TIMING AND DISTRIBUTION OF ATTACK BY THE BANANA WEEVIL (COLEOPTERA:CURCULIONIDAE) IN EAST AFRICAN HIGHLAND BANANA (*MUSA* SPP.)

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ABSTRACT

Timing and distribution of attack on East African highland banana (Musa AAA-EA) by the banana weevil, *Cosmopolites sordidus* (Germar), (Coleoptera: Curculionidae) was studied in a field trial at a farm 25 km NE of Kampala, Uganda. Weevils were released at three densities (5, 20 and 40 females per mat) in 324 m² banana plots (cv *Atwalira*) that had been established 18 months earlier and maintained relatively free of weevils. Two weeks after release, entire mats were removed and examined for weevil eggs and first instar larvae. At a density of 20 weevils per mat, oviposition oc curred on 25% of plants less than 6 six months old (suckers) with an average of three eggs (range 0-16) per infested plant. At the same time, 85% of flowered plants were attacked with mean oviposition of 15 eggs (range 0-41) per plant. An inverse relationship existed between weevil population density and eggs/female/plant. Five females per mat produced an average of 7.2 eggs per flowered plant, whereas 20 females produced 15 eggs per flowered plant and 40 females produced 12.5 eggs. This suggests the existence of density-dependent factors in weevil oviposition. Over 90% of the oviposition occurred in the base of the pseudostem, with the remaining eggs found in the corm and roots near the soil surface. However, in stands displaying high mat, (a condition in which part of the corm appears above the soil surface) more eggs were found on the corm than pseudostem.

Key Words: highland banana, banana weevil, $Cosmopolites\ sordidus$, high mat, oviposition

RESUMEN

Se estudió la época y distribución del ataque del barrenador del plátano, Cosmopolites sordidus (Germar), (Coleoptera: Curculionidae) al plátano de montaña de Africa del Este (Musa AAA-EA) en una plantación ubicada 25 km al NE de Kampala, Uganda. Se liberaron tres densidades de barrenadores (5, 20, y 40 hembras por mata) en lotes de 324 m² del cv. Atwalira plantados 18 meses antes y mantenidos relativamente libres de barrenadores. Dos semanas despues de liberar los barrenadores, se examinaron matas completas para determinar la presencia de huevecillos y larvas en primer instar. La densidad de 20 hembras/mata resultó en oviposición (0-16 huevecillos/planta) en 25% de plantas de menos de 6 meses de edad (chupones). El 85% de las plantas con floración fueron atacadas, encontrándose un promedio de 15 huevecillos/ planta (rango 0-40 huevecillos/planta). Se encontró una relación inversa entre la densidad de población del barrenador y la cantidad de huevecillos/hembra/mata. La densidad de 5 hembras/mata resultó en un promedio de 7.2 huevecillos/planta florecida, mientras que 20 y 40 hembras/mata produjeron 15 y 12.5 huevecillos/planta florecida, respectivamete. Los resultados sugieren que el nivel de oviposición depende de la densidad de hembras. Mas del 90% de la oviposición ocurrió en la base del pseudotallo, mientras que el resto de los huevecillos se encontró en el cormo y raices cercanas a la superficie del suelo. Sin embargo, en aquellas plantas con cormos ubicados arriba de la superficie del suelo, se encontraron más huevecillos en el cormo que en el pseudotallo.

All of the indices developed for weevil assessment (Mitchell 1978, Taylor 1991, Gold et al. 1994) evaluate cumulative larval damage in corm residues soon after harvest. None of these methods discern timing of attack. There may be critical developmental periods when plant sensitivity to weevil damage is heightened. If so, two plants displaying similar levels of weevil damage at harvest may differ in yield loss if attack occurred at dissimilar times. Thus, it is critical to gain insight into the timing of weevil attack under natural conditions as a first step towards understanding dam-

The banana weevil, *Cosmopolites sordidus* Germar, is a primary production constraint of highland cooking banana (*Musa* AAA-EA) in the Great Lakes region of eastern Africa (Gold et al. 1993; Bosch et al. 1995). Weevil larvae bore into the corm and the lower pseudostem causing mortality of suckers, through snapping and toppling (Wright 1977, Bosch et al. 1995, Rukazambuga 1996). Larvae also interfere with root initiation (Shillingford 1988). Damage is usually greater in ratoon crops (Mitchell 1980, Rukazambuga 1996, Gold 1998) and sustained attack over several crop cycles may prolong maturation rates and reduce yield by up to 60% (Rukazambuga 1996).

age thresholds. At present, no information is available on oviposition preferences for different host phenological stages.

Research results suggest that no single control strategy is likely to provide complete control for banana weevil (Gold 1998). Therefore, a broad integrated pest management (IPM) approach encompassing major components of pest control and plant resistance mechanisms might provide the best chance for success in controlling this pest (Gold 1998). Information on timing and location of weevil attack and vulnerable stages will be essential to the development of any IPM program.

Classical biological control of banana weevil in Africa may be possible. The banana weevil evolved in southeast Asia and is not considered a pest in much of its area of origin (Neuenschwander 1988, Gold 1998). This suggests that natural enemies may be important in the control of the weevil in Asia. Based on the weevil's biology, Neuenschwander (1988) suggests the egg stage may be most vulnerable to natural enemies. Of particular interest would be the possible existence of egg parasitoids. Efficacy of egg parasitoids, in turn, would be affected by egg density, oviposition sites, and exposure of eggs. For example, eggs placed above the soil surface should be more vulnerable to natural enemies than those underground. The objectives of this study were to establish timing of banana weevil attack, and spatial and temporal egg distribution in highland banana plants under field conditions.

MATERIALS AND METHODS

Site Description

The research was conducted in field trials at Sendusu Farm $(0^{\circ}32' \text{ N}, 1260 \text{ m.a.s.l.})$ of the International Institute of Tropical Agriculture (IITA) and at the Kawanda Research Station $(0^{\circ}19' \text{ N}, 1195 \text{ m.a.s.l.})$. Both sites have two rainy seasons (March-May and Sept.-Nov.), with an average precipitation of 1,219 mm per year. Daily mean temperature is 21°C at both sites.

Sendusu trial-timing of weevil attack

The research was carried out in an 18-month-old banana plantation (24 plots of 36 plants each) at Sendusu farm, established in July 1993. Plots consisted of six rows of six mats (cv*Atwalira*, AAA-EA) spaced at 3 m with 20 m grass alleys to minimize weevil movement between plots. The trial was established in a fallow field with no history of recent banana production. Suckers were pared and hot water-treated before planting to remove immature weevil immature stages, which are the main source of infestation in new plantations. At the time of this study, experimental plots contained 25-36 mats with three to seven plants per mat. Plants were characterized as (1) "peeper" (1-3 mo), (2) "maiden suckers" (4-6 mo), (3) "pre-flowered" (7-9 mo), (4) "flowered" and (5) "residues" (standing post-harvest plants). Desuckering was not undertaken for a month prior to weevil release to prevent plant injury. Timing of banana weevil attack, in relation to growth stage, was studied by destructively sampling entire banana mats and determining egg numbers and density on plants at different phenological stages.

Weevil Release and Sampling

Mature weevils were collected from pseudostem traps in farmers' fields in Masaka district (120 km SW of Kampala) and maintained on corm pieces in the IITA entomology laboratory at the Kawanda Research Station for two weeks. Female weevils were

released into plots at densities of 5, 20, or 40 females per mat. Each treatment was replicated twice. The weevils were released during the evening of 1 February 1995 into shallow holes around the base of each mat.

Data from previous trials at the same site suggest that banana weevil movement between plots was limited. In one study, for example, more than 15,000 weevils were marked to identify plot of release. Over a three year period, fewer than 3% of marked weevils captured in pseudostem traps were recovered from plots other than those in which they had been initially released (Gold & Night, unpubl.). Therefore, the number of released weevils which may have moved between plots during the relatively brief period of our study was likely to have been very low. The experiment was repeated in June 1995 using similar treatments and replication numbers.

Sampling commenced two weeks after weevil release and lasted for a three week period during which all mats were sampled. Mats were selected in random order, uprooted in their entirety, and separated into plants grouped by phenological stage. Plant girth at the collar (i.e., junction of pseudostem and corm) and the depth of the collar relative to the soil surface were recorded for each plant. All plants on a mat were sampled.

Since weevil oviposition is relatively low, both eggs and first instar larvae (i.e., < 1.5 mm head capsule width) were counted. Field observations suggested that first instar larvae did not move more than a few cm from eclosion sites. Preliminary observations suggested that few eggs were found more than 10 cm from the plant collar. Therefore, the roots were first inspected for eggs after which the first 10 cm of corm and the first 20 cm of pseudostem (relative to the collar) were gently pared to expose immature weevil stages. The number and location (i.e., root, corm pseudostem, distance from soil surface) of all eggs and first instar larvae were then recorded.

Kawanda trial-influence of high mat on egg distribution

The effect of high mat on weevil egg distribution was studied in an established field trial at the Kawanda Research Station. The trial was planted in November 1991 and consisted of 24 adjacent plots (i.e., no alleys) containing five rows of five plants in a 3 m \times 3 m arrangement. Treatments included (1) continuous intercropping with finger millet; (2) control with neither intercrop nor soil amendments; (3) manure placed in planting holes; (4) manure plus continual grass mulching. Weevils were released at a mean rate of 10 males and 10 females per mat in August 1992 and remained high throughout the entire trial (Rukazambuga, 1996).

Egg and first instar larval distribution were studied during the fourth ration (April 1996) in the manure plus mulch plots. This treatment was selected because it supported the highest densities of weevil adults (Rukazambuga, 1996) and >60% of the plants had developed high mat. Existing field populations of weevils were used. At the time of sampling, weevil density, using mark and recapture methods (Southwood, 1978), was estimated at a mean density of 30 weevils/mat.

Sampling

Destructive sampling was undertaken on flowered plants. This stage displayed a greater degree of high mat than younger plants and supported the highest levels of weevil eggs. Plants were categorized as "high mat" if the corm appeared above the soil surface or "normal" if the corm was totally covered by soil. Six plants of each category were uprooted in each of the six mulched plots. Distribution of eggs and first instar larvae were recorded with respect to plant location (i.e., root, corm, pseudostem) and position (above or below) relative to the soil surface.

Data analysis included border plants since host stage preferences were likely to be independent of mat location. Egg and first instar larval numbers were combined; hereafter, "egg" refers to these combined values. Chi square analysis indicated that oviposition levels and egg distribution trends were similar for the February and June sampling periods; therefore, analyses (ANOVA) were conducted on pooled data. To stabilize the variance, data on oviposition were transformed to $\log_{10} (x + 1)$. Egg density was estimated as (1) number per plant for each banana stage; (2) total numbers per stage; and (3) numbers per unit pseudostem surface area (i.e., 100 cm²) presented to gravid females. Surface area was estimated for the first 10 cm of pseudostem (where most oviposition occurred) by treating this section as a cylinder (i.e., girth \times 10 cm). Standing post harvest plants on mats are referred to as crop residues and considered as a plant stage in the results.

Oviposition on different host phenological stages was compared through analysis of variance procedures (General Linear Model under SAS) for 1) egg number per plant; 2) egg number per plot and 3) egg density per unit surface area. Presented means are adjusted based on least square means procedure in SAS and compared using standard error. Oviposition per female under field conditions was calculated for the different treatments. Categorical mode regression analysis in SAS was used to determine the probability of a given plant stage being associated with oviposition

A T-test was used to compare the effect of high versus low mat on oviposition. Within each mat condition, egg placement on the corm versus the pseudostem was compared using a matched pair T-test. Egg location relative to the soil surface was estimated as the percentage of total eggs that were encountered above or below the soil surface.

RESULTS

Sendusu trial—Timing of attack

Plants in trial plots were desuckered on a periodic basis such that peepers and maiden suckers were two to three times as abundant as flowered plants at the time of study (Table 1). At each of the three tested pest densities, banana weevils oviposited on all stages of the host plant including crop residues (Table 1). Weevils displayed a preference for older, larger plants with pre-flowered or flowered stages being utilized two to four times more than maiden suckers or peepers (Table 1).

Oviposition was highest on flowered plants and crop residues at all weevil densities (Table 2). Egg number per flowered plant was 2 to 2.4 times that of pre-flowered plants and 8 to 20 times that of peepers and maiden suckers. Adjusting for differential plant number per mat, 10-12% of oviposition occurred on peepers and maiden suckers, 27-34% on pre-flowered plants, 22-37% on flowered plants and 19-32% on crop residues (Table 3).

Egg distribution appeared to be affected by both stage preference and availability. For example, egg number per 100 cm^2 of plant was greatest on crop residues (Table 2) although a higher percentage of total oviposition was on the more abundant pre-flow-ered plants (Table 3).

Analysis of host plant association with oviposition using categorical mode regression gave probabilities less than 0.5 for peepers and maiden suckers. Pre-flowering plants were associated with an oviposition probability of 0.77, flowered plants with a probability of 0.79 and crop residues with a probability of 0.6. Peepers and maiden suckers carried a negative sign which was an indication of very low association with egg presence.

		5	20		40 $^{\circ}/mat$	
Stage	No./plot	% utilized	No./plot	% utilized	No./plot	% utilized
Peeper	48	21	58	26	54	24
Maiden sucker	26	35	69	36	47	51
Pre-flowered	36	81	53	81	62	77
Flowered	18	78	27	93	17	94
Crop residues	15	67	23	92	25	100

TABLE 1. EAST AFRICAN HIGHLAND BANANA (MUSA AAA-EA) UTILIZATION FOR OVIPOSITION AT THREE DENSITIES OF BANANA WEEVIL FEMALES IN A 2 YEAR OLD BANANA STAND AT SENDUSU RESEARCH FARM, NAMULONGE, UGANDA.

Effect of Weevil Density

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Fewest eggs were found following release of 5 females weevils per mat. However, increasing weevil density from 20 to 40 females per mat did not result in corresponding increases in oviposition. Thus treatment means at the two weevil densities were not significantly different (Table 4). Increasing weevil density per mat had little effect on the percentage of plants attacked (Table 1), while egg density per plant (Table 2) and egg number per plot (Table 3) increased only until 20 weevils per mat. Weevil density had a quadratic (F = 23.66, P < 0.01) influence on oviposition.

There was a treatment-stage interaction (F = 3.24, P < .01) that suggested the number of eggs encountered in different host stages at five females per mat were limited by weevil number (Table 5). Since plant size was similar across treatments, egg density per unit surface area followed the same trends as eggs per plant.

Weevils produced more eggs per female at lower densities. Oviposition averaged 1.4 eggs/female/week at a weevil release density of five females per mat, 0.8 eggs/female/week at a density of 20 females per mat, and 0.5 eggs/female/week at a density of 40 females per mat.

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Stage	Eggs	$\text{Log}_{10}(\text{eggs+1})$	$Eggs/100cm^2$
Peeper	0.6	0.11 ± 0.03	0.16 ± 0.09
Maiden sucker	1.2	0.22 ± 0.03	0.24 ± 0.09
Preflowered	4.5	0.57 ± 0.03	0.75 ± 0.09
Flowered	11.6	0.93 ± 0.04	1.74 ± 0.14
Crop residues	10.1	0.82 ± 0.04	1.93 ± 0.14
F value		108.01**	49.13**

TABLE 2. DISTRIBUTION OF BANANA WEEVIL EGGS PER PLANT IN A 2 YEAR OLD BANANA STAND AT SENDUSU RESEARCH FARM, NAMULONGE, UGANDA (LSMEANS \pm SE).

***P* < 0.01; df = 4, 577.

Stage	Η	Banana Weevil Eggs/H	Plot
	5	20	40 °/mat
Peeper	9	12	23
Maiden sucker	8	49	36
Preflowered	61	154	160
Flowered	63	202	107
Crop residues	35	151	158

TABLE 3. DISTRIBUTION OF BANANA WEEVIL EGGS PER PLOT IN A 2 YEAR OLD BANANASTAND AT SENDUSU RESEARCH FARM, NAMULONGE, UGANDA.

Oviposition Sites

On a mat basis, 95% of the oviposition was in the pseudostem, 4% in the corm and 1% in roots (Table 6). Weevil density did not affect egg location. On peepers and suckers oviposition never occurred in the roots while only 1 egg was found in the root system of a pre-flowered plant. Most oviposition on the pseudostem was <5 cm above the collar with eggs rarely encountered >15 cm above the plant collar. Oviposition on the corm was usually within five cm from the collar.

In this trial, the collar was, on average, 10 cm below the soil surface for all plant stages. Eggs in peepers and suckers were most commonly found 0-5 cm below the soil surface and rarely above ground (Table 7). In plants more than six months old, oviposition ranged from 10 cm below to 10 cm above the soil surface. Older plants with the collar near the soil surface supported significant above-ground oviposition. As a result, at least 37% of the eggs in flowered plants and crop residues were found close enough to the soil surface to be accessible to natural enemies.

Kawanda trial-Effect of high mat on oviposition

Plants with high mat received more eggs (28.0) than plants without high mat (17.4) (T = 2.8; P < 0.01). On plants with high mat, more eggs were placed on the corm

Weevils/mat	Eggs per plant			
	Eggs	$\text{Log}_{10} (\text{eggs} + 1) \pm \text{SE}$	Eggs/100cm ² ± SE	
5	3.19	0.38 ± 0.03	0.57 ± 0.09	
20	7.16	0.61 ± 0.03	1.29 ± 0.08	
40	6.57	0.59 ± 0.03	1.03 ± 0.09	
F value		19.11**	16.23**	

TABLE 4. EFFECT OF ADULT BANANA WEEVIL DENSITY ON INTENSITY OF OVIPOSITION PER PLANT IN A 2 YEAR OLD BANANA STAND AT SENDUSU RESEARCH FARM, NAMULONGE, UGANDA (LSMEANS ± SE FOR TRANSFORMED VALUES).

** P < 0.01; df = 2, 577.

Eggs per plant Log_{10} $\begin{array}{c} Log_{_{10}} \\ (eggs + 1) \end{array}$ $\begin{array}{c} Log_{_{10}} \\ (eggs + 1) \end{array}$ 5^1 20^{1} (eggs + 1) 40^{1} Stage Peeper 0.3 0.1 ± 0.05 0.4 0.1 ± 0.04 0.9 0.1 ± 0.05 Maiden suckers 0.6 0.2 ± 0.07 1.6 0.2 ± 0.04 1.6 0.3 ± 0.05 Preflowered 3.3 0.5 ± 0.06 5.8 0.6 ± 0.05 5.3 0.6 ± 0.04 Flowered 7.2 0.7 ± 0.08 15.0 1.0 ± 0.07 12.5 1.0 ± 0.08 1.0 ± 0.07 1.0 ± 0.07 Crop residues 0.5 ± 0.09 13.112.74.4

TABLE 5. INFLUENCE OF ADULT BANANA WEEVIL DENSITY AND PLANT PHENOLOGICAL STAGES ON OVIPOSITION PER PLANT IN A 2 YEAR OLD BANANA STAND AT SENDUSU RESEARCH FARM, NAMULONGE, UGANDA (LS MEANS \pm SE FOR TRANSFORMED VALUES).

¹Female weevils/mat.

(17.3) than on the pseudostem (10.6) (matched pair T-test 2.6; P < .01). By contrast, plants with normal mat had only 33% of the eggs on the corm (5.8) and 67% on the pseudostem (11.6) (matched pair t test 2.8; P < 0.01).

DISCUSSION

Plant age was an important factor in determining the number of eggs encountered. Older (i.e., flowered) plants received more eggs than other plant stages. Additionally, egg density per unit surface area of the plant was greater on older plants suggesting that oviposition was not based on random encounter with hosts. Instead, flowered plants were either more easily located or accepted at higher levels than peepers, suckers and pre-flowered plants. Standing crop residues also attracted high levels of oviposition.

TABLE 6. BANANA WEEVIL OVIPOSITION SITES IN A 2 YEAR OLD BANANA STAND AT SEN-DUSU RESEARCH FARM, NAMULONGE, UGANDA (EGGS PER 10 PLANTS).

	Pseud	ostem		Corm	
	Distance from collar of				
Plant stage	6-15cm	0-5cm	0-5cm	6-15	Roots
Peeper	0.8	2.2	0	0	0
Maiden sucker	2.9	2.4	0.6	0	0
Preflowered	20.7	29.5	2.9	0.1	0.1
Flowered	50.9	93.4	7.8	0.2	2.9
Crop residues	42.1	69.2	8.8	0	2.9

F value 20.99**; for plant stage- site interaction.

**P < 0.01; df = 16, 1199.

Standard errors: Peeper = 3.5; Maiden sucker = 3.3; Preflowered = 3.4; Flowered = 5.4; Crop Residues = 5.5.

	Egg site				
	Soil s	Paired T-test			
Plant stage	Below	Above	T - value		
Peeper	0.14	0	2.11^{*}		
Maiden sucker	0.15	0.02	2.30^{*}		
Preflowered	4.13	2.00	4.71**		
Flowered	9.88	5.83	5.39**		
Crop residues	9.34	5.55	7.44**		

TABLE 7. DISTRIBUTION OF BANANA WEEVIL EGGS IN RELATION TO THE SOIL SURFACE IN A 2 YEAR OLD BANANA STAND AT SENDUSU RESEARCH FARM, NAMULONGE, UGANDA.

*P < 0.05.

**P < 0.01; df = 2, 577.

Standing crop residues supported higher egg densities than growing plants although numbers of eggs encountered per plant suggested diminishing levels with time after harvest. The results in this study contrast with those of Gold & Bagabe (1994) in Uganda and our observations in Indonesia where heavy weevil attack was observed on prostrate corms and pseudostems, while little damage was observed on standing (i.e., uncut) residues.

Close examination of banana plants revealed small scars on all plant stages which may have been oviposition chambers or signs of exploratory feeding and in older plants, eggs or first instar larvae were commonly found in or around these scars. Although similar scars were common in peepers and maiden suckers, they rarely contained eggs. This suggests that host plant acceptance may be more important than host plant location in determining egg distribution across different aged plants. If this is true, it remains unclear whether or not host acceptance is related to oviposition stimulants or deterrents.

Although weevil oviposition on peepers and suckers was low, such plants are still highly vulnerable to weevil damage. In many cases, weevil larvae pass from the mother plant into followers through a shared corm. In a heavily infested weevil trial at Kawanda, we observed this type of attack on 46% of suckers. Such attack causes poor sucker growth, early plant death, and contamination of planting material, which is the primary source of infestation of new stands.

The cause of high mat in cooking banana is unclear. In West Africa, high mat in plantain is believed to reflect general plant stress, including low soil fertility and high pest pressure (Swennen 1984). In Uganda, high mat is most common in aging plantations. In this study, corm exposure above the ground increased susceptibility to weevil attack. This would further exacerbate overall plant stress and would likely hasten plantation decline.

Observed egg densities in our study of 0.5-1.4 eggs per female per week suggest that oviposition in the field may be considerably less than that obtained in the laboratory. Differences between our results and laboratory studies might be explained by emigration of adults, failure to detect eggs or reduced fecundity under field conditions. Follow-up studies suggested that weevil emigration was limited (Gold et al. unpubl.). Similarly, we believe that our examination for eggs was quite thorough and that we detected a high percentage of the eggs in study plots.

Thus, it appears that banana weevil fecundity is lower in the field than under laboratory conditions. Oviposition also seems to be affected by density dependent factors (i.e., reduced oviposition per female at higher weevil densities) In our study, total oviposition was similar in plots with 20 versus 40 females per mat. This might help explain why damage estimates may be similar in farms with disparate populations of adult weevils (Gold et al.1997).

The data suggest that banana weevils do not achieve their oviposition potential under field conditions. Density dependent factors may further limit fecundity in highly infested fields. Such reduced fecundity at high densities may contribute to the slow population build-up commonly observed in banana weevil and may also explain the poor relationship observed between weevil adult densities and damage (Rukazambuga 1996; Gold et al. 1997).

ACKNOWLEDGMENTS

Paul Speijer and Daniel Rukazambuga assisted in problem definition and proposal development. Advice on data analysis was given by S. Nokoe. Funding was provided by the Rockefeller Foundation through IITA.

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