PEANUT SCIENCE

VOLUME 19 JULY - DECEMBER 1992 NUMBER 2

Feeding-Site Preference of Fall Armyworm, Corn Earworm, and Granulate Cutworm (Lepidoptera:Noctuidae) on Florunner Peanut[1]

S. S. Deitz[2], J. W. Chapin[3]*, and P. H. Adler[4]

ABSTRACT

The feeding-site preferences of fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), corn earworm (CEW), *Helicoverpa zea* (Boddie), and granulate cutworm (GCW), *Agrotis subterranea* (F.) were studied on excised laterals and entire plants of Florunner peanut. Six larval size classes, based on head-capsule widths, were distinguished for FAW and GCW, and five for CEW. FAW and CEW larvae had very similar feeding behaviors. Both species fed primarily on the terminal three leaves of peanut laterals, but this preference for young foliage declined with larval age. All FAW and CEW size classes fed on blooms, with greatest incidence (21% of feeding observations) occurring in the second through fourth size classes. Axillary-bud feeding by FAW and CEW was greatest (23 and 17% of feeding observation, respectively) in the third size class. The last two larval size classes of FAW and CEW spent 20% of feeding time on R2 pegs. GCW fed primarily on blooms through the first four size classes. Foliage feeding by GCW remained ≤10% of feeding observations until the fifth size class. GCW did not feed on axillary buds in whole plant studies. Peg feeding by GCW peaked in the fourth and fifth size classes (36% of feeding observations). On whole plants, each FAW consumed 4.8± 1.2 tetrafoliate leaves, severed 6.3±1.6 pegs, and damaged an additional 3.6±1.7 pegs. Each CEW consumed 4.7± 0.8 leaves, severed 7.1±1.6 pegs, and damaged 2.4±1.4 pegs. Each GCW consumed 3.9±0.5 leaves, severed 8.5±2.0 pegs, and damaged 3.5±1.3 pegs.

Key Words: Peanut, *Arachis hypogaea*, fall armyworm, *Spodoptera frugiperda*, corn earworm, *Helicoverpa zea*, granulate cutworm, *Agrotis subterranea*, defoliators, feeding behavior.

Corn earworm (CEW), *Helicoverpa zea* (Boddie), fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), and granulate cutworm (GCW), *Agrotis subterranea* (F.) are primary defoliating insects on peanut, *Arachis hypogaea* L., in the southeastern United States (15, 16, 25, 30). Several studies have referred to the feeding behavior of these noctuids. FAW larvae prefer young leaves that have been unfolded from the terminal bud for two days or less; the last two instars account for more than 80% of defoliation (2, 11). CEW larvae also prefer to feed on terminals and young peanut foliage (15, 16); over 70% of total CEW peanut-foliage consumption occurs during the last two instars (14). Pencoe and Lynch (22) found that 93% of first-instar CEW feeding occurred on terminal foliage, while 5% occurred on blooms. Older GCW larvae feed on foliage and become nocturnal feeders, hiding during the day in the soil or under debris on the soil surface (25). GCW larvae also sever leaf stems and feed on those leaves in contact with the soil during daylight hours (25).

Other than foliage-consumption studies, where only foliage was offered, little is known about the feeding behavior of these species on peanut. Our field observations indicate that canopy-inhabiting larvae feed on many plant parts other than leaves. The purpose of this study was to determine age-specific feeding preferences of CEW, FAW, and GCW on peanut. A better understanding of the peanut-feeding behavior of these insects should be useful in the development of plant damage models and pest management practices.

Materials and Methods

All tests were conducted on Florunner peanut. Colonies of all three species were established in August 1990, with larvae collected from peanut fields in Barnwell County, S. C. The CEW colony failed that winter, and a new colony was established with 100 pupae obtained from the U.S.D.A. laboratory in Stoneville, Miss. Tests prior to August 1990 were conducted with colonies established from field collections in August 1989. Colonies were maintained on a modified pintobean-soyprotein-wheatgerm diet. (12)

Crisper Tests

Two tests were conducted with each species. FAW, CEW, and GCW larvae were reared in 27.5- X 19.5- X 9.5-cm covered plastic crispers on peanut laterals. Lateral branches were clipped from field plants and placed in 10-mL vials containing water, and plugged with cotton. Each lateral branch provided young terminal foliage, older foliage, axillary buds, flowers, and R2 pegs (newly formed gynophores, (6)). Pegs older than R2 were not supplied because they would not be available above the soil line. In test 1, plants were in the R5 growth stage at 73 days after planting (DAP).

[1]Technical Contribution No. 3257 of the South Carolina Agriculture Experiment Station, Clemson University, SC.

[2]Former Graduate Research Assistant, Current Address: 39200 Millwood Drive, Woodlake, CA 93286.

[3]Professor of Entomology, Edisto Research and Education Center, Blackville, SC 29817.

[4]Associate Professor of Entomology, Department of Entomology, Clemson University, Clemson, SC 29634-0365.

*Corresponding author.

Plants used in test 2 were in the R6 growth stage at 90 DAP. Two vials, each supporting one horizontal lateral branch, were place in each crisper so that all plant parts were accessible to the larvae. Four neonate larvae of the same species were placed on terminal, folded leaflets in each crisper and reared to pupation. Previous studies have reported that first-instar larvae are found predominantly on the terminal leaves (11, 15, 22, 25). Seven crispers were used for each species (n=28 larvae), and all species were reared concurrently. Crispers were placed side-by-side, with species position determined at random for each group of three crispers. Sunlight was augmented with fluorescent lighting from 0900 to 1630 hours (14:10 L:D). Room temperature ranged from 26 to 32 C. Throughout its lifespan, each larva was observed daily at 0800 and 2100 hours to provide one day and one night observation. At night, each crisper was observed under a desk lamp. Larval size, behavior, location on the plant, and feeding site were recorded at each observation. Behavior was classified as feeding, molting, or other nonfeeding. If a larva was found on a freshly damaged plant part, that part was recorded as a feeding site, except when larvae were molting.

Plant parts were divided into five main categories: terminal foliage, flowers, axillary buds, pegs, and other. Terminal foliage included the terminal three leaves on each lateral. Axillary buds are regions of new growth that lie between an older leaf and the lateral or vertical stem. These produce foliage, reproductive tissue, or both (13). The "other" category included older foliage, leaf petioles, bracts, lateral stems, and floral hypanthia ("bloom stalks").

CEW, FAW, and GCW develop through a variable number of instars on peanut foliage (14, 21, 25). Reference collections of larval instars were established for each species from diet-reared specimens. Larvae in the behavioral studies were placed in size classes by comparing head-capsule widths to these reference specimens. Due to the variability in number of molts on peanut, this technique is unreliable for identifying the true larval instar after the first two. However, it does show age-specific trends in feeding behavior which should closely correspond to the true larval instars. Five size classes for CEW larvae had mean (±S.E., n=10) head-capsule widths (mm) of 0.28±0.025, 0.52±0.026, 0.93±0.036, 1.72±0.06, and 3.03±0.11. Six FAW size classes had mean head-capsule widths (mm) of 0.30±0.015, 0.48±0.036, 0.72±0.048, 1.19±0.035, 1.85±0.081, and 2.84±0.097. Six GCW size classes had head-capsule widths (mm) of 0.32±0.013, 0.49±0.023, 0.80±0.057, 1.24±0.056, 1.79±0.086, and 2.84±0.125.

Lateral branches in the crispers were replaced every 2-3 days to keep plant parts fresh and to ensure that all plant parts were available throughout larval development. Each time plant material was replaced, the number of pegs severed or damaged was recorded. Pegs with meristematic tips removed were classified as severed. In a separate study, all pegs with tip feeding from naturally occurring FAW populations failed to develop. Those pegs not severed, but with feeding injury along the length of the peg, were counted as damaged. Dead larvae were replaced with the same size class, from colonies maintained on peanut foliage. All larvae were placed on terminal foliage when plant material was changed and when dead larvae were replaced.

The Z test for proportions (26) was used to determne differences in plant-part preference among size classes. To analyze differences in feeding-site preference between species, larvae were grouped into three categories: small, medium, and large. The first two size classes of each species were designated as small larvae and the last two sizes as large larvae. The middle two size classes of FAW and GCW, and third-size larvae of CEW were considered medium-size larvae. The Z test for proportions was then used to determine significant differences among species. Any calculated Z score greater than 1.96 (P=0.05) was statistically significant.

Whole-Plant Tests

Peanut plants were grown in an inflated, plastic greenhouse in plastic tubs (50-cm diameter, 45-cm depth) containing a sandy-loam soil over 20 cm of vermiculite. Soil fertility parameters fell within the recommended range for peanut production. Seed were coated with Nitragen® *Rhizobium* inoculant. Five tubs, each containing a single plant, were spaced around the periphery of a wooden table (2.4m x 1.2m x 0.9-m height). Plants were grown with a photoperiod of 14:10 (L:D). Greenhouse daily temperature ranged from 18-35 C. Thrips were controlled with aldicarb (0.15 gm/pot). The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) and twospotted spider mites, *Tetranychus urticae* Koch, were controlled when necessary, with Safers® insecticidal soap (20mL/L$H_2$0); one 15-X 30-cm yellow sticky card (Hummert Seed Co.) per plant; and with the release of predatory mites, *Phytoseiulus persimilus* Athias-Henriot and *Neoseiulus californicus* (McGregor), and the whitefly parasite, *Encarsia formosa* Gahan. Insecticidal soap was used only on tests 2 and 5 (35d and 21d prior to larval stocking, respectively).

Neonate larvae of all three species were reared in 27.5- X 19.5- X 9.5-cm crispers on young Florunner peanut foliage. The foliage was kept fresh as previously described. Five larvae of the second or third size class were subsequently transferred to separate, terminal, folded leaflets of each plant. Some lateral branches were pruned to the edge of the tub to prevent larvae from dropping outside the tub. Tanglefoot® was used to create borders around each tub to identify migration losses.

Five whole-plant tests were conducted:

Test 1. 7-26 April 1990. Ten plants were each stocked with five third-size FAW larvae.

Plants were in the R5 growth stage at 78 DAP.

Test 2. 29 June - 14 July 1990. Ten plants were each stocked with five third-size FAW larvae. Plants were in the R5 growth stage at 86 DAP.

Test 3. 22 April-11 May 1991. Five plants were each stocked with five second-size CEW larvae, and five plants were each stocked with five second-size FAW larvae.

Plants were in the R8 growth stage at 107 DAP.

Test 4. May-22 June 1991. Five plants were each stocked with five second-site GCW larvae, and five plants were each stocked with five second-size CEW larvae.

Plants were in the R6 growth stage at 91 DAP.

Test 5. 18 September - 8 October 1991. Five plants were each stocked with five second-size GCW, larvae, and five plants were each stocked with five second-size FAW larvae. Plants were in the R5 growth stage at 65 DAP.

Each larva was observed twice daily until pupation, beginning at approximately 0700 and 1900 hours. GCW larvae were observed at 0530 and 1900 hours due to their nocturnal feeding habit. A battery-powered headlamp was used to make predawn observations. Larval size, behavior, location on the plant, and feeding site were recorded as before.

Dead larvae and migrants were replaced with the same size class, from colonies maintained on peanut foliage. As with the crisper studies, all larvae were placed on terminal foliage. Due to high mortality of CEW on peanut, some replacement CEW larvae were retained in individual diet cups through the third size class to ensure enough replacements. After all larvae had pupated, each plant was uprooted and examined for peg damage and defoliation. Severed and damaged pegs were counted on each plant. The number of leaves consumed was determined by examining all tetrafoliate leaves, assigning each a defoliation rating (0-100%), summing all defoliation, and dividing by 100. A Delta-T leaf area meter (model #PM-910A) was used to calculate a mean leaflet area (cm^2) for intact leaves. The Z test for proportions (P=0.05) was used to determine differences in plant-part preference among size classes. Larval voucher specimens for each species were deposited in the Clemson University Arthropod Collection.

Results

Crisper Tests

Fall Armyworm

A total of 1,382 FAW larval observations were made, and a feeding site was determined for 1,075 of these observations (Fig. 1A). Subsequent reference to percentage of observations pertains to observations for which a feeding site could be determined, not total larval observations. All larval sizes fed more on the terminal three leaves than any other plant part. Terminal-foliage feeding was greatest for first and second sizes (81 and 77% of observations, respectively), and declined with larval age to 58-65% of observations in the last three sizes. This shift in feeding preference occurred despite continued availability of fresh terminal foliage.

Flower feeding by FAW was numerically greatest for the second size class (16% of observations) and declined with larval age to 2% occurrence in the sixth size class. Only minor axillary-bud feeding was observed (1-7%) in the crisper studies. Very little peg feeding occurred during the first two size classes (1-2%), but this behavior increased with larval age to 25 and 22% fifth-and sixth-size larvae, respectively. Peg-feeding larvae fed primarily on the distal tips of R2 pegs. First-to fifth-size larvae fed on other plant parts in 2-6% of observations. In the sixth size class, other-plant-part feeding was 15%, primarily due to the consumption of older foliage.

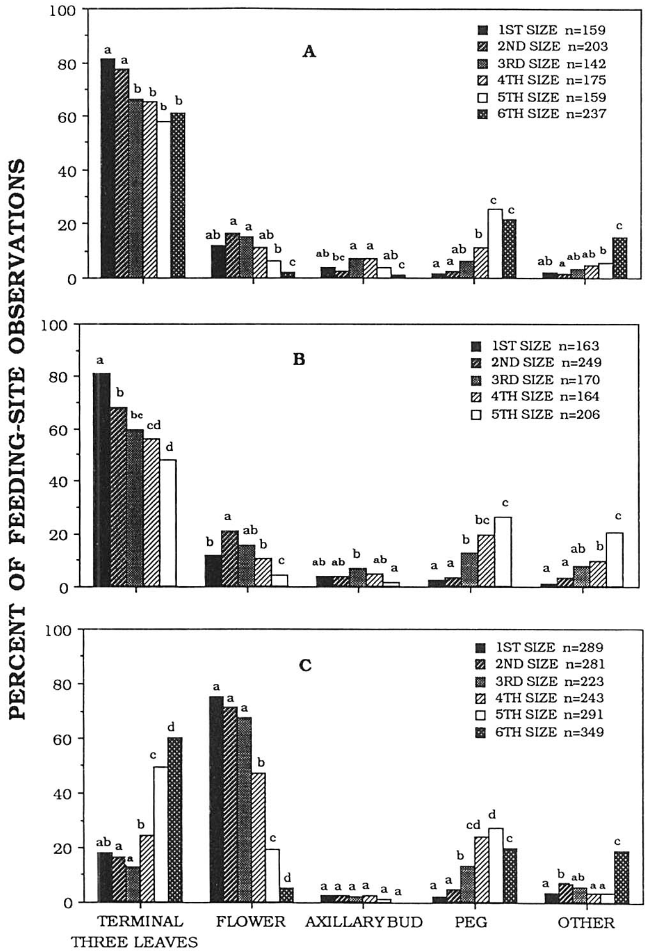

Fig. 1. Feeding-site preferences of FAW (A), CEW (B), and GCW (C), on Florunner peanut in crisper tests. Bars having the same letter within each plant-part category are not significantly different (P = 0.05).

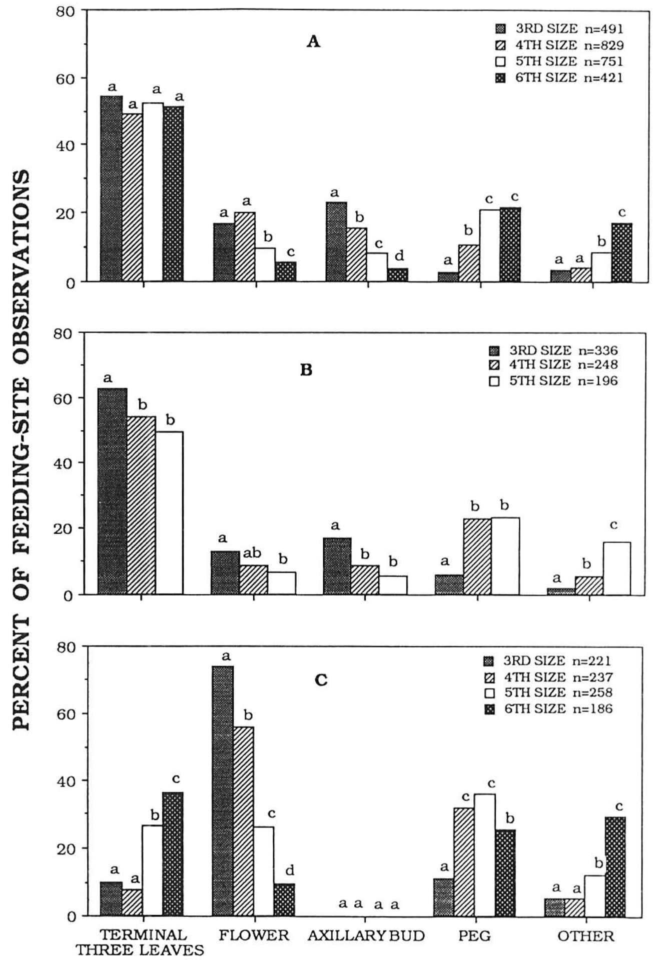

Fig. 2. Feeding-site preferences of FAW (A), CEW (B), and GCW (C), on Florunner peanut in whole-plant tests. Bars having the same letter within each plant-part category are not significantly different (P = 0.05).

FAW larvae pupated after 13-16 days of feeding. Over this interval, each larva severed a mean of 6.0±1.3 pegs and damaged an additional 1.1±0.3 pegs.

Corn Earworm

A total of 1,320 CEW larval observation were made, and a feeding site was determined for 952 of these observation (Fig. 1B). Similar to FAW, all CEW larval sizes fed more on the terminal three leaves than any other plant part. Terminal-foliage feeding by CEW was greatest for first-size larvae (81% of observations) and declined with larval age.

As with FAW, CEW flower feeding peaked during the second size class (21%), and then declined with larval age, to 6% in the fifth. Very little axillary-bud feeding (1-7%) was observed for all larval sizes in the crisper tests. Peg feeding was very low (2-4%) in first two size classes, but increased to 22% in the last size class. Like FAW, CEW usually fed on R2 peg tips. First- and second-size larvae fed on other plant parts in only 1-3% of observations. However, feeding on other parts increased with larval age to 20% (primarily older foliage) in the fifth size class.

Since diet-fed replacement larvae may have artificially reduced larval development time, a development time was not calculated for CEW. Each CEW larva severed a mean of 6.2±1.0 pegs and damaged an additional 1.1±0.5 pegs.

Granulate Cutworm

A total of 2,301 GCW larval observations were made, and a feeding site was determined for 1,676 of these observations (Fig. 1C). Unlike CEW and FAW, terminal-foliage feeding in the first three GCW size classes was limited to 13-18% of observations. However, terminal-foliage feeding increased to 49 and 60% in the fifth and sixth size classes, respectively.

First-, second-, and third-size GCW larvae fed on flowers in 67-75% of observations. Feeding on flowers declined with each subsequent size class to only 5% of observations in the sixth. Early size class larvae were usually found feeding within older, wilted flowers. Very little axillary-bud feeding was observed for all larval sizes of GCW. Peg feeding by first-size larvae occurred in 2% of observations and increased with larval age, peaking in the fifth size class at 31% of observations. As with CEW and FAW, peg feeding was concentrated on R2 peg tips. Other-plant-part feeding constituted only 3-7% of observations in the first five size classes, but increased to 19% of observations (primarily older foliage) in the sixth.

GCW larvae pupated after 23-26 days of feeding. Over this interval, each larva severed a mean of 7.9±1.4 pegs and damaged an additional 2.2±0.7 pegs.

Interspecies Comparisons

Small GCW larvae fed less on terminal foliage than small CEW (Z=15.05) or FAW larvae (Z=16.10). Conversely, small GCW larvae fed more on flowers than small CEW (Z=15.95) or FAW larvae (Z=16.25).

Medium GCW larvae fed less on terminal foliage than medium sized CEW (Z=7.76) or FAW larvae (Z=10.02). Medium GCW larvae also fed significantly more on flowers than medium CEW (Z=9.57) or FAW larvae (Z=11.81). Medium CEW larvae fed on axillary buds more than medium GCW larvae (Z=3.28).

Large CEW larvae fed less on terminal foliage than large FAW (Z=2.50). Large FAW larvae fed less on flowers than either large CEW (Z=2.18) or large GCW larvae (Z-2.21). Both large FAW and CEW larvae fed more on axillary buds than large GCW larvae (Z=2.50, Z=3.10, respectively).

Whole-Plant Tests

Fall Armyworm

A total of 3,127 FAW larval observations were made, and a feeding site was determined in 2,492 of these observations (Fig. 2A). All larval sizes fed more on the terminal three leaves (49-54% of observations) than any other plant part and no consistent trend among size classes was apparent.

Flower feeding by third- and fourth-size larvae occurred in 17 and 20% of feeding observations, respectively, and declined with larval age to 6% of observations in the sixth. Axillary-bud feeding comprised 23% of third-size larvae, observations, and declined with larval age to 4% in the sixth size. Very little peg feeding was observed for third-size FAW larvae (3%). However, peg feeding by later sizes increased to 20-21% of observations in the fifth and sixth size classes. Larvae usually fed on the tips of R2 pegs that had not yet penetrated the soil surface. Minimal feeding destroyed the meristem and effectively severed the peg. Larvae also fed to a lesser extent along the peg length, and there was a slight incidence of feeding on exposed pods (<1%). Although feeding on other plant parts was minor among third- and fourth-size larvae, it increased to 17% in the sixth size class. Older leaves were the primary component of the other category, accounting for 65% of other feeding in the sixth size class.

Each FAW larva consumed a mean of 4.8±1.2 tetrafoliate leaves, severed 6.3±1.6 pegs, and damaged an additional 3.6±1.7 pegs.

Corn Earworm

A total of 1,011 CEW larval observations were made, and a feeding site was determined in 780 of these observations (Fig. 2B). All larval sizes fed more on the terminal three leaves (50-63% of observations) than any other plant part. Foliage feeding by fourth- and fifth-size larvae was significantly less than that of the third. As with FAW, third-size CEW larvae preferred to feed within the folded, terminal leaflets. Older larvae fed either on the underside of younger foliage or on the leaf edge.

Flower feeding by third-size CEW larvae accounted for 13% of observations, decreasing to 6% in the fifth size class. Axillary-bud feeding in the third size class was greater (17%) than the fourth or fifth sizes (9 and 7%, respectively). Peg feeding by third-size larvae constituted only 6% of observation, but increased to 23% of observations in the fourth and fifth size classes. As with FAW, CEW usually fed on R2 peg tips. Very little other plant-part feeding was observed by third-size CEW larvae (2%). However, other feeding increased for each subsequent size class to 16% in the fifth. Older foliage was the primary component (80%) of other-plant-part feeding for fifth-size larvae.

Each CEW larva consumed an average of 4.7±0.8 leaves, severed 7.1±1.6 pegs, and damaged 2.4±1.4 additional pegs.

Granulate Cutworm

A total of 1,475 GCW larval observations were made, and a feeding site was determined in 902 of these observations (Fig. 2C). Third-size larvae overwhelmingly preferred flowers (74% of observations) and were usually found within older, wilted flowers or within the youngest flowers that had yet to unfold. Older larvae fed less on flowers with each subsequent size class, declining to 10% of observations for sixth-size larvae.

Terminal-foliage feeding was relatively minor during the third and fourth size classes (10 and 8% of observations, respectively), but increased to 26% and 36% of observations in fifth- and sixth-size GCW larvae, respectively. Unlike FAW and CEW, axillary-bud feeding was not observed for any size larvae. Peg feeding by third-size larvae occurred in only 11% of observations, and increased to 36% in the fifth size class. Similar to FAW and CEW larvae, peg feeding was greatest on R2 peg tips, although there was a greater incidence of exposed pod feeding (5% for fifth and sixth size classes). Other-plant-part feeding by third- and fourth-size GCW larvae was negligible, but increased to 12 and 29% of observations in the fifth and sixth size classes, respectively. Plant debris accessible from the soil surface accounted for 53 and 73% of other feeding for fifth- and sixth-size larvae, respectively.

The diel movement of GCW larvae on the peanut plant changed with larval age (Fig. 3). During the day, 62% of third-size larvae were located on the plant, usually on the lower third of the canopy. Less than 15% of older larvae were on the plant during the day. Most fourth-, fifth-, and sixth-size larvae (87, 90, and 96%, respectively) were found on the soil surface. Some were slightly buried in loose soil or under plant debris. At night 47, 45, and 35% of fourth-, fifth-, and sixth-size larvae were found on the plant. This represents a net larval movement onto the plant of 34, 35, and 31%, respectively.

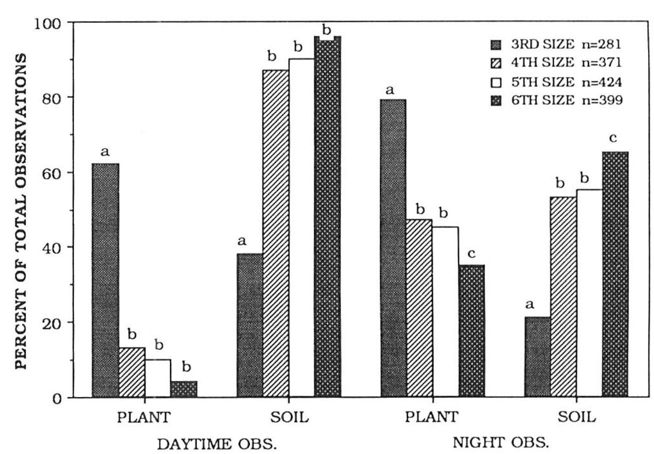

Fig. 3. Diel movement of GCW on potted Florunner peanut plants. Bars having the same letter within each location category are not significantly different (P = 0.05).

Each GCW larva consumed a mean of 3.9±0.5 leaves, severed 8.5±2.0 pegs, and damaged 3.5±1.3 additional pegs.

Discussion

Feeding-Site Preference

Fall Armyworm and Corn Earworm

FAW and CEW exhibited very similar feeding-site preferences, both in the crisper and whole-plant studies. Both species were predominantly foliage feeders throughout all larval sizes, feeding primarily on the terminal three leaves. This agrees with previously cited studies reporting that FAW and CEW preferred young peanut foliage (2, 11, 15, 16, 22). FAW and CEW bloom feeding was greatest for the second and third size classes in the crisper studies. The lower incidence of bloom feeding by first-size larvae was probably biased by initial larval placement in the terminal leaf.

Peg feeding by FAW and CEW increased with larval age, as bloom and axillary-bud feeding decreased. Young FAW and CEW preferred the concealed feeding sites within terminal, folded leaflets and flowers. Peg-feeding larvae are exposed as they crawl out to the tips of these structures. Greater mobility, reduced susceptibility to natural enemies, and changing nutritional requirements may be factors in the increased peg feeding of older larvae. Studies on other host crops have shown similar age-specific shifts in larval-feeding preference for FAW (1, 18, 19) and CEW (10, 20, 23, 27).

Granulate Cutworm

Unlike FAW and CEW, GCW fed predominantly on flowers rather than leaves during the first four size classes. Flower feeding apparently affords small GCW larvae protection from natural enemies. Even when not concealed within blooms, flower-feeding larvae seemed well-camouflaged by the orange gut contents visible through the larval skin. However, we attempted to exclude natural enemies and have no measure of actual site-specific mortality.

GCW peg feeding reached higher levels than that of FAW and CEW. GCW occupies a distinctly different feeding niche than that of CEW or FAW. The greater accessibility of pegs from the soil surface may explain the higher percentage of GCW peg feeding and damage in the whole-plant study. In contrast, pegs were equally accessible to all species in the crisper tests and this may explain the similar frequency of peg feeding among species.

Snow and Callahan (25) reported GCW severing leaf stems, and we have observed clipped leaflets on the soil surface in the field. Severed leaflets provide a food resource and a refuge for GCW during the day. The near absence of petiole feeding in this study (1-2% of all size classes) may indicate that this behavior is density dependent. Eden *et al.* (9) reported that GCW caused the worst damage in peanut fields by feeding on the "underground portions" of the plant. In our study, very little pod damage occurred in the whole-plant tests. There was also no evident injury to the plant crown or roots. As with FAW and CEW, almost all peg feeding occurred on R2 pegs. In this study, only pods brought to the soil surface during plant manipulation were fed on by GCW. However, we have observed some subterranean pod feeding by GCW in the field.

By occupying a different feeding niche, GCW larvae reduce competition with CEW and FAW, even though older larvae of all three species vie for some of the same resources (i.e., terminal foliage and R2 pegs). CEW and FAW have nearly identical feeding niches on peanut throughout their lifespan, but are often temporally isolated. In the South Carolina Coastal Plain, CEW larvae typically appear in peanut around the first week of August. FAW larval populations usually become established about two weeks later. Although mixed larval populations occur, the oviposition timing of these two species tends to reduce competition for early-instar feeding sites in terminal leaflets.

Foliage Consumption and Larval Development

In this study, FAW, CEW, and GCW consumed a mean of 4.8, 4.7, and 3.9 tetrefoliate leaves, corresponding to 19.2, 18.8, and 15.6 leaflets, respectively. GCW larvae consumed less foliage than the other two species, primarily because it relied more on flowers, pegs, and plant debris. Higher foliage-consumption values reported by Nickle (21), particularly for GCW, can be explained by the fact that only foliage was available. Based on a mean leaflet area of 8.00±0.32 cm^2 (n=312); FAW, CEW, and GCW consumed an average of 192, 188, and 125 cm^2 of foliage, respectively. Previous leaf-consumption studies reported an average of 95 cm^2 for FAW (11), 176 cm^2 for CEW (14), and 157 cm^2 for GCW (25).

Estimates of larval development time on peanut for FAW (11, 21, 29) and GCW (21, 25) are based on foliage diets. The diversity of plant parts actually consumed by these species may significantly shorten development time in the field. Todd *et al.* (29) found that CEW reared in petri dishes on peanut blooms and foliage developed two days sooner, had higher pupal weights, and lower mortality than those reared on foliage alone.

Management Implications

Larval location on the host plant influences the feasibility of field-sampling procedures used in pest management procedures. Linker *et al.* (17) reported that small CEW larvae in the terminal bud of peanut cannot be recovered as consistently as larger larvae exposed on leaves. Small CEW and FAW larvae feeding in blooms and axillary buds may also be harder to dislodge. In this study, a majority of small GCW larvae were found on the plant. Thus, small GCW larvae could be sampled with a shake cloth, but canopy sampling probably would not dislodge all larvae feeding within blooms, and others would be on the soil surface. Scouting for older GCW larvae would require soil sampling.

Larval location and feeding behavior influence insecticidal efficacy. Because small GCW are located within blooms on the lower third of the plant, and larger larvae are found on or slightly beneath the soil surface during the day, foliar sprays may be less effective against GCW than FAW or CEW.

Treatment thresholds for CEW, FAW, and GCW are currently based on foliage-consumption and artificial-defoliation studies. The treatment threshold for all three species is 13 larvae per row meter (30). The economic impact of canopy-inhabiting insects feeding on flowers, axillary buds, and pegs is unclear. Flower feeding is probably not economically important, since pollination occurs almost simultaneously as the flower opens. Smith (24) found that breaking the floral hypanthium at its base 4 h after the flower opened did not prevent fruit development. Axillary bud feeding prevents development of new leaves and reproductive branches. Thus, larval defoliation and peg removal are underestimated.

The economic significance of R2 peg severance is unknown. In this study, larvae were place on whole plants at R5 to R8 growth stages (65-107 DAP). This approximates the infestation interval of these three species in the field. On Florunner peanut, pod addition levels off about 90 DAP (7). Therefore, populations of CEW and FAW causing high rates of R2 peg severance after 90 d may have no effect on yield. However, GCW larvae are often found in peanut as early as June, when plants are in the early pegging stage (R2). High rates of peg severance at this point might delay maturity and have significant yield impact. GCW peg feeding from the soil surface and the fact that GCW often colonizes peanut earlier in the growing season, indicate that peg feeding by this species may be more significant than FAW or CEW peg feeding. Early, proximal R2 pegs attacked by GCW may contribute more to yield than later maturing, more distal pegs typically attacked by FAW and CEW. Because the feeding behavior of GCW is different than that of CEW and FAW, the economic thresholds for these species might also be different. Rates of peg severance by lepidopterous larvae are dependent on plant phenology (i.e., peg availability and condition of foliage), as well as larval density over time and competition for this resource. In field studies, peg-severance rates of 5-7 pegs/larva have been observed for CEW populations of 16-20 larvae/m (J. W. Chapin, unpublished data). Although pruning of lateral branches to the tub edge in our whole-plant studies could have affected plant growth and peg availability, the levels of peg severance observed in this study appear to be realistic.

Damage from larval feeding may also reduce yields indirectly. *Rhizoctonia solani* Kuhn is a major peanut pathogen that attacks all plant structures (28); however, peg infection accounts for the greatest yield loss (5, 8). Although *R. solani* is found abundantly in soils, Brenneman and Sumner (4) and Barnes *et al.* (3) found that wounding the plant significantly increases *Rhizoctonia* incidence. Thus, pegs fed on by canopy-inhabiting larvae, even though not severed, might be more susceptible to *Rhizoctonia* infection. A better understanding of the yield consequences of larval feeding on pegs and axillary buds will improve confidence in larval treatment thresholds for peanut.

Acknowledgment

We appreciate the assistance of J. S. Thomas, W. C. Bridges, Jr., and J. A. Brittain. We thank K. J. Boote and R. E. Lynch for preliminary reviews and suggestions on the manuscript. Partial funding was provided by the South Carolina Peanut Board and the Clemson University IPM Committee (SL 3d IPM grant).

Literature Cited

1. Ali, A., R. G. Luttrell, and H. N. Pitre. 1990. Feeding sites and distribution of fall armyworm (Lepidoptera:Noctuidae) larvae on cotton. Environ. Entomol. 19:1060-1067.
2. Barfield, C. S., J. W. Smith, Jr., C. Carlysle, and E. R. Mitchell. 1980. Impact of peanut phenology on select population parameters of fall armyworm. Environ. Entomol. 9:381-384.
3. Barnes, J. S., A. S. Csinos, and W. D. Branch. 1990. Sensitivity of *Rhizoctonia solani* isolates to fungicides and evaluation of peanut cultivars to Rhizoctonia limb rot. Peanut Sci. 17:62-65.
4. Brenneman T. B., and D. R. Sumner. 1989. Effects of chemigated and conventionally sprayed tebuconazole and tractor traffic on peanut diseases and pod yields. Plant Dis. 73:843-846.
5. Bell, D. K. and D. R. Sumner. 1984. *Rhizoctonia* diseases. p. 23-25 in D. M. Porter, D. H. Smith, and R. Rodriguez-Kabana (eds.), Compendium of Peanut Diseases. Am. Phytopathological Soc. St. Paul, MN.
6. Boote, K. J. 1982. Growth stages of peanut (*Arachis hypogaea* L.). Peanut Sci. 9:35-39.
7. Boote, K. J. and D. L. Ketring. 1990. Peanut. p. 675-717. in B. A. Stewart and D. R. Nielson (eds.), Irrigation of Agricultural Crops-Agronomy Monograph no. 30. Amer. Soc. of Agron. Madison, WI.
8. Csinos, A. S. 1987. Control of southern stem rot and *Rhizoctonia* limb rot of peanut with flutolanil. Peanut Sci. 14:55-58.
9. Eden, W. G., C. A. Brogden, and M. Sconyers. 1964. The granulate cutworm in peanuts and its control. Highlights Agric. Res. Ala. Agric. Exp. Stn. 11:13.
10. Farrar, R. R. and J. R. Bradley. 1985. Within plant distribution of *Heliothis* spp. (Lepidoptera: Noctuidae) eggs and larvae on cotton in North Carolina. Environ. Entomol. 14:205-209.
11. Garner, J. W. and R. E. Lynch. 1981. Fall armyworm leaf consumption and development on Florunner peanut. J. Econ. Enotomol. 74:191-193.
12. Greene, G. L., N. C. Leppla, and W. A. Dickerson. 1976. Velvetbean caterpillar: a rearing procedure and artificial medium. J. Econ. Entomol. 69: 487-488.
13. Gregory, W. C., B. W. Smith, and J. A. Yarbrough. 1951. Morphology, genetics, and breeding. pp. 28-87. *in* The Peanut - The Unpredictable Legume. Arant, F. S. (Arr.). National Fertilizer Assoc. Washington.
14. Huffman, F. R. and J. W. Smith, Jr. 1979. Bollworm: Peanut foliage consumption and larval development. Environ. Entomol. 8:465-467.
15. King, D. R., J. A. Harding, and B. C. Langley. 1961. Peanut insects in Texas. Misc. Publ. 550 Tex. Agric. Exp. Stn.
16. Leuck, D. B., R. O. Hammons, L. W. Morgan, and J. E. Harvey. 1967. Insect preference for peanut varieties. J. Econ. Entomol. 60:1546-1549.
17. Linker, H. M., F. A. Johnson, J. L. Stimac, and S. L. Poe. 1984. Analysis of sampling procedures for corn earworm and fall armyworm in peanuts. Environ. Entomol. 13:75-78.
18. Morrill, W. L. and G. L. Greene. 1973a. Distribution of fall armyworm larvae 1. Regions of field corn plants infested by larvae. Environ. Entomol. 2:195-198.
19. Morrill, W. L. and G. L. Greene. 1973b. Distribution of fall armyworm larvae 2. Influence of biology and behavior on selection of feeding sites. Environ. Entomol. 2:415-418.
20. Mueller, A. J. and B. W. Engroff. 1980. Effects of infestation levels of *Heliothis zea* on soybean. J. Econ. Entomol. 73:271-275.
21. Nickle, D. A. 1976. The peanut agroecosystem in central Florida, economic thresholds for defoliating noctuids; associated parasites; hyperparasitism of the *Apanteles* complex. Ph.D. dissertation. Univ. of Florida, Gainesville.
22. Pencoe, N. L. and R. E. Lynch. 1982. Distribution of *Heliothis zea* eggs and first instar larvae on peanuts. Environ. Entomol. 11:243-245.
23. Pitre, H. N. and T. L. Hillhouse. 1980. Establishment of infestation and behavior of *Heliothis zea* on soybeans in the greenhouse. J. Ga. Entomol. Soc. 16:28-34.
24. Smith, B. W. 1950. *Arachis hypogaea*: Aerial flower and subterranean fruit. Amer. J. Bot. 37:802-815.
25. Snow, J. W. and P. S. Callahan. 1968. Biological and morphological studies of the granulate cutworm, *Feltia subterranea* (F.), in Georgia and Louisiana. Res. Bull. 42 Univ. Ga. Exp. Stn.
26. Steele, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics, 1st ed. McGraw-Hill, New York.
27. Schmidt, K. M., J. H. Benedict, and M. H. Walmsley. 1988. Behavioral responses (time budgets) of bollworm (Lepidoptera: Noctuidae) larvae for three cotton cultivars. Environ. Entomol. 17:350-353.
28. Tabor, R. A., and Pettit, R. E. 1970. Characteristics of *Rhizoctonia* isolates from peanuts. Proc. Am. Peanut Res. Educ. Soc. 2:143 (Abstr.).
29. Todd, J. W., R. M. Beach, and W. D. Branch. 1991. Resistance in eight peanut genotypes to foliar feeding of fall armyworm, velvetbean caterpillar, and corn earworm. Peanut Sci. 18:38-41.
30. Womack, H., J. C. French, F. A. Johnson, S. S. Thompson, C. W. Swann. 1981. Peanut pest management in the Southeast. Univ. of Ga. Coop. Ext. Ser. Bull. 850.

Accepted June 5, 1992