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Components of resistance to banana weevil (*Cosmopolites sordidus*) in *Musa* germplasm in Uganda

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Abstract

A field screening trial undertaken in Uganda showed that a number of *Musa* L. (Musaceae) cultivars and hybrids displayed high levels of resistance to banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), while most highland banana cultivars tended to be susceptible to weevil attack. In this study, research was undertaken to determine modalities of resistance to banana weevil. Laboratory studies suggested that all cultivars were attractive to the weevil and that females freely oviposited on all cultivars. While some differences were found between cultivars in attractivity and egg numbers, these were not related to subsequent damage. Therefore, antixenosis does not appear to play an important role in host-plant resistance to banana weevil. Larval survivorship rates in living corms were, for the most part, low on resistant cultivars, suggesting that antibiosis mechanisms offer the primary avenues of resistance. In the laboratory, development was slower on some resistant cultivars although survivorship rates on excised corm material were not as well related to levels of resistance as that on living material. Sap appeared to play a minor role in reducing egg eclosion rates on some resistant cultivars. Methanol extracts from Kayinja, a resistant cultivar, inhibited larval development on corms of susceptible cultivars in the laboratory.

Introduction

The banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), is a principal production constraint in subsistence highland cooking banana (*Musa* spp., AAA-EA genome group) and plantain (AAB) (Musaceae) based cropping systems in Africa (Sengooba, 1986; Gold et al., 1999a, 2001). For example, banana weevil attack is one of the primary causes of the decline and disappearance of highland cooking banana in central Uganda (Gold et al., 1999a).

Host-plant resistance is an important component in the development of an integrated pest-management strategy for the control of this pest (Gold et al., 2001). In recent years, some progress has been achieved in screening banana germplasm against banana weevil and a number of cultivars have been identified as possible sources of resistance for breeding programs (Pavis & Lemaire, 1997; Kiggundu et al., 1999, 2003). Screening studies, based on weevil damage to the corm central cylinder and cortex, showed up to 100-fold differences in damage levels between clones (Kiggundu et al., 2003). Clones were categorized as susceptible, intermediate, or resistant based on cluster analysis using different weevil damage parameters (Kiggundu et al., 2003). While highland bananas and plantains are considered highly susceptible to the weevil (Ortiz et al., 1995; Kiggundu et al., 2003), many other cultivars such as Yangambi-Km5 (AAA), Cavendish (AAA), Gros Michel (AAA), Kayinja (ABB), Ndiizi (AAB), and Kisubi (AB) appeared to be moderately to highly resistant (Kiggundu et al., 2003). However, a real understanding of the mechanisms underlying host-plant resistance to banana weevil remains unclear.

Bananas are rhizomatous herbaceous plants that reproduce vegetatively. A mat consists of an underground corm from which one or more plants (shoots) emerge. The shoot is actually a pseudostem comprised of leaf petioles. The

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true stem arises from the apical meristem after leaf production has terminated and grows through the center of the pseudostem, eventually producing the flower and, later, the bunch. Upon harvest of the bunch, the shoot dies back to the corm. Banana is a perennial crop that is most commonly propagated by suckers (lateral shoots from the corm). Subsequent crop cycles are known as ratoon crops.

The banana weevil adults are free living but most often closely associated with banana mats and crop residues (Gold et al., 1999c). Banana weevils are attracted to freshly cut banana pseudostems and corms (Mitchell, 1978; Budenberg et al., 1993). This attractiveness has been used for monitoring populations of banana weevil through placement of pseudostem traps and for population control (Gold et al., 2001).

The banana weevil inserts its eggs in the corm and the base of the pseudostem (Abera, 1997; Gold et al., 2001). Eggs are placed singly in cavities made by the female's rostrum. The oviposition rate is 0.5–4 eggs per female per week (Abera, 1997; Gold et al., 2001). On hatching, the larvae bore into the corm. Pupation is within the plant tissue. Under ambient conditions in Uganda, the developmental period from egg to adult has been estimated at 6–8 weeks (Gold et al., 1999b). This mode of development (i.e., inside the corm) exposes the immature stages to plant biotic defense mechanisms, such as tissue hardness and toxic secondary metabolic substances. High mortality rates are believed to occur in the egg and larval stages (Gold et al., 2001), especially in resistant cultivars (Abera et al., 1999).

Larval damage can impede establishment in the plant crop (McIntyre et al., 2002), lengthen the crop cycle, reduce bunch weight (Rukazambuga et al., 1998), and shorten stand longevity (Gold et al., 2004). Weevil damage tends to increase over time, such that problems are more pronounced in ratoon crops (Rukazambuga et al., 1998). Yield losses of up to 100% have been reported for highland cooking banana in eastern Africa (Sengooba, 1986). In response to weevil pressure, many farmers have shifted from susceptible highland bananas to more resistant brewing cultivars (i.e., Kayinja, Kisubi) (Gold et al., 1999c).

Successful attack of bananas by banana weevils involves finding host plants, host-plant acceptance (oviposition), and host-plant suitability (larval survival, developmental rate, and fitness). Host-plant resistance may affect any of these processes. Most commonly host-plant resistance modalities have been attributed to antixenosis (nonpreference), antibiosis, and/or host-plant tolerance (Painter, 1951). The role of these different factors in host-plant resistance to banana weevil have been reviewed by Kiggundu et al. (1999) and Gold et al. (2001).

Antixenosis suggests that resistant cultivars avoid banana weevil attack by reducing the adult insect's ability to find and/or accept host plants; the combined effects of these two processes would be reduced oviposition (Gold et al., 2001). Pavis & Lemaire (1997) suggested that antixenotic factors may also deter adult feeding. Budenberg et al. (1993) identified banana kairomones as important in attracting banana weevils to their host plants. In field and laboratory studies, however, attraction to banana corms and pseudostems did not reflect host-plant susceptibility (Minost, 1992; Musabyimana, 1995; Abera, 1997; Sumani, 1997; Kiggundu, 2000). Moreover, Abera et al. (1999) found oviposition rates on the resistant cultivar Kayinja to be similar to those on five highland banana cultivars. These studies seem to indicate that antixenosis is not an important component of weevil resistance in *Musa*.

Antibiotic factors are those which negatively influence larval performance (i.e., poorer survivorship, slower development rates, reduced fitness) (Gold et al., 2001). These factors may include physical (e.g., sticky sap and latex, and corm hardness), antifeedants, toxic secondary plant substances, and nutritional deficiencies. Abera et al. (1999) estimated larval survivorship on five highland banana cultivars to be 5–25 times greater than that on Kayinja. Mesquita & Alves (1983), Mesquita et al. (1984), and Mesquita & Caldas (1986) found that banana weevil immatures developed faster and had fewer ecdyses on some cultivars than on others. Lemaire (1996) reported slower larval development and higher larval mortality on the resistant cultivar Yangambi-Km5.

Owing to its long crop cycle and increasing importance of the banana weevil in ratoon crops (Rukazambuga et al., 1998), most studies on resistance in *Musa* examine damage levels on different cultivars rather than yield loss. As a result, little is known about host-plant tolerance to banana weevil, as such studies would require large trials and several years.

The objective of this study was to investigate modalities of weevil resistance within a representative sample of *Musa* germplasm in Uganda.

Materials and methods

Site description and source of materials

Studies on host-plant resistance modalities to banana weevil were conducted in the banana entomology laboratory at the Kawanda Agriculture Research Institute. Kawanda (0.19N, 32.38E, 1195 m above sea level, 12 h day length throughout the year) is 13 km north of Kampala. Average daily temperatures in the field and laboratory were 16 °C minimum and 29 °C maximum.

The plant materials used in laboratory studies were collected from the Uganda National Banana Research Program germplasm collection at Kawanda. The collection

is well maintained by application of manure and mulching. Insecticides are occasionally applied to control pests. All laboratory studies were conducted in the banana entomology laboratory at Kawanda under ambient room temperatures (i.e., between 16 and 29 °C).

Collection and maintenance of weevils for laboratory experiments

Banana weevils were collected from farmer's fields, using pseudostem traps, and held in the laboratory in 3 l plastic containers. These were maintained with fresh corm material that was changed regularly. Since the provided material was small, weevil oviposition was uncommon in these containers. The containers were also washed regularly to prevent the buildup of rotting food material. All test weevils were kept in containers for at least 1 week before use in experiments. Each weevil was used in a single experiment and then discarded.

Antixenosis

Experiment 1: acceptance of different cultivars for oviposition. Pieces of corm material (16 × 14 cm) from 16 *Musa* cultivars were placed in 500 ml plastic containers (one piece per container), the sides of which were perforated to provide adequate ventilation. Ten female weevils were released into each container and left covered for 24 h. The corm pieces were then removed and dissected by peeling off thin layers of tissue to expose eggs, which were then counted. The experiment was repeated 10 times, each with a different set of weevils, with the resulting data pooled for analysis.

Antibiosis

Four laboratory experiments were designed to investigate the suitability of corm material from different cultivars on the development of banana weevil eggs and larvae. In Experiment 2, developmental bioassays were carried out in excised corm pieces starting from less than 1-day-old larvae through the time the larvae entered into the pupal stage. In Experiment 3, development was followed in undisturbed corms for 27 days. The effect of sap on egg eclosion was studied in Experiment 4, and finally the effect of fresh corm methanol extracts on eclosion and early larval development was studied in Experiment 5.

Experiment 2: postembryonic development to pupal stage on corm material from different Musa *cultivars.* Mature banana weevil eggs were obtained by inducing females to oviposit on fresh, field-collected corms with 30 cm of pseudostem, and then extracting and incubating the eggs in Petri dishes. The oviposition substrates were placed with 100 females in 10 l plastic buckets. These were left covered for 24 h, after which the banana material was removed and thin layers of tissue were slowly pared to expose the eggs. These eggs were carefully extracted and kept in distilled water during extraction. They were then washed in a 40% solution of ethanol for 5–10 s after which they were rinsed several times with distilled water from a spray bottle. The eggs were then arranged on distilled water moistened pieces of tissue paper in clean plastic Petri dishes (the Petri dishes were previously washed in detergent, rinsed, disinfected by spraying with 75% ethanol, and dried). The Petri dishes were placed in a cool place and eggs allowed to incubate at room temperature until the first-instar larvae emerged (5–6 days). These larvae were then reared on corm pieces from each of the 12 different test cultivars.

With the help of a fine brush, newly eclosed first-instars were each placed on a small piece of corm tissue (5 × 5 × 3 cm) (one larva per corm piece; 100 replicates per cultivar) taken from medium-sized preflowered plants. A small notch was made into the corm piece to simulate a gallery, thus making it easier for the small larvae to initiate feeding and bore into the plant. This notch was covered with a thin piece of corm material. Every few days, larval condition was monitored with minimal disturbance by removing the thin corm covering. Deteriorated corms were changed as necessary. Data on mortality and days to pupation were recorded. Pupation was determined when larvae ceased feeding and constructed a pupal chamber. These were opened a few days later and the pupae were removed and weighed using a Mettler AE50 digital analytic balance (precision 0.0001 g).

Experiment 3: postembryonic development in intact corms of different cultivars. Corms (30 cm in diameter) with 30 cm pieces of pseudostem from each cultivar were placed in 20 l plastic buckets (one corm per bucket) with sterilized sawdust at the bottom. (The sawdust had been sterilized with steam for 1 h). Fifty female weevils that had been maintained apart from ovipositional substrates for 10 days were released into each bucket for 24 h and then removed. The corms were then superficially inspected for eggs (visual observations of leaf sheaths, paring of small sections of corm surface) to ensure that the weevils had sufficiently oviposited on each of them. The corm pieces were moistened regularly with a hand spray bottle to keep them fresh and to encourage them to sprout and root. After 27 days, the corms were removed and dissected. The number of immatures was recorded and larval stage estimated. At this time, most were expected to be in the last instar or pupal stage (Gold et al., 1999b). The experiment was replicated three times with one corm per cultivar per replicate.

Experiment 4: effect of sap and latex on egg eclosion. Sap was collected from 14 test cultivars and then applied to

banana weevil eggs to determine if sap viscosity or constituents might influence eclosion rates. Sap was collected from maiden plants from the germplasm collection at Kawanda by making a diagonal cut across the area around the plant collar. The exuding sap was allowed to drip into small plastic vials. The sap was immediately transferred to the laboratory and dabbed onto 1-day-old eggs that were being maintained on moist tissue paper in Petri dishes. Two Petri dishes were used for each test cultivar. Each Petri dish contained 50 eggs arranged in rows and columns on moist filter paper. One drop of fresh sap was applied to each egg. Controls consisted of eggs dabbed with one drop of distilled water. The fates of these eggs and the condition of emerging larvae were then determined.

Experiment 5: effect of methanol extracts on early development of banana weevil larvae. Three cultivars, Kayinja (resistant), Atwalira (susceptible), and Musakala (intermediate), were selected for this experiment. For each cultivar methanol extracts were made by blending 100 g of fresh corm material in 100 ml of methanol. The mixture was incubated at room temperature for 24 h and then filtered with Whatman no. 4 filter paper (Whatman International Ltd., Maidstone, UK).

In Experiment 5a, corn meal agar (Sigma-Aldrich Co., St. Louis, MO, USA) media, comprised of 0.17 g corn meal agar in 25 ml water, was autoclaved for 15 min at 120 °C. The hot liquid agar medium was allowed to cool to 50 °C. For each cultivar, we mixed 1 ml of each respective extract to the agar medium and poured the mixture into sterile glass Petri dishes (10 cm in diameter). The following day, 25 5-day-old eggs were placed on the medium and left to incubate. Percentage eclosion and percentage tunneling were recorded over a 4-day period only, as the larvae could not sustain development longer than this due to lack of nutrients in the agar media.

In Experiment 5b, 5 ml of each extract were poured over fresh corm pieces of another susceptible highland banana cultivar (Ndiibwabalangira). Extracts were applied to the entire corm piece and were allowed to absorb into the tissue surface for 24 h. Thereafter, newly hatched first-instar larvae were introduced on the corm pieces and allowed to develop for 15 days, after which the larvae were extracted, measured, and weighed as in Experiment 4.

Data analysis

Data from all laboratory experiments was analyzed using one-way analysis of variance (ANOVA) in STATISTICA version 5.0 (StarSoft, 1995). Means were separated using the least significant difference (LSD), at the 5% probability level.

Results

Antixenosis

Experiment 1: acceptance of different cultivars for oviposition. Mean oviposition ranged from 9.2 to 17.9 eggs per corm piece (Table 1). Oviposition levels were statistically similar for resistant and susceptible cultivars. Banana weevils freely oviposited on resistant cultivars such as Cavendish, Yangambi-Km5, and Kayinja, while the susceptible cultivars Atwalira, Nakyetengu, and Muvubo received the fewest eggs.

Antibiosis

Experiment 2: postembryonic development to pupal stage on corm material from different Musa *cultivars.* Larval mortality ranged from 5% in the susceptible highland banana Ndiibwabalangira to 100% in the resistant cultivar Kayinja (Table 2). Larval mortality was not related to resistance levels. For example, there was 78% mortality in the highly susceptible cultivar Mbwazirume and less than 50% mortality in resistant Cavendish. High mortality (≥75%) was also experienced in Kabula (intermediate), FHIA03 (intermediate), Mbwazirume (susceptible), Ndiizi (resistant), and Yangambi-Km5 (resistant).

Table 1 Mean number of banana weevil eggs collected from corm pieces of different cultivars in oviposition choice experiments. Means (± SE) followed by the same letter are not significantly different at P<0.05 by least significant difference (LSD) (Experiment 1)

Cultivar[1]	Eggs
Gonja	17.9 (± 3.6)a
Nakitembe	15.7 (± 2.7)ab
Nakabululu	15.1 (± 3.2)ab
Nalukira	14.6 (± 3.0)ab
Ndiizi	14.6 (± 2.1)ab
Cavendish	13.6 (± 2.7)ab
Kibuzi	13.6 (± 2.3)ab
Yangambi-Km5	13.4 (± 2.6)ab
Kabula	12.6 (± 3.2)ab
Kayinja	12.1 (± 1.8)ab
Mbwazirume	11.7 (± 1.7)ab
Ndiibwabalangira	11.7 (± 2.0)ab
FHIA-03	10.3 (± 3.2)b
Atwalira	10.0 (± 2.7)b
Nakyetengu	9.4 (± 1.5)b
Muvubo	9.2 (± 2.3)b
LSD (P<0.05)	34.8

[1]Cultivar susceptibility to banana weevil (adapted from Kiggundu et al., 2003): bold, resistant; italic, intermediate susceptibility; normal, susceptible.

Table 2 Percentage larval mortality, mean number (± SE) of days to pupation, and pupal weights (± SE) of banana weevils reared on corm material of different *Musa* cultivars (Experiment 2)

Cultivar[1]	Percentage mortality[2]	Days to pupation	Pupal weight (g)
Kayinja	100	–	–
FHIA-03	90	32.5 (± 3.1)	0.064 (± 0.014)
Kabula	90	37.8 (± 0.5)	0.067 (± 0.010)
Mbwazirume	78	33.4 (± 0.7)	0.086 (± 0.005)
Ndiizi	75	31.7 (± 1.4)	0.084 (± 0.010)
Yangambi-Km5	75	39.6 (± 0.9)	0.088 (± 0.007)
Nakabulu	73	31.7 (± 1.2)	0.063 (± 0.007)
Nakawere	60	31.4 (± 1.3)	0.093 (± 0.005)
Nakyetengu	50	32.0 (± 1.0)	0.067 (± 0.005)
Nalukira	50	35.6 (± 0.7)	0.095 (± 0.004)
Cavendish	48	35.0 (± 0.7)	0.084 (± 0.003)
Tereza	48	31.0 (± 0.7)	0.098 (± 0.004)
Muvubo	45	30.6 (± 0.2)	0.081 (± 0.004)
Gonja	40	29.0 (± 0.5)	0.077 (± 0.006)
Kisansa	18	31.4 (± 0.6)	0.073 (± 0.004)
Ndiibwabalangira	5	31.2 (± 0.9)	0.078 (± 0.004)
LSD (P<0.05)	–	0.67	ns

[1]Cultivar susceptibility to banana weevil (adapted from Kiggundu et al., 2003): bold, resistant; italic, intermediate susceptibility; normal, susceptible.
[2]Mortality was derived from counts and hence no statistic is provided.

The number of days to pupation was significantly different among cultivars, while there were no significant differences in pupal weights (Table 2). The number of days to pupation was longest in highly resistant Yangambi-Km5 followed by Kabula (intermediate), Nakabulu (susceptible), and Cavendish (resistant). It is interesting to note that the relatively susceptible Muvubo, Gonja, Kisansa, and Ndiibwabalangira germplasms all showed low mortality and shortest days to pupation. Surprisingly Kabula, a brewing EAHB, was found to cause 90% mortality and significantly increase weevil developmental time, even though it showed field susceptibility in previous studies (Kiggundu et al., 2003).

Experiment 3: postembryonic development in intact corms of different cultivars. Following 27 days of development, the greatest number of immatures were found in susceptible or intermediate cultivars, while survivorship on resistant or nearly resistant (i.e., FHIA-03) cultivars was low (Figure 1). The only aberrant cultivar to this trend was Kibuzi for which a mean of one immature was found per corm. More than 80% of the immatures had reached the pupal stage in the susceptible cultivars Nakitembe, Muvubo, Atwalira, and Nakyetengu. By contrast, only 18% of the immatures had pupated in resistant Ndiizi and no pupae were encountered in FHIA-03, Yangambi-Km5, and Kayinja.

Experiment 4: effect of sap and latex on egg eclosion. Sap and latex that exude from banana plants apparently show some effect on the survival of banana weevil eggs and larvae although the lowest eclosion rate was still >70% (Table 3). Eggs treated with sap/latex from Kayinja, FHIA 03, and Yangambi-Km5 had lower eclosion rates than controls. Most of the unhatched eggs appeared deformed and blackened.

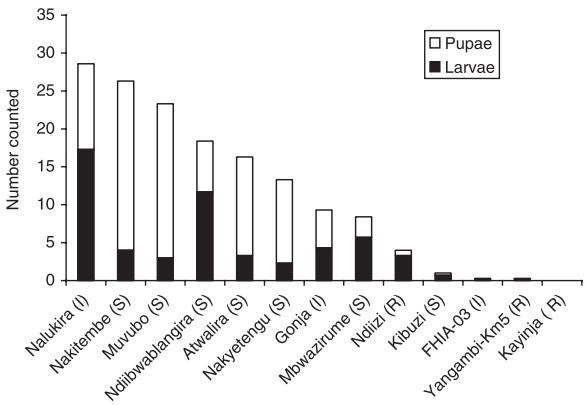

Figure 1 Mean number of larval and pupal stages of banana weevil collected after 27 days of development on corms of different *Musa* cultivars. R, resistant, I, intermediate, and S, susceptible (number replicates = 3) (Experiment 3).

Experiment 5: effect of methanol extracts on early development of banana weevil larva. In Experiment 5a, there were no differences in eclosion of eggs incubated on the surface of corn meal agar-containing methanol extracts of Kayinja (resistant), Atwalira (susceptible), and Musakala (susceptible) (Figure 2A). However, Kayinja extracts significantly reduced levels of larval tunneling in comparison to extracts from Atwalira and Mukasala (Figure 2B). There were no significant differences between the susceptible cultivars. Larvae tunneling in the agar-containing Kayinja extract were sluggish and most appeared moribund by the third day. By contrast, larvae in agar-containing extracts from Atwalira and Musakala continued to actively tunnel throughout the study period. Developing larvae had significantly higher body weights on corm pieces treated with extracts from Atwalira and Musakala than on Ndiibwa-balangira corm pieces treated with Kayinja (Figure 2C).

Discussion

Field surveys and screening studies suggest that highland cooking banana and plantains are highly susceptible to banana weevil, while a range of other *Musa* cultivars are resistant (Gold et al., 1994; Kiggundu et al., 1999, 2003). Successful attack of bananas involves host-plant location,

Table 3 Hatchability (%) of banana weevil eggs incubated in contact with sap/latex collected from 13 *Musa* cultivars (Experiment 4)

Cultivar[1]	Percentage hatchability
Control (dist H_2O)	95 (± 1.0)a
Ndiizi	90 (± 2.6)ab
Cavendish	89 (± 1.0)ab
Nakitembe	89 (± 3.0)ab
Nakyetengu	89 (± 1.9)ab
Nakabululu	88 (± 1.6)abc
Nalukira	88 (± 1.6)abc
Gonja	86 (± 2.6)abc
Mbwazirume	86 (± 2.6)abc
Ndiibwabalangira	85 (± 3.4)abc
Kabula	83 (± 5.7)abc
Kayinja	75 (± 3.8)bc
FHIA-03	74 (± 3.7)bc
Yangambi-Km5	72 (± 6.6)c
LSD (P<0.05)	22.3

[1]Cultivar susceptibility to banana weevil (adapted from Kiggundu et al., 2003): Means (± SE) followed by the same letter are not significantly different (P<0.05), ANOVA F = 4.04 and P = 0.0003. Mean separation based on least significant difference (LSD). bold, resistant; italic, intermediate susceptibility; normal, susceptible.

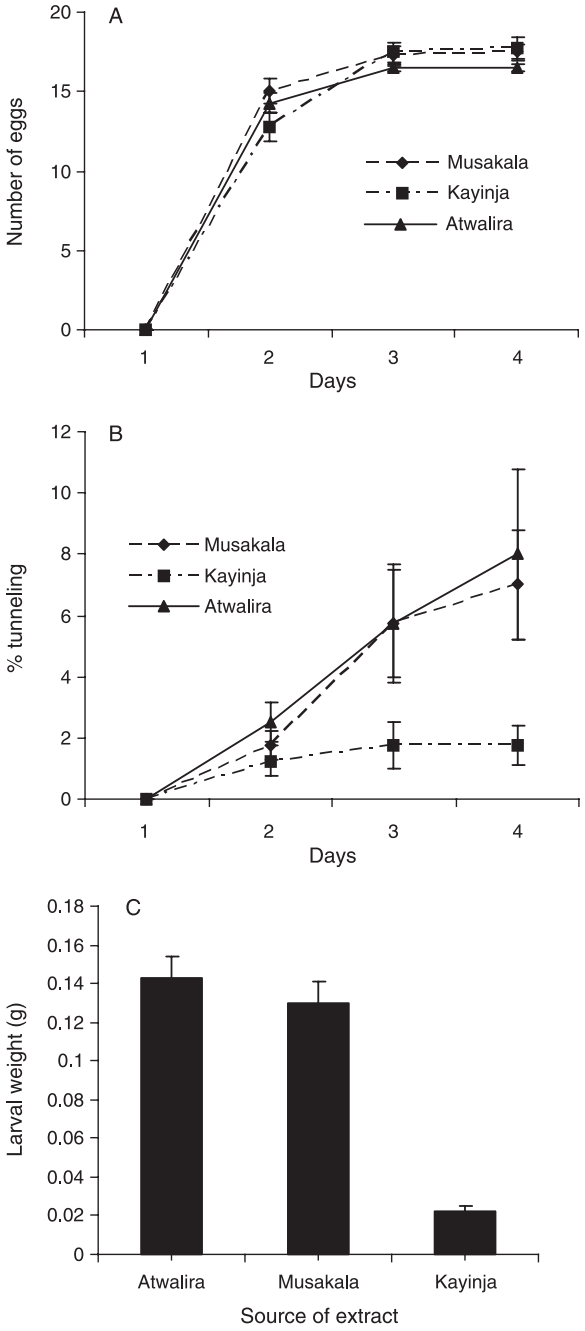

Figure 2 (A) Mean eclosion (± SE) of banana weevil eggs incubating on corn meal agar with crude methanol extracts of three different cultivars (Experiment 5a); (B) Estimated mean percentage (± SE) of agar surface tunneled by banana weevil larvae after hatching on corn meal agar containing crude methanol extracts of three different cultivars (Experiment 5a); (C) Mean (± SE) larval weights of banana weevil larvae developing on Ndiibwabalangira corm pieces treated with methanol extracts from three different cultivars (Experiment 5b).

acceptance, and suitability. Resistance modalities interfering with these processes include antixenosis (nonpreference) and antibiosis, while host-plant tolerance concerns the plant's ability to withstand attack (Painter, 1951).

The results of this study suggest that antibiosis is the primary means by which banana plants defend themselves against banana weevil, while antixenosis seems of little importance. Banana weevil oviposition on corm pieces was not related to cultivar susceptibility. Similarly, in laboratory studies, Budenberg et al. (1993) found that females were equally attracted to volatiles from cut corms of susceptible and resistant cultivars. Under field conditions, trap catches of adult weevils at the base of banana plants can be seen as an indicator of host-plant attraction and retention. These varied among cultivars, but there was no relationship between the weevil captures and host-plant susceptibility (Kiggundu, 2000). At the same time, weevil attraction to corm pieces in laboratory choice experiments were not related to host-plant susceptibility (Kiggundu, 2000). Finally, Minost (1992), Pavis & Minost (1993), Musabyimana (1995), Abera (1997), Sumani (1997), and Abera et al. (1999) found no relationship between host-plant attractivity and weevil damage levels under field conditions.

Little work has been done on host-plant acceptance by banana weevil. Abera et al. (1999) found field oviposition on Kayinja to be similar to that on five highland banana cultivars, even though the latter displayed much higher levels of damage. In laboratory choice and no-choice experiments in this study, there was no relationship between oviposition levels and host-plant resistance: females freely placed eggs on all resistant cultivars tested including Yangambi-Km5, Kayinja, Cavendish, and Ndiizi. Given that the weevils are largely sedentary and that adult dispersal is primarily by crawling, it might be unrealistic for gravid females to move far looking for a suitable host.

The results suggest that if ovipositing banana weevils do not discriminate between susceptible and resistant bananas, low levels of damage on resistant cultivars must reflect reduced larval success (i.e., antibiosis). For example, Abera et al. (1999) estimated larval survivorship to be 10–23 times higher on highland banana cultivars than on Kayinja. However, factors resulting in reduced survivorship on Kayinja were not determined. Gold et al. (2001) speculated that antibiotic factors might include physical factors (e.g., sticky sap and latex, or corm hardness), antifeedants, toxic secondary plant substances, and nutritional deficiencies.

In this study, poor weevil growth, development, and survivorship on resistant cultivars suggest that these may contain substances that are antibiotic to banana weevil. Attempts to rear immatures on Yangambi-Km5, Kayinja, and FHIA 03 consistently resulted in poor larval performance including high mortality, low body weights, and/or extended stage duration. These results are consistent with those of Lemaire (1996) who also found developmental time to be greater on Yangambi-Km5 than on other cultivars.

The nonsignificance of pupal weights from different cultivars has previously been observed in banana weevil by Silva & Fancelli (1998) and in sweetpotato weevil (*Cylas puncticollis*) by Anota & Odebiyi (1984). Increased developmental time could be an adaptation by these two insects to attain an optimum required weight for pupation to take place. This means that there might also be no significant differences in the weights and probably the fitness of the adults that emerge.

There is need to develop laboratory bioassays to be used as early screening methods for resistance to banana weevil. This is especially important in a long cycle crop such as banana, as current methods require extended field studies (Kiggundu, 2000). However, this requires a strong relationship between laboratory and field results. Poor larval development in corm material from intermediate (e.g., Kabula) and susceptible cultivars (Kibuzi and Mbwazirume) are therefore problematic. These results require confirmation and further study.

Gold & Bagabe (1997) found that recently harvested Kayinja largely escaped weevil attack, while crop residues supported high levels of weevil attack. Similarly, CS Gold (unpubl.) found recently harvested Pisang awak to have very low levels of weevil damage, but that prostrate residues could support more than 100 larvae, of which many had entered the fifth instar or pupal stage. This suggests the presence of a resistant factor that breaks down after crop harvest.

This might explain the success of some larvae on Yangambi-Km5 and Kayinja on excised pieces of corm in the laboratory. By contrast, the strongest relationship between larval performance and cultivar susceptibility was found when banana weevils were reared undisturbed on living corm material (Experiment 6).

Although significant differences were limited in this study, the data suggest that sap extracted from the resistant cultivars Yangambi-Km5, FHIA 03, and Kayinja might reduce eclosion rates of banana weevil eggs. Chemically, sap has been found to be rich in ions, especially K^+, Mg^{2+}, Cl^-, and NO_3^- (Baker et al., 1990). These, plus other inclusions such as globular vesicles and crystalloid vesicles have been found to be osmotically active (Kallarackal et al., 1986). These ions and inclusions may have either acted as desiccants or toxins to the eggs. More work is needed to elucidate if sap does serve as a plant defense mechanism against weevil attack.

Pavis & Minost (1993) found a negative correlation between corm hardness and infestation rate and hypothesized mechanical resistance to oviposition or larval development. Ortiz et al. (1995) assessed five plantains cultivars, videlicet, 2 AAA dessert, Calcutta 4 (AA), Bluggoe (ABB), and Fougamou (ABB), plus 97 euploid hybrids derived from diploid vs. triploid crosses, for corm hardness. All plantains were equally susceptible to the weevil and significant differences were found among the euploid hybrids for weevil damage levels and corm hardness. However, phenotypic correlations between corm hardness and weevil damage were not significant in segregating progenies suggesting that other resistance modalities, such as biochemical compounds, may be as important in weevil damage as corm hardness. Kiggundu (2000) also found no phenotypic relationship between corm hardness and weevil damage.

Methanol extracts from Kayinja reduced larval survivorship on a susceptible cultivar. From this study, it was unclear whether components of these extracts acted as toxins or feeding inhibitors. Following the strong suggestion of a biochemical basis of resistance from methanol extract experiments, biochemical analysis, using high performance liquid chromatography (HPLC), has suggested the presence of antibiotic compounds in resistant cultivars containing contribution from the B genome (e.g., Kayinja, ABB) (Kiggundu, 2000). Further analysis and separation has shown at least two bioactive fractions, related to these peaks, that cause high levels of weevil mortality (A Kiggundu, A Hassanali & CS Gold, unpubl.).

These results suggest that several factors may contribute to antibiosis-based resistance against banana weevil and that resistance modalities might vary among cultivars and or genome groups. Further work should be centered on identification and characterization of the biochemical basis of resistance with a view of identifying the active compounds. Such compounds can serve at least in part as biochemical resistance markers for use in rapid selection. Work is also wanting in the development of rapid laboratory based methods for early evaluation of resistance. Because indications are towards banana weevil being controlled by more that one gene, molecular marker assisted breeding and selection should be developed. This later strategy would require a complete quantitative trait locus mapping study.

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