Oviposition by fall armyworm, Spodoptera frugiperda (J. E. Smith): effects of moth age and sorghum maturation stage

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Abstract. Fall armyworm (FAW), Spodoptera frugiperda (J.E. Smith), oviposition preferences for sorghum in various stages of development were measured in 48h choice and 72h no-choice studies in cages in the greenhouse and in the field, respectively. Moths aged 3, 6 and 9 days old (mated at days 1, 4 and 7 posteclosion, respectively) deposited more eggs on mid-whorl and late whorl than on early whorl stage sorghum in the greenhouse choice oviposition study. Numbers of egg masses laid by moths in the three moth age groups during their initial 48h or 72h oviposition periods in the two studies were not significantly different. A total of 176 egg masses was laid on plants in the greenhouse, of which 72% and 28% were deposited on the abaxial and adaxial surfaces of the leaves, respectively. From field cages, a total of 291 egg masses were collected, of which 79%, 5% and 16% were deposited on the abaxial and adaxial surfaces of the leaves, and the saran screen cage, respectively. Average egg mass weight was not significantly different among female ages or stages of sorghum maturity. Because FAW moths in the early to late stages of reproduction laid more eggs during their initial 48-72h oviposition period in consistently larger egg masses on taller whorl stage sorghum, and on the abaxial compared to the adaxial leaf surface, sampling procedures to determine field infestations of this insect for making pest management decisions should take into consideration these insect-plant biological relationships.

Keywords: Fall armyworm, oviposition, sorghum, Spodoptera frugiperda.

Resumen. La preferencia del cogollero, *Spodoptera frugiperda* (J.E. Smith), de ovipositar en sorgo en varios estados de desarrollo de la planta se midió en estudios de 48 horas de preferencia y 72 horas sin preferencia en jaulas en invernadero y el campo, respectivamente. Las palomillas de 3, 6 y 9 días de edad (cruzadas los días 1, 4 y 7 después de la eclosión, respectivamente) depositaron más huevos en plantas medianamente maduras y maduras que en plantas más jóvenes en el estudio de oviposición del invernadero. La cantidad de masas de huevos puestas por las palomillas de los tres grupos de edad, durante las 48 ó 72 horas iniciales del periodo de oviposición en los dos estudios, no fueron significativamente diferentes. Fueron puestas 176 masas de huevos en planta en el invernadero, de las cuales el 72% y 28% fueron depositadas en el envés y el haz de las hojas, respectivamente. En las jaulas del campo se recolectaron 291 masas de huevos, de las cuales 79%, 5% y 16% fueron depositadas en el envés y el haz de las hojas y la tela saran de las jaulas, respectivamente. El peso de las masas de huevos no fue significativamente diferente entre la edad de las hembras o el estado de madurez del sorgo. Debido a que las palomillas del cogollero en los estados de reproducción temprano a tardío ponen más huevos en masas de huevos consistentemente más grandes durante las 48-72 horas iniciales del periodo de oviposición, en plantas de sorgo más altas que en las más bajas, y en el envés que en el haz de las hojas, los procedimientos de muestreo para determinar las infestaciones en el campo de este insecto para tomar decisiones de manejo de plagas se debe tomar en consideraciones estas relaciones biológicas de insecto-planta.

Palabras claves: Cogollero, oviposición, sorgo, Spodoptera frugiperda.

INTRODUCTION

The fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith), is a major pest of several crops in the south and central United States (Vickery, 1929). Sorghum, Sorghum bicolor (L.) (Moench), is attacked by FAW because it prefers hosts belonging to the grass family (Luginbill, 1928). Information on oviposition by FAW on sorghum with respect to various stages of crop maturation and insect age is limited. Pitre *et al.* (1983) reported that taller sorghum (0.99 m) is preferred for oviposition over shorter sorghum (0.28, 0.46, and 0.58 m). Similarly, taller corn (1.27 and 1.09 m) had more eggs than shorter corn (0.30, 0.36, and 0.74 m) (Pitre et al., 1983). However, Harrison (1984) reported that young corn plants in the early whorl stages were preferred for oviposition over older, taller plants. Observations on oviposition generally agree that most FAW eggs are deposited on the abaxial

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sorghum in groups of 20 pairs at days 1,

(bottom) surface of the leaves of corn and sorghum (Luginbill, 1928; Pitre *et al.*, 1983). Since the literature reports conflicting views on egg laying behavior of FAW on sorghum and maize in relation to age (size) of the plants, there is need for information on maturation stage of the grain crops as a factor influencing plant acceptability for oviposition by moths of different ages.

Knowledge of the oviposition potential of FAW throughout its adult stage and interaction of oviposition with maturation stage of sorghum and other crops could assist in making the most effective insect pest management decisions. This research was, therefore, designed to determine the oviposition preferences of FAW moths of different ages on sorghum plants at various stages of maturation.

MATERIALS AND METHODS

Choice oviposition study. This study was conducted in a greenhouse at Mississippi State University. Sorghum variety 'Funks DR 522' was planted in 7.6 L pots filled with Promix B® soil and Black Kow® topsoil. Seeds were planted on three dates at 14-d intervals. Seedlings were thinned to two per pot. The plants were watered daily and fertilized weekly with Peter's® 20: 20: 20 NPK nutrient solution using an equivalent application rate of 134 kg N/ha. Dimethoate spray was applied to control aphids. No insecticide sprays were applied less than 14 days prior to confinement of moths with the sorghum plants. The oviposition study was initiated when the three plantings were at early whorl, mid-whorl, and late whorl stages of vegetative growth. At this time the plant heights were 38.5 ± 7.3 , 67.9 ± 4.3 and 75.2 ± 3.3 cm (mean \pm SD) and the plants were at 6, 7, and 8 node stages, respectively.

FAW moths used were from a corn strain (Pashley et al., 1992) colony maintained at the USDA ARS Crop Science Research Laboratory in Starkville, Mississippi (Davis, 1989). The colony had developed through seven generations after it was infused with wild males collected as larvae on maize plants in Oktibbeha County, MS. Larvae were raised on a wheat-germ casein diet (a mixture of Biomix # F 0635 and # F 0717, Bio- Serv Inc., Frenchtown, N. J.) at 26.7° C, 50-60% RH, and 16:8h (L:D) photoperiod. Pupae were sexed and males and females were placed separately in 3.75 L glass jars covered with cotton cloth and moist paper towel on the inside at the bottom. Dates of eclosion of the moths were recorded. Female moths were allowed to mate for 2 nights in groups of 20 pairs at days 1, 4 and 7 posteclosion to produce moths in 3-, 6- and 9-day age groups, respectively. Conditions during the mating period included 14:10h (L:D) photoperiod and temperature 26.7°C. Five moths from each age group were dissected to determine presence of spermatophores which would indicate that each group of females successfully mated in the glass jars. Forty females of a given test age group were placed in each 1.8 x 1.8 x 1.8 m saran cage (Chicopee Mfg. Co., Gainesville, GA), each cage representing a replication with three replications per treatment.

Three pots of sorghum at each growth stage were placed at random in each cage to give a total of nine pots per cage and a total of 81 pots for the study. A split plot design was used with moth age as main-plots and sorghum maturation stage of sorghum maturity as sub-plots. Moths were released into the cages at 19:00 h, provided a 10% honey-water food source and allowed to lay eggs for 48h. On day 3 after the moths were released in the cages, all plants were searched for egg masses using a whole plant destructive sampling technique. The number of egg masses on each plant was counted after which the egg masses were removed from the plants and weighed using an electronic balance to estimate the number of eggs per mass (Lynch et al., 1983). Number of egg masses and average weight per egg mass were analyzed using GLM procedures for analysis of variance (SAS Institute, 1985), and means were separated by Fisher's Protected LSD (Steel and Torrie, 1980).

No-choice oviposition study. The no-choice oviposition study was conducted in a small field of 'Funks DR 522' sorghum planted in 96.5 cm rows on the Mississippi Agriculture and Forestry Experiment Station Plant Science Research Farm in Oktibbeha County in 1992. Tworow plots (1.47 m^2) were established to observe oviposition by 3, 6 and 9-d-old moths on sorghum at three stages of development. Treatments were arranged in a randomized complete block design with three replications. Recommended agronomic practices for sorghum production in Mississippi were used. Nine 1.8 x 1.8 x 1.8 m saran screen cages were placed over the plants in designated plots. The study was initiated when the crop developed to early whorl, mid-whorl, and late whorl stages. At these times the early, mid and late whorl stages were 36.4 ± 2.7 , 50.2 ± 3.7 and 58.0 ± 3.3 cm tall and had 6, 8 and 10 nodes, respectively. The cages were moved and

placed over the plots at each successive stage of plant development. Moths were from the same source as those used in the choice oviposition study. Procedures for handling larvae, pupae and moths prior to release in the cages, as well as plant samples for eggs (18 plants examined per cage) and analysis of the data were the same as in the choice oviposition study. Thirty moths of a given age were released into each cage at 19:00 h to oviposit for 72h when the plants were in mid-whorl and late whorl. At early whorl, only 15 females were released in each cage. The reduced number of moths used in the nochoice study, compared to the greenhouse study, was due to larval mortality in the colony, resulting in fewer moths available for the no-choice test. Moths were provided a honey-water food source as in the previous study. Data were analyzed as in the choice oviposition study.

RESULTS

Choice oviposition study. Spermatophores were identified in 47 to 67% of the females dissected from the three moth age groups prior to release, indicating that mating was successful in the glass jar mating containers.

FAW females 3, 6 and 9 days old did not differ significantly (F = 3.58; df = 2, 4; P = 0.1284) in the number of egg masses deposited on sorghum during their initial 48h oviposition period in the choice oviposition study. The moth age-plant stage interaction was not significant (F = 0.82; df = 4, 12; P = 0.5376). A trend was observed for females in combined age groups to deposit more egg masses on midwhorl and late whorl stages (53.3 and 31.8% of total, respectively), than on early whorl stage (14.9%) sorghum in this choice oviposition study (F = 7.80; df = 2, 12; P = 0.01) (Table 1). Weight per egg mass did not differ significantly among FAW female ages within plant growth stages (F =1.93; df = 2, 4; P = 0.26) or for female age across plant growth stages (F = 0.47; df = 2, 12; P = 0.64). Mean egg mass weights across plant growth stages were pooled for females within 3, 6 and 9-day-old age groups on all stages of sorghum. A total of 176 egg masses was counted, of which 72% and 28% were deposited on the abaxial (bottom) and adaxial (top) surface of the leaves, respectively. The eggs were located from nodes 3 to 8 (3 being the lowest). The average number of eggs/egg mass was 366.4 \pm 26.0 (mean \pm SE) calculated using a weight of 0.064 mg/egg (Lynch et al., 1983).

Table 1. Oviposition by fall armyworm (FAW) moths in three combined age groups (3, 6 and 9-d-old females) on sorghum in various stages of development in choice (greenhouse) and no-choice (field) cage studies.

	Crop development			
Study	Stage	No. of nodes	Plant height (cm)	Mean (± SD) number of egg masses per observed plants ^a
Choice	Early whorl	6	38.5	2.9 ± 2.0 a
	Mid-whorl	7	67.9	10.4 ± 7.4 b
	Late whorl	8	75.2	6.2±5.3b
No choice	Early whorl	б -	36.4	1.0 ± 1.1 a
	Mid-whorl	8	50.2	3.7 ± 3.9 a
	Late whorl	10	58.0	2.3 ± 1.9 a

^aMean of nine treatment replications (3 pots with 2 plants each = 1 replication in choice study), (18 plants = 1 replication in no-choice study). Means followed by the same letter are not significantly different (P = 0.05, LSD).

No-choice oviposition study. In this field cage study, the number of egg masses laid on sorghum by 3, 6 and 9d-old FAW moths during their initial 72h oviposition period did not differ significantly at early whorl (F = 0.80; df = 2, 4; P = 0.5102), mid-whorl (F = 4.55; df = 2, 4; P = 0.932) or late whorl (F = 3.50; df = 2, 4; P = 0.1322) (Figure 1). However, the total number of egg masses deposited during the 72h egg laying period by 6- and 9day-old females on early whorl stage sorghum plus the saran screen cage covers was significantly (F = 8.68; df = 2, 4; P = 0.0351) greater than that deposited by 3-d-old females (Figure 2). The number of egg masses laid on sorghum plus the saran screen cage covers was not significantly different among moth ages on mid-whorl (F = 4.48; df = 2, 4; P = 0.0951) or late whorl (F = 0.48; df = 2, 4; P = 0.6487) sorghum.

The mean weight (g) of egg masses laid by 3, 6 and 9day-old females in the cages (on sorghum plus the saran screen cage covers) was not significantly different when plants were at early whorl (F = 0.07; df = 2, 4; P = 0.9296), mid-whorl (F = 0.44; df = 2, 4; P = 0.6712) or late whorl stages (F = 1.97; df = 2, 4; P = 0.2544). A total of 291 egg masses was laid of which 79, 5 and 16% were on the abaxial and adaxial surfaces of the leaves, and on the saran screen, respectively. The average number of eggs/ egg mass was 334.1 ± 37.3 (mean ± SE).



Figure 1. Mean (\pm SD) number of egg masses laid by 3, 6, and 9-day-old fall armyworm (FAW) (Spodoptera frugiperda) moths during their initial 72h oviposition period on sorghum at early whorl (36.4 cm tall), mid-whorl (50.2 cm), and late whorl (58.0 cm) stages in no-choice oviposition study in field cages. Bars with the same letter within plant growth stage are not significantly different (P=0.05, LSD).

DISCUSSION

The results obtained in the choice oviposition study corroborate the observations by Pitre et al. (1983), where taller sorghum was preferred by FAW for oviposition over shorter sorghum. In the same study, FAW moths were observed to prefer taller corn over shorter corn for oviposition. In other studies, the corn earworm, Helicoverpa zea (Boddie), was reported to prefer taller corn over shorter corn for oviposition (Johnson et al., 1975), and similar observations were reported for oviposition by the European corn borer, Ostrinia nubilalis (Hubner), on cotton (Everly, 1959). Adult ovipositional preference for taller and older plants may be an adaptation to allow larvae to feed on the fruit of maturing crop plants (Johnson et al., 1975; Pitre et al., 1983). Another hypothesis, proposed by Claycomb (1954), suggests that FAW moths lay eggs on taller objects because larvae disperse on silk



Figure 2. Mean (\pm SD) number of egg masses laid by 3, 6, and 9-day-old fall armyworm (FAW) (Spodoptera frugiperda) moths during their initial 72h oviposition period on sorghum plus the saran screen cage covers at early whorl (36.4 cm tall), mid-whorl (50.2 cm), and late whorl (58.0 cm) stages in no-choice oviposition study in field cages. Bars with the same letter within plant growth stage are not significantly different (P=0.05, LSD).

threads on which they drop and are spread by the wind from the ovipositional sites to surrounding vegetation.

Oviposition of more egg masses on abaxial than adaxial surface of leaves agrees with observations by Pitre et al. (1983) and Ali et al. (1989) on FAW oviposition on corn, sorghum or cotton. With most of the eggs being deposited on the abaxial surface of leaves, ovicides used to control this pest on crops like sorghum and corn could have reduced efficacy because the insecticide would have little opportunity to come in contact with most of the eggs.

Examinations for FAW egg masses may be conducted by whole plant sampling and shadow casting techniques (Waddill, 1977). Oviposition studies indicate that procedures to determine infestation of FAW egg masses on sorghum should concentrate on the abaxial rather than the adaxial surface of the leaves, as has been suggested for cotton (Ali et al., 1989). FAW moths 3, 6 and 9 days old laid about the same number of egg masses during either their initial 48 or 72h oviposition test periods. The females laid eggs from day 3 posteclosion through 9 days of age. This agrees with the observations by Simmons and Lynch (1990) that FAW moths fed honey-water solution laid eggs over a 8.6-day period. Our observations indicate that FAW moths can lay about the same number of egg masses during the 48 or 72h initial oviposition periods as 3, 6 or 9-day-old moths (moths mated during previous two days), even as they age from days 3 to 9, but this study does not consider the total fecundity or reproductive potential of moths when mated at various ages.

The reproductive potential of FAW moths was reported to be influenced by age of the insects at first mating (Rogers and Marti, 1994). Young mated females 1 day old had greater reproductive potential than 3-day-old mated females. Females older than 10 days had a low reproductive potential (avg. 607 eggs/female). The reproductive potential of other lepidopterous species has been reported to be influenced by age of the female at mating. The pink bollworm, Pectinophora gossypiella (Saunders) (Gelechiidae), lays greater numbers of eggs when mated on day 1 posteclosion than when mated at an older age (Proshold 1996), as does Spodoptera littoralis (Boisduval) (Noctuidae) when mated two days after eclosion rather than when older (Ellis and Steele, 1982). Similar observations were recorded for beet armyworm, Spodoptera exigua (Hübner) (Noctuidae) (Rogers and Marti, 1997). The optimum time for beet armyworm mating is day 2 after female eclosion to achieve maximum egg laying.

Simmons and Lynch (1990) reported that peak egg deposition of FAW and other species, including corn earworm and lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller), occurred 2 to 3 days after eclosion with most of the eggs being deposited during the first half of the oviposition period. Pashley *et al.* (1992) reported that the FAW corn and rice strains had oviposition periods of 8 and 9 days, respectively, with most of the eggs being laid during the first four days. FAW females aged 3 and 6 days laid a greater number (although not significant at P=0.05 level) of egg masses than 9-day-old females in our 48h choice oviposition study, a trend similar to observations by Simmons and Lynch (1990) and Pashley et al. (1992).

These oviposition studies indicated that FAW females laid eggs on sorghum from 3 to 9 days after eclosion,

deposited more eggs on the abaxial than adaxial leaf surfaces and on taller plants (late whorl) than shorter plants (early whorl), and laid about the same number of egg masses during the 48 or 72h initial egg laying periods as 3, 6 or 9-day-old moths having mated during the previous 48h. It is significant to recognize that the age of FAW moths at mating, as with many other closely related insects, is a contributing factor to the reproductive potential of the species. The ability of FAW females to lay eggs for nine or more days allows this insect to have a high fecundity level. A single female may lay as many as 2375 eggs (Simmons and Lynch, 1990). A consistent high fecundity level during the oviposition period provides the FAW with an increased probability of survival of some eggs in spite of egg mortality factors such as predation, parasitization and adverse weather conditions.

Since the FAW is a migratory species and may immigrate into specific geographical locations from source areas at different times during the sorghum growing season when the crops are in various stages of plant development, it is beneficial to know the relationship between crop maturation stage and oviposition behavior of the moths. This information can be used in defining sampling programs for this pest, as well as developing season-long insect management strategies for sorghum.

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