

Recent advances in banana weevil biology, population dynamics and pest status with emphasis on East Africa

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Introduction

The banana weevil, *Cosmopolites sordidus* Germar, is the most important insect pest of banana and plantain. Plantain and highland banana are especially susceptible (Gold *et al.* 1994). The weevil has been implicated in the decline and disappearance of highland banana from traditional growing zones in central Uganda (Gold *et al.* 1998) and western Tanzania (Bosch *et al.* 1995).

The foundation of any integrated pest management (IPM) programme is a clear understanding of the biology, behaviour, population dynamics and pest status of the target insect. Studies on pest biology will provide insight into intrinsic mortality, dispensable mortality, stages best targeted for control, and interpretation of the effects of control methods on pest populations and damage. For example, reductions in adult weevil numbers (e.g. by trapping or use of entomopathogens) may not result in corresponding decreases in damage if oviposition is strongly density-dependent or if there are high levels of immigration from surrounding fields. Similarly, the effects of a natural enemy attacking weevil eggs may be less important if there is already high mortality in the egg and early instars.

Banana weevil biology

Banana weevils are narrowly oligophagous, attacking only plants in the genera *Musa* and *Ensete* (Zimmerman 1968, Arleu and Neto 1984, Esquivel 1990). The adult is free-living (i.e. not confined to the host plant) but rarely encountered outside of banana stands.

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Eggs are placed singly in chambers excavated in the base of the host plant. The emerging larvae tunnel into the corm and, occasionally, the pseudostem and true stem. The larvae are the only damaging stage of the insect. Pupation is within the host plant. The adult passes its teneral stage within the corm or pseudostem and may exit from the plant as much as a week after emergence.

Adult population density, sex ratio and size

Banana weevil populations and damage levels show considerable variation both within and between sites (Gold *et al.* 1994, 1997). For example, population estimates in Ntungamo district, Uganda (0.53oS latitude) (N = 50 farms) ranged from 1600 to 149,000 adults/ha. In this study, populations on all farms may have been underestimated as a proportion of the population may be sedentary, not attracted to traps and therefore not included in population estimates (S. Lux, personal communication).

Delattre (1980) found a 1:1 sex ratio (male:female) of reared banana weevils in Cameroon. However, he encountered more females than males in the field during the rainy season, suggesting sexual differences in behaviour patterns. In contrast, Sponagel *et al.* (1995) found sex ratios of field collected weevils in Honduras to be 2.2:1. In the Ntungamo survey, sex ratios ranged from 0.60 to 1.56 with a mean value of 0.90 (C. Gold *et al.*, unpublished data). Females were, on average, larger than males on 46 of 48 farms and the average weight of the females (0.090 g) was significantly higher than that of the males (0.079 g).

Adult longevity, distribution and movement

The banana weevil displays a classical "k" selected life cycle (Pianka 1970), with long lifespan and low fecundity. Adults have been reported to live up to two years (Froggatt 1925, Waterhouse and Norris 1987, Gowen 1995), while in Uganda a few marked weevils were recovered in experimental trials 4 years after release (N. Rukazambuga and C. Gold, unpublished data).

Banana weevils are negatively phototrophic and active between 18.00 and 06.00 hours with greatest activity periods between 21.00 and 04.00 hours (Uzakah 1995). Adults are not commonly observed in the field unless recovered in traps. In distribution studies in Uganda, most banana weevils were associated with the plant (mainly in leaf sheaths) or in the soil at the base of the mat (Table 1) (C. Gold and G. Night, unpublished data). Weevil density was greatest on flowered plants, although more total weevils were associated with preflowered plants and stumps. A few marked weevils had reentered the corm or pseudostem of living plants through existing galleries. Many weevils were attached to cut residues (i.e. pseudostems or corms), while a negligible number were found in the leaf trash or burrowed in the soil away from the mats. Thus, crop sanitation practices will influence weevil distribution. Distribution patterns of males and females were similar.

The adults feed on crop debris and may survive for extended periods without feeding (Froggatt 1925, Simmonds 1966). However, they commonly die within 72 hours when

Table 1. Distribution of adult banana weevils in experimental plots at Namulonge Agricultural Research Institute, Uganda, 1997.

A. Within field			
Location	Female (%)	Male (%)	
Plants	62	67	
Mat	(36)	(45)	
Soil	(26)	(22)	
Cut residues	30	27	
Trash	6	5	
Soil	2	1	
B. Within mat			
Plant stage	Female (%)	Male (%)	Numbers/Plant
Sucker	14	13	0.8
Preflower	44	48	3.3
Flowered	12	9	7.3
Stump	30	30	3.4

Source: C. Gold and G. Night (unpubl. data)

maintained on dry substrates. This suggests that they are very sensitive to soil moisture. The weevils are positively hygrotrophic (Roth and Willis 1963, Delattre 1980). Rainfall is believed to increase adult activity (Delattre 1980) and, in Uganda, trap catches tend to be higher in the rainy season (C. Gold *et al.*, personal observations).

This may also explain why weevil populations are often greater in mulched rather than in unmulched fields (Price 1993, Rukazambuga 1996). For example, Rukazambuga (1996) allowed weevils to move freely between mulched, unmulched and intercropped banana plots. From 4 to 36 months after release, weevil density was 1.7 to 2.5 times as high in the mulch as in other plots (Fig. 1). With this in mind, farmers often place mulches away from the base of a banana mat as a means of reducing weevil damage. The utility of such practices is currently under study in Uganda.

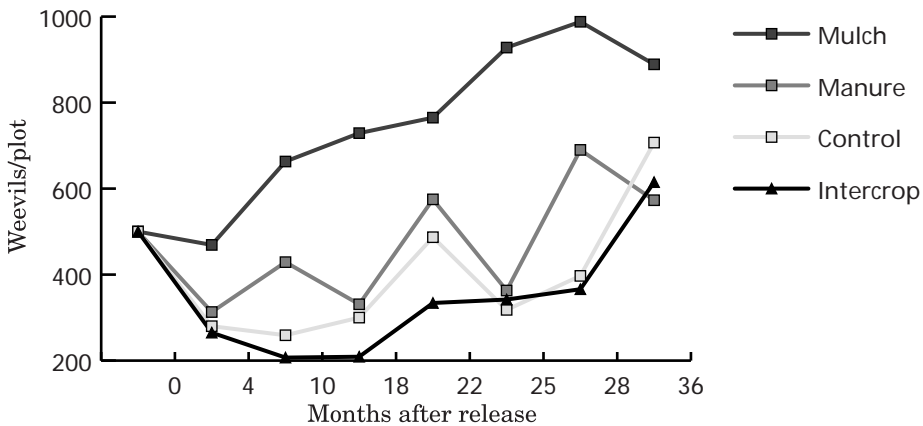


Figure 1. Weevil density in mulched, manured and intercropped plots.

Although banana weevils have functional wings, they rarely fly. Most commonly, dispersal is passive by movement of infested planting material containing eggs, larvae, pupae and/or adults. The adults may also move over limited distances by walking. Behavioural studies at the International Centre for Insect Physiology and Ecology (ICIPE) in Kenya suggest that only a small percentage (6-8%) of weevils might be active on the soil surface at any time (S. Lux, personal communication).

Trivial movement of adult banana weevils is currently under study in an ongoing trial in Uganda. Two thousand weevils were marked individually and released at recorded locations in adjacent mulched and bare soil plots. Plot size was 4368 m² and weevil density was 4-5 adults/mat. At 2- to 3-week intervals, pseudostem traps were placed at the base of banana mats and the location of marked weevils was recorded. Observations were made in each trap for 4 consecutive days. The distance moved and time elapsed since their last observation were determined for marked weevils found in the traps.

In mulched plots, the percentage of trapped weevils captured at the site of release decreased from 49% at 2 weeks after release to 17% at 6 and 9 weeks after release (C. Gold and G. Kagezi, unpublished data). For trapped weevils which had been last observed 1-7 days earlier, 75% were recorded on the same mat and 17% had moved less than 9 m. A few weevils moved 30-50 m in less than a week. In contrast, only 16% of weevils last observed 6-10 weeks earlier were on the same mat, while 60% had moved more than 10 m.

In bare soil plots, the percentage of weevils captured at the site of release decreased from 79% at 2 weeks to 25% at 13 weeks (Table 2). For all time intervals, a higher percentage of weevils were captured on the original mat than in mulched plots, while fewer weevils moved more than 10 m. Thus, activity and trivial movement appear greater in mulched rather than unmulched plots. This suggests that high soil moisture stimulates movement. The data also suggest that many weevils are sedentary for extended periods of time.

Similarly, in a field trial, more than 15,000 weevils were marked to identify plots (15 x 30 m) of release. Over a 3-year period, less than 3% of marked weevils later recaptured in pseudostem traps were recovered from plots other than those in which they had been initially released (C. Gold and G. Night, unpublished data). Nevertheless, it is a common belief among farmers that the efficacy of control methods may be reduced because of weevil invasion from neighbouring fields.

Movement patterns of banana weevils have management implications. Use of traps for collecting adults or infecting them with biopesticides (e.g. *Beauveria bassiana*) will most likely capture only those weevils in the immediate vicinity of the traps.

Trapping efficacy might be increased by the use of pheromones and plant volatiles although it remains to be seen over what distances such semiochemicals might be attractive.

Similarly, non-host plants, including intercrops and green manures, may interfere with host plant location or serve to repel specialized herbivorous insects. Thus, diversified cropping systems often reduce herbivore pressure by decreasing immigration and/or increasing emigration rates (Risch *et al.* 1983). However, sedentary insects, such as the banana weevil, may be less likely to come in contact with and be affected by intercrops and green manures.

Table 2. Trivial movement of banana weevils in mulched and unmulched experimental plots at the Kawanda Agricultural Research Institute, Uganda, August-November 1998.

A. Percentage of weevils on original mat						
Weeks after release	Mulched (%)			Unmulched (%)		
2	49			79		
5	31			48		
7	17			26		
10	17			36		
13	-			25		

B. Distance moved since previous observation						
Days after last observation	Mulched			Unmulched		
	Distance moved (%)			Distance moved (%)		
	0	1-9	>10 m	0	1-9	>10 m
1-7	75	17	8	86	11	3
15-21	36	33	31	49	39	11
22-28	34	35	31	53	35	12
36-42	22	37	41	43	42	16
43-49	19	44	37	31	37	32
57-70	16	24	60	33	39	27

Source: C. Gold and G. Kagezi (unpubl. data)

Oviposition

Sexual maturity is attained by male banana weevils at 18 to 31 days after emergence (DAE) and by females at 5 to 20 DAE and the first oviposition occurred 27 to 41 DAE (Uzakah 1995). The first oocytes were recorded at 11-28 DAE, while chorionated eggs first appeared at 25 DAE. This suggests that it takes around 2 weeks for an oocyte to mature.

Egg production of the banana weevil is low, with oviposition in the laboratory estimated from 1 to 2.7 eggs/week in the laboratory (Cuille 1950, Delattre 1980, Arleu and Neto 1984, Koppenhofer 1993) and 10 to 270 in the lifetime of the insect (Cuille 1950, Viswanath 1976, Arleu and Neto 1984, Castrillon 1989). Further studies in Uganda have found laboratory oviposition rates of 4 to 11.2 eggs/week (Abera 1997, M. Griesbach and C. Gold, unpublished data; C. Gold and P. Nemeje, unpublished data). Under field conditions, oviposition was estimated at 0.5-1.2 eggs/week under field conditions (Abera 1997). Oviposition rates appear to be related to temperature but not to relative humidity or precipitation (Uzakah 1995).

Although Uzakah (1995) found no relationship between female size and egg production, research in Uganda suggests that smaller weevils produce fewer eggs. Field collected banana weevil females were divided into "large" (mean weight 0.11 g) and "small" (0.06 g) individuals. Large females laid significantly more eggs (mean = 0.43/day) than small

females (0.28/day) ($T=4.76$; $p<0.01$) (M. Griesbach and C. Gold, unpublished data). Larger weevils also produced significantly larger eggs (0.47 mg) with higher rates of eclosion (81%) than eggs produced by smaller weevils (0.41 mg; 73%). After being held in the laboratory for 2 weeks, large females contained 7.2 chorionated eggs and 4.8 developing oocytes, while smaller females had 4.6 chorionated eggs and 4.0 developing oocytes.

In a separate experiment, Abera *et al.* (unpublished data) found that large and small field-collected weevils contained similar numbers of chorionated eggs (4.0 and 4.3). However, when held in the laboratory for 2 or 6 weeks without exposure to an oviposition substrate, larger weevils maintained twice as many chorionated eggs (10.5 and 11.3, respectively) as did small weevils (5.0 and 4.6). The data suggests that small weevils resorb eggs or oocytes when unable to oviposit. It is unclear why egg number was the same following 2 and 6 weeks without exposure to an oviposition substrate.

Uzakah (1995) reported up to 17 (mean 5) chorionated eggs retained in the calyx, while in Uganda, A. Abera and C. Gold (unpublished data) found up to 22 chorionated eggs (mean 10). These data suggest that realized oviposition in the field may be considerably less than the weevil's potential fecundity.

The effect of population density on oviposition was studied in laboratory trials in Uganda. Five, 10, 20 and 40 females were placed in drums containing corm material. Total oviposition was greater at higher population densities (Table 3a) although egg production per female was greater at the lowest density (C. Gold and P. Nemeje, unpublished data). Dissections at the end of the experiment showed that weevils at lower population densities also contained a greater number of eggs and developing oocytes (Table 3b).

Under field conditions, weevils were released into small plots (36 mats) at densities of 5, 10, and 20 females per mat. Prior to release, these plots supported few if any banana weevils. Plots were then uprooted in their entirety 2-5 weeks after weevil release. Oviposition per female declined with increasing weevil density with averages of 1.4 eggs/female/week at a density of 5 females/mat, 0.8 eggs/female/week at 20 females/mat, and 0.5 eggs/female/week at 40 females/mat (Abera 1997).

Timing and distribution of attack in highland banana by the banana weevil was studied in field trials in Uganda (Abera 1997). At a density of 20 weevils per mat, oviposition occurred on 26% of peepers, 36% of suckers, 81% of preflowered plants, 93% of flowered plants and 92% of standing residues. Egg density increased with plant age (Table 4). In Brazil, however, younger plants were shown to be more suitable for developing larvae (Mesquita and Caldas 1986). Almost all oviposition was on the pseudostem and the majority of eggs were placed below the soil surface (Table 5). Subterranean placement of eggs suggests that predators such as ants might be more effective than (yet undiscovered) egg parasitoids.

Number of stadia and stage duration

The banana weevil has been variously reported to have 5 (Cendana 1922, Beccari 1967), 6 (Koppenhofer and Seshu Reddy 1994, Traore *et al.* 1996), 7 (Viswanath 1976), 5 to 7 (Schmitt 1993), and 5 to 8 (Mesquita *et al.* 1984, Mesquita and Caldas 1986) instars. The variable number of larval instars suggest that banana weevils may display developmental

Table 3a. Weevil oviposition at different densities for 30 days.

Weevil density	Mean total oviposition	Mean eggs/female/day
5 Female:5 Male	233.0c	1.6a
10 Female:10 Male	262.8c	0.9b
20 Female:20 Male	485.0b	0.8b
40 Female:40 Male	736.5a	0.6b
F value	46.3*	23.1*

* P < 0.01

Means within a column followed by the same letter are not significantly different (P<0.05) - test by Student Newman Keuls (SNK).

Table 3b. Banana weevil fecundity indices under different densities after 30 days exposure to oviposition substrate.

Weevil density	Mature medium eggs	Small oocytes	Total oocytes	Fecundity
5 Female:5 Male	2.4ab	3.0a	5.3ab	10.7ab
10 Female:10 Male	3.5a	2.0b	5.4a	10.8a
20 Female:20 Male	1.6b	1.9b	5.6a	9.1ab
40 Female:40 Male	1.8b	2.0b	5.2a	8.9b
F value	5.6*	2.3	0.6	2.4

* P < 0.01

Means within a column followed by the same letter are not significantly different (P<0.05) - Contrast by LSMEANS.

Table 4. Banana weevil oviposition by plant stage in field trials at the Namulonge and Kawanda Agricultural Research Stations.**A. Namulonge (following release of 20 weevils per mat)**

Stage	% acceptance	Eggs/plant	Eggs/100 cm ²
Peeper	26	0.6c	0.2c
Maiden	36	1.3c	0.3c
Preflowered	81	4.5b	0.7b
Flowered	93	12.0a	1.9a
Residue	92	10.5a	1.9a
F value		144.27**	74.47**

** P < 0.01; df = (4, 696)

B. Kawanda (field population)

Stage	Eggs/plant	Eggs/100 cm ²
Peeper	2.4c	1.9c
Maiden	5.1bc	2.6bc
Preflowered	9.5b	3.6b
Flowered	15.6a	4.7a
F value	83.7**	17.2**

** P < 0.01; df = (3,19)

Values within a column with same letter are not significantly different by Tukey multiple range test. Source: Abera (1998).

Table 5. Banana weevil oviposition sites in East African highland banana in a 2-year-old banana stand at Namulonge Agricultural Research Institute, Uganda.

A. Location on plant			
Plant stage	Pseudostem		Corm
Peeper	2.3		0.1
Maiden sucker	3.1		0.2
Preflowered	5.8		0.4
Flowered	10.5		1.0
Residues	10.6		0.8

B. Location relative to soil surface			
Plant stage	Soil surface		Paired T-test
	Below	Above	
Peeper	0.1	0.0	2.11*
Maiden sucker	0.2	0.0	2.30*
Preflowered	4.1	2.0	4.71**
Flowered	9.9	5.8	5.39**
Crop residues	9.3	5.6	7.44**

* P < 0.05; ** P < 0.01

Source: Abera (1998)

polymorphism, i.e., the occurrence of "supernumerary" instars other than those which are thought to be customary for a particular species (Schmidt and Lauer 1977).

Larval stages can then be separated on the basis of head capsule widths. Separation of banana weevil larvae to instar was determined by model fitting to frequency distributions of larval head capsule widths of laboratory-reared and field-collected larvae (C. Gold, P. Nemeje and R. Coe, unpublished data). In the laboratory population, most weevil larvae passed through 5-7 instars, with 74% pupating after 6 instars. A few individuals had 8 or 9 instars. Mean head capsule widths for the first four instars showed close agreement among both laboratory and field collected populations. The method of analysis was not sensitive enough to separate later instars.

Studies on banana weevil developmental rates (reviewed by Schmitt 1993, Traore *et al.* 1993) have been conducted under ambient temperatures and show wide variability in stage duration: 4-36 days for eggs, 12-165 days for larvae, 1-4 days for prepupae, 4-30 days for pupae and 24-220 days from egg to adult. While temperature is certainly the most critical factor in determining developmental rates, relative humidity, cultivar, age of plant, food quality and population density may also be involved (Mesquita *et al.* 1984, Schmitt 1993).

Traore *et al.* (1993) determined the duration of the egg stage under six constant temperatures and found eclosion time ranged from 4.9 days at 30°C to 34.9 days at 15°C. Using linear regression, it was determined that the eggs had a developmental threshold of 120°C and a thermal requirement of 89 day-degrees.

Traore *et al.* (1996) estimated the duration of individual instars under five constant temperatures. He found that the total larval period ranged from 33.7 days at 30°C to 69.7

days at 16°C. Developmental thresholds and degree-day requirements were not determined. The larvae passed through 6 instars with mean relative stage durations of 10.6%, 10.1%, 14.0%, 16.9%, 18.3% and 29.5%, respectively. No data were presented on the prepupal stage (which may have been included in L6). Larval mortality, under experimental conditions, ranged from 59 to 77%. The pupal stage ranged from 5.5 days at 30°C to 23.0 days at 16°C, with 10 to 19% mortality.

In India, banana weevil larvae passed through seven instars with estimated mean durations of 4.1, 5.6, 5.8, 5.8, 5.9, 5.9, and 6.8 days, respectively, with a 2.7 day prepupal period and 7.2 day pupal period (Viswanath 1976). Although the total larval period varied by season (ranging from 36.6-44.4 days), the relative time spent in each instar was fairly constant.

Stage duration for banana weevil eggs and larvae was determined under ambient conditions in three experiments in Uganda. The egg stage lasted 6-8 days. Larvae completed development in 23-33 days and spent between 3 and 5 days in each instar. The mean relative stage duration was 14.9%, 12.5%, 15.6%, 17.0%, 18.2% and 22.2% for the 6 instars, respectively. Mortality ranged from 56% to 73%. The prepupal period averaged 4.6 days, while the pupal stage averaged 7.0 days. Overall, the egg to adult period lasted 6-8 weeks. In both this and the Traore *et al.* (1996) studies, mortality may have been inflated by lower food quality and by repeated handling of the larvae.

Population dynamics, natural enemies and survivorship curves

Rukazambuga (1996) monitored banana weevil populations for 3 years following release of adults at densities of 19,250 and 11,111 weevils/ha, respectively, into 9- and 11-month-old banana stands. In the first trial, weevil numbers peaked 32 months after release at 2.25% the original population. In the second trial, the population peaked 36 months after release at 1.4 times the release rate.

Such slow rates of population buildup suggest high mortality in the egg and larval stages. For example, Abera (1997) found 6-12 times as many eggs as mid- to late-instar larvae during dissections of banana mats. A net emigration from the field would also contribute to retarded population increase, although the available data suggest limited movement of adult weevils. Thus, if a banana weevil female produces 1 egg/week, one would expect >92% loss (immature mortality and/or net adult emigration) for population doubling within a year.

The banana weevil is largely protected by virtue of its secluded lifestyle. The adults are heavily sclerotized and not known to be attacked by arthropod natural enemies. The egg, larval and pupal stage all occur within the host plant or crop residues. Although weevil immatures developing in crop residues may be vulnerable to predation by histerids, staphylinids, hydrophilids and dermaptera as the plant tissues break down (Koppenhofer *et al.* 1992), eggs and larvae in standing plants may be inaccessible to parasitoids and most opportunistic predators. However, ants in the genera *Tetramorium* and *Pheidole* have been reported as effective predators on banana weevil eggs and larvae

(Castineiras 1982, Bendicho and Gonzalez 1986, Castineiras *et al.* 1991). These ants may enter both crop residues and living plants in search of weevil eggs and larvae.

Neuenschwander (1988) suggests the egg stage may be most vulnerable to natural enemies. Of particular interest would be the possible existence of egg parasitoids. Success in establishment and efficacy of egg parasitoids (if they exist) would be affected by population density, oviposition sites and exposure of eggs.

In Uganda, survivorship studies have been designed to determine levels of intrinsic mortality in the egg and larval stages of banana weevil. Eight plots were planted in November 1996. Half of the plots will exclude predatory Myrmicine ants (e.g. *Tetramorium* and *Pheidole*) by application of a selective pesticide (Amdro). Maiden suckers and flowered plants will be systematically sampled to set up population curves.

Pest status

Banana weevil is often severe in newly planted fields where heavy attack can kill a high percentage of suckers and lead to crop failure (Mitchell 1980, Ambrose 1984). After crop establishment, the weevil may not be an important pest for several crop cycles. With slow population buildup, most weevil problems are seen in ratoon crops (Mitchell 1980, Lescott 1988, Rukazambuga 1996).

Damage to banana plants is caused by larvae feeding within the corm and pseudostem. Larval galleries weaken the plant and provide entry points for ants and secondary pests, including fungi, which accelerate the destruction and decomposition of the rhizome tissues. Damage may also be manifested in weakened root systems, retarded and stunted growth, premature leaf drop and decreased bunch size. In extreme cases, plants topple (uproot) or snap at the base. Toppling is generally associated with nematode damage, but has been observed in fields with low levels of nematodes and heavily infested with banana weevils in Tanzania (N. Rukazambuga, personal observation) and Uganda (Rukazambuga 1996). Finally, attack may affect suckers, including their number and vigour, and the proportion of water suckers.

Yield loss in highland banana due to the banana weevil was studied in field trials in Uganda (Rukazambuga *et al.* 1998). Adults were released at the base of banana mats 9 months after planting at a rate of 19,250/ha. Weevil populations, corm damage, plant growth and yield were assessed over four crop cycles. Banana weevil damage increased with crop cycle, with high levels of attack and related plant loss in the third ratoon cycle (Table 6). The effects of banana weevil damage on plant growth were negligible in the first two crop cycles, while very heavy levels of damage (>20%) caused reductions in plant height, girth, and number of functional leaves in later ratoon crops.

In general, the effect of damage was greater on bunch weight (Table 7) than on plant growth and rate of development. When plants failing to produce bunches are included, there was an average bunch weight reduction of 8% (range 0-13%) for plants with low damage (5-10%), 18% (range 13-27%) with moderate damage (10-15%), 34% (range 17-57%) with heavy damage (15-20%) and 65% (range 57-72%) with very heavy damage (>20%).

Table 6. Banana weevil damage and plant loss in banana (cv. Atwalira) yield loss trial at Kawanda Agricultural Research Station, Uganda, 1991-1995.

A. Weevil damage distribution (%)				
Damage (%)	Plant crop	Ratoon crops		
		First	Second	Third
0-5	74	38	24	6
>5-10	19	31	30	14
>10-15	5	18	19	18
>15-20	2	4	8	10
>20	-	8	19	52
Plants	428	450	458	307
B. Plants lost² without producing harvestable bunches				
Damage (%)	Plant crop	Ratoon crops		
		First	Second	Third
0-5	2	5	10	0
>5-10	4	13	14	0
>10-15	2	5	14	3
>15-20	4	3	6	7
>20	-	13	43	80
Subtotal	12	39	87	90
% loss	3	9	19	29

¹ *C. sordidus* damage scored in the central cylinder of harvested plants.

² Dead, snapped and toppled plants.

Source: Rukazambuga *et al.* (1998).

Table 7. Bunch weights (kg) for harvested plants suffering different levels of banana weevil attack in banana (cv. Atwalira) yield loss trial at Kawanda Agricultural Research Station, Uganda, 1991-1995.

A. By within-cycle damage				
Damage (%)	Plant crop	Ratoon crops		
		First	Second	Third
0-5	9.5 ± 0.2	11.9 ± 0.3	12.4 ± 0.4	16.7 ± 1.3
>5-10	8.6 ± 0.3	11.5 ± 0.3	12.5 ± 0.4	17.4 ± 0.8
>10-15	8.8 ± 0.6	10.0 ± 0.4	11.5 ± 0.5	13.6 ± 0.7
>15-20	6.0 ± 1.1	11.1 ± 0.9	10.5 ± 0.8	12.5 ± 1.0
>20	- - -	7.3 ± 0.8	7.8 ± 0.6	10.6 ± 0.6
F-value	5.10**	10.64**	12.62**	14.10**

** P < 0.01

B. By cumulative damage for current and preceding cycles

Damage(%)	Ratoon crops		
	First	Second	Third
0-5	12.2 ± 0.3	12.9 ± 0.4	16.8 ± 0.7
>5-10	10.1 ± 0.3	11.7 ± 0.3	14.3 ± 0.6
>10-15	9.8 ± 0.8	9.3 ± 0.6	11.2 ± 0.8
>15-20	7.1 ± 1.7	9.9 ± 1.4	8.3 ± 1.0
>20	7.0 ± 1.0	7.4 ± 1.0	9.1 ± 1.5
F-value	15.27**	10.76**	16.17**

** P < 0.01

¹ Mean weevil damage by mat to central cylinder of current and preceding crop cycles.

Source: Rukazambuga *et al.* (1998).

Yield loss increased with crop cycle. Using plants with negligible damage as controls, yield losses were estimated at 5% in the plant crop, 9% in the first ratoon, 17% in the second ratoon and 44% in the third ratoon (Table 8) (Rukazambuga *et al.* 1998). The cumulative effect of heavy damage sustained over several crop cycles resulted in greater reduction in bunch weight than that inflicted by similar levels of damage in a single cycle. These results suggest that *C. sordidus* damage may affect both field productivity and longevity.

Table 8. Estimated banana yield loss to *Cosmopolites sordidus* in different crop cycles at Kawanda Agricultural Research Station, Uganda, 1991-1995.

	PC	1	2	3
Negligible damage mean yield ¹	9.4	11.5	11.2	16.7
Expected yield ²	4153	5175	5130	5127
Actual yield	3961	4709	4281	2896
Yield loss	5%	9%	17%	44%

¹ Mean yield for all plants with 0-5% weevil damage

² Mean yield for plants with negligible damage multiplied by number of plants in crop cycle (Adapted from Rukazambuga *et al.* 1998)

Effects of management

A parallel study on the effects of management on banana weevil population levels, damage and related yield loss in highland banana was also undertaken in Uganda (Rukazambuga 1996). Four treatments were used to create different levels of host plant vitality, viz. (1) intercrop with finger millet; (2) control; (3) addition of manure at planting; and (4) addition of manure plus continuous mulch. Adult banana weevils were released at the base of the banana mats 11 months after planting. Plant growth, yield and banana weevil damage to the corm were assessed over four crop cycles and compared among management systems.

Banana performance was influenced by field management with larger, more vigorous plants and largest bunches in mulched plots, while intercropped bananas displayed the poorest growth and produced the smallest bunches. However, banana weevil populations were greatest in the mulched systems and lowest in the intercrop (Rukazambuga 1996). Damage, expressed as percent corm tissue consumed, was similar among treatments. However, the total area consumed was greater in the mulched plants, reflecting the larger size of plant corms in this system.

Plants were divided into categories according to the level of banana weevil damage. Yield loss attributable to the weevil was inferred from the yield differences between infested and uninfested plants. The effect of weevil damage was greater on bunch weight (yield) than on plant size and growth in all treatments. The yield loss increased with crop cycle irrespective of host vigour, with greatest loss in the fourth crop cycle. The percentage yield loss was similar for mulched and intercropped bananas (Table 9). However, the reduction in tons/ha was greatest in the mulched system.

Table 9. Total yield loss in four crop cycles in bananas grown under different management regimes at Kawanda Agricultural Research Station, Uganda, 1991-1995.**A. Percentage yield loss**

Cycle	Intercrop	Control	Manure	Mulch
Plant crop	10.0	10.0	4.4	8.5
Ratoon 1	13.9	15.7	17.6	18.9
Ratoon 2	25.8	16.4	9.5	15.5
Ratoon 3	25.5	15.2	17.1	27.4

B. Tons per hectare lost

Cycle	Intercrop	Control	Manure	Mulch
Plant crop	0.8	1.0	0.5	1.4
Ratoon 1	1.6	1.7	2.5	3.7
Ratoon 2	3.4	2.0	1.2	2.3
Ratoon 3	2.5	2.2	3.0	6.3

Source: Rukazambuga (1998)

Discussion

Banana and *Ensete*, the host plants of the banana weevil are perennial crops which are commonly grown in semi-permanent stands. Thus, host plants are continuously available for ovipositing females.

The bioecology of the weevil is well suited for such a system. The adults are long-lived and produce low numbers of eggs over extended periods of time. Since host plants are normally abundant, dispersal capacity should be of restricted importance. In fact, the weevil has limited mobility as it rarely flies. The adults feed on plant residues and can go extended periods without feeding. While the weevils require soil moisture, they are able to burrow in the soil or find refuge in leaf sheaths, plant tissues or crop residues. Finally, the weevil is largely immune from many opportunistic predators by placement of the eggs beneath the soil level and the protected nature of the larval feeding niche.

Banana weevils normally gain entrance into newly planted fields by movement of infested planting material or immigration from established neighbouring fields. With low oviposition rates and (most probably) high mortality in the larval stage, population buildup is slow. The banana weevil is attracted to cut corms (Treverrow 1993) and this may explain why detached suckers used as planting material are especially susceptible to attack. Otherwise, pest problems most often appear in ratoon crops. In heavy attacks, the weevil can cause failure of new plantations, increasing yield loss and reducing plantation life.

Control methods being recommended, tested or proposed target the adult (trapping, sanitation, mulch placement, entomopathogens, entomophagous nematodes, intercrops, botanicals), egg (predators, parasitoids and endophytes) and larvae (predators, endophytes, botanicals and resistant varieties). Understanding the population dynamics of the banana weevil will be essential for evaluating the efficacy or potential of these methods.

For example, only poor to modest relationships have been shown between adult weevil numbers and damage (Gold *et al.* 1997). Thus, it is unclear how reductions in weevil numbers will be reflected in damage and yields. Similarly, crop sanitation has been proposed to eliminate weevil breeding grounds, reduce weevil populations and, subsequently, decrease damage to maturing banana plants. However, residues may also act as traps, being more attractive to ovipositing females than standing plants. In addition, it is unclear how much intrinsic mortality occurs in the egg and larval stages and whether density-dependent processes may be in play in determining oviposition levels or larval success. Thus, it would seem that control methods targeting the damaging larval stage may have greater impact than those methods directed at adults.

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