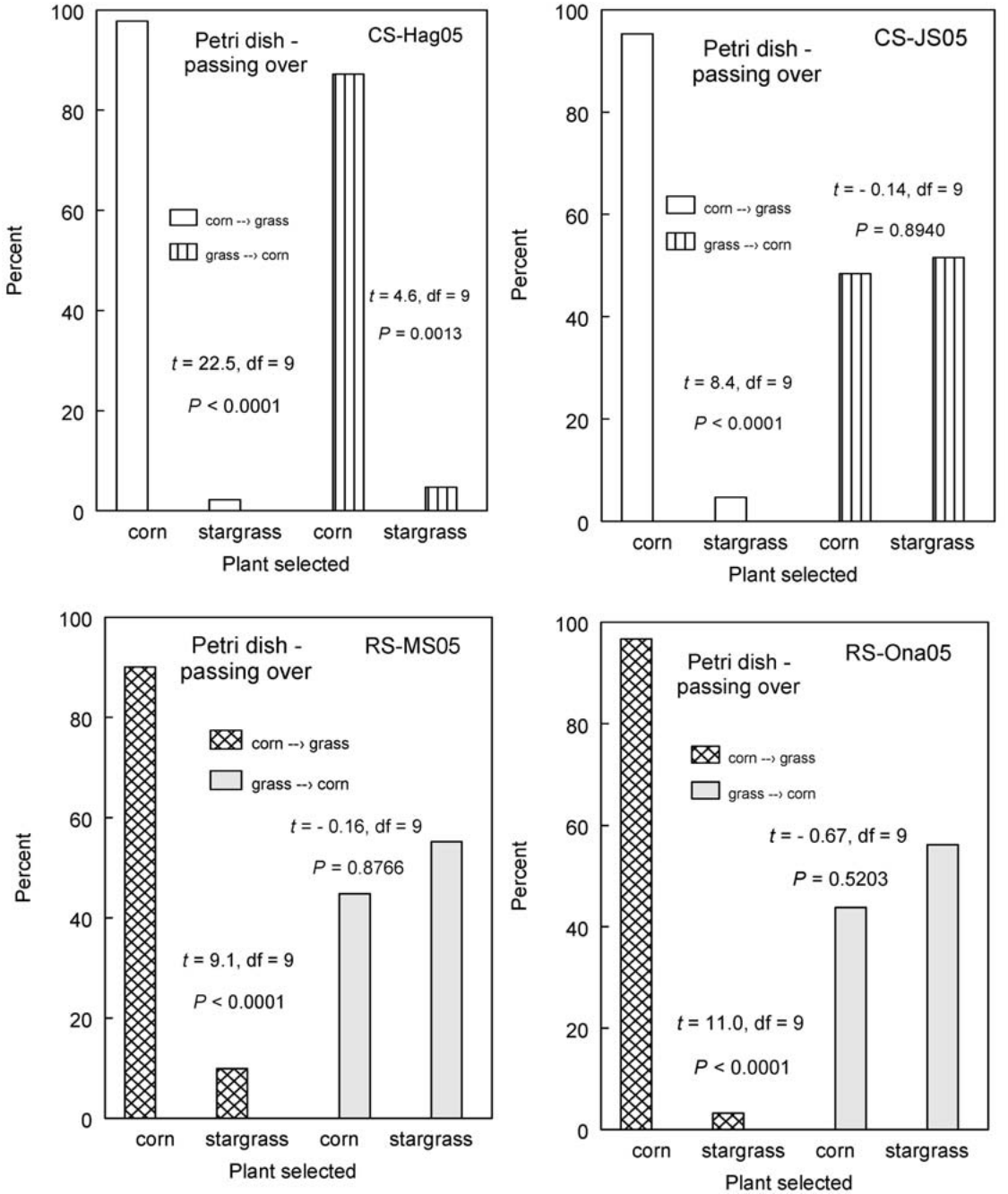


Fig. 5. Percentage of corn strain (CS-Hag05 and CS-JS05) or rice strain (RS-MS05 and RS-Ona05) larvae that chose either corn or stargrass in a petri dish passing over bioassay. Larvae encountered either corn (corn → grass) or stargrass (grass → corn) first and then dispersed to the second plant.

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Discussion

Our objective in this study was to assess variation among different independently-isolated fall armyworm populations based upon simple behavioral bioassays targeted at the youngest larval stage. Since the colonies were treated identically for several generations, the presumption is that any observed differences will most likely be the result of genetic variation.

The attraction of fall armyworm neonates to corn plant sections was previously observed by Pashley et al. (1995), who found that most neonate larvae of both strains preferred corn over bermudagrass. Our findings that this phenotype can be reproduced consistently with 6 independently-isolated colonies generated over a two-year period strongly suggest that this behavior is ubiquitous and relatively insensitive to the influences of artificial culturing and genetic inbreeding. Why the rice strain should exhibit this bias toward corn is not clear.

Interestingly, a simple change in the orientation of the plant sections in the petri dish, so that physical contact with one must occur before the other can be reached resulted in significant behavioral differences among colonies. The first stage of the experiment was designed to have neonates first encounter corn. Based on the choice test results, it was expected that both strains would tend to remain on the corn section. This was observed for 5 of the 6 colonies tested. Larvae from the 1 exception, RS-Ona03, were equally distributed over the 2 plant sections, suggesting this colony might have lost its attraction to corn volatiles.

We anticipated several possible outcomes when stargrass was encountered first, depending on the relative strength of the attraction to corn volatiles compared to the tactile or taste attractiveness of the intervening stargrass sections. In particular, since the rice strain is the predominant fall armyworm population in stargrass, we anticipated that a substantial proportion of the neonates would recognize it as an acceptable host and remain on the stargrass section. This was the case for 2 of the 3 rice strain colonies tested, where a statistically equal proportion of larvae was found on both plant materials. Larvae from the third colony, RS-Ona03, showed the same tendency but to a much greater degree, consistent with the proposition that attraction to corn volatiles was lost in this colony. Our initial expectation with the corn strain colonies was that these would always show a preference to corn, the presumed preferred plant host. This was not the case, as each of the 3 corn strain colonies gave a different response when the stargrass section was encountered first.

Overall, the passing-over experiments with 6 different colonies uncovered 4 distinct behavioral patterns with no clear indication of strain-specific behavior. One simple way of explaining these results is to assume variability in the attraction to corn sections relative to the attraction to stargrass sections. Larvae from CS-Hag05 were always biased to the corn section, regardless of which plant type was encountered first. In the next 3 colonies (CS-JS05, RS-MS05, RS-Ona05), the attraction to corn appeared reduced such that when stargrass was first contacted, a substantial number of larvae remained rather than move to the corn section. Further reduction in corn attraction was found with larvae from CS-Hag03, where now a majority of the neonates remained on stargrass when it was encountered first. Finally, attraction to corn was so low with RS-Ona03 larvae that a substantial number moved onto stargrass even when corn was first encountered.

We conclude from this study that while there is a consistent attraction of neonates to damaged corn, there is substantial variability in the relative strength of that attraction that can be uncovered in the passing-over experiments. Since the 6 colonies were cultured under the same laboratory conditions, we believe these differences most likely reflect genetic and phenotypic variability in wild populations in addition to that associated with strain differences.

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