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Evidence for the presence of chemicals attractive to the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) in dead banana leaves

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Abstract

The effects of host and non-host plant odours on the foraging responses of the banana weevil, *Cosmopolites sordidus* (Germar), were investigated in the laboratory through arena and olfactometer bioassays. Contrary to previous reports that banana rhizome and pseudostem were the most attractive parts to the weevil, dead leaves were most preferred. Comparison of dead banana leaves with dead leaves of other plants showed that attractant odours were present in yam, cocoyam and dead grasses but absent in cocoa and soybean leaves. Complete leaf senescence while the leaf was attached to the mother plant proved necessary for the development of the dead-leaf-based odours but the involvement of microbial organisms could not be demonstrated. It is possible that dead-leaf-based attractants could be used in combination with microbials such as entomogenous fungi and nematodes in integrated management of *C. sordidus*.

Introduction

Bananas and plantains are the main source of regular dietary carbohydrate for more than 400 million people in the humid tropical and subtropical regions of the world (Stover & Simmonds, 1987; Gold *et al*., 1994). They are known to tolerate considerable neglect and also fit well into the farming systems of resource poor farmers (Johnston, 1958; Jones, 1986).

The production of bananas and plantains is hampered by several factors, of which attack by the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae) is one of the most important (Ostmark, 1974; Koppenhöfer *et al*., 1994; Gold *et al*., 1994).

Unfortunately, because the weevil remains mostly concealed and its larvae feed by mining the banana rhizome and pseudostem, control either by conventional insecticides or even classical biological control methods is difficult (Waterhouse & Norris, 1987; Treverrow, 1993). More importantly, smallholder farmers, who are the main producers and consumers of the crop, lack both the money to purchase modern insecticides and the technical knowledge and machinery for their effective application (Sikora *et al*., 1989). Further, hardly any varieties of bananas and plantains have been identified as tolerant or resistant to *C. sordidus* (Stover & Simmonds, 1987).

The control of the weevil by cultural methods such as mulching or the use of split pseudostem traps to catch and kill resident and invading weevil populations (Koppenhöfer *et al*., 1994) has been only partially successful. Crop rotation has been practised (Seshu-Reddy *et al*., 1993; Price, 1994), but is not practical because of the perennial growth habit of banana and increasing pressure on land.

The above problems associated with control of the weevil have led to attempts to develop effective means of trapping it. One way to achieve this is with semiochemicals.

Foraging responses of several phytophagous insects are stimulated by semiochemicals released by their host plants. The semiochemicals are usually by-products of the normal biological processes of the host plant or chemicals that emanate from them following damage caused by insect attack or other physical damage (Angst & Lanier, 1979; Bartlet *et al*., 1993).

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Attractive host plant chemicals (kairomones) have been used as baiting materials for several weevils (Evans & Allen-Williams, 1989; Dowd & Bartelt, 1991). The banana weevil has been reported to respond to banana rhizome material in both olfactometer and electroantennogram bioassays (Budenberg *et al.*, 1993) probably because of the presence in the rhizomes of mono- and sesquiterpenes (Ndiege *et al.*, 1991). This evidence and earlier observations that female *C. sordidus* deposit their eggs in rhizomes and pseudostems (Froggatt, 1925) gave impetus to the use of rhizomes and pseudostems as trapping materials (Mitchell, 1980; Treverrow, 1993). Prior to the work reported here, the aerial parts of the banana plant had not been examined as possible sources of attractant chemicals of the weevil. This work was carried out to ascertain whether parts of the banana plant other than the rhizomes and pseudostems were sources of attractants for the weevil.

Materials and methods

Y-tube olfactometer

A 'Y' tube olfactometer (fig. 1), based on the design of McIndoo (1926), was constructed to suit the size of *C. sordidus*. It was constructed from three Perspex boxes, each measuring 130 × 75 × 55 mm. Two such boxes (test chambers, tc) held the test materials while the third (main chamber, mc) constituted the arena into which the weevils were liberated. The boxes were linked with 10 mm internal diameter Perspex tubes held in position with silicon sealant. The ends of the tubes were flush with the walls of the arena, but extended into the test chambers for about 20 mm. As they were also raised above the floors of the boxes, they trapped weevils that moved into them in response to a test material.

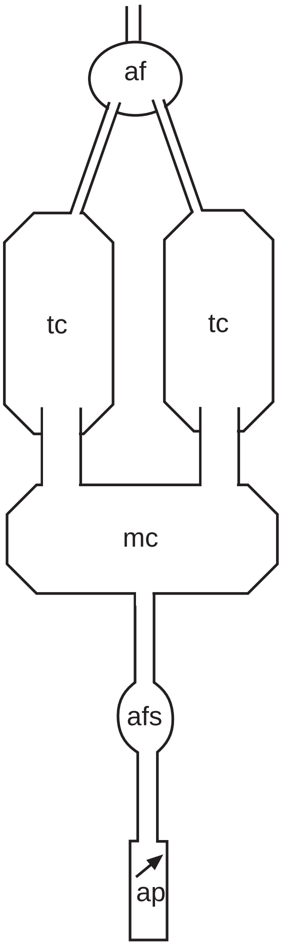

Fig. 1. The Y-olfactometer (not to scale). af, air filter; afs, air-flow stabilizer; ap, air pump; mc, main chamber; tc, test chambers.

An activated charcoal filter (af) in a plastic jar was connected to the test chambers by means of a Y-junction and silicon tubing of about 5 mm internal diameter. An air pump (ap) was connected to the main chamber and drew air through the apparatus.

To stabilize the flow of air, a 250 ml flask (afs) was connected between the pump and the main chamber. Smoke was generated from sticks of incense in the test chambers, and the speed of the pump was adjusted until the smoke was drawn into the main chamber equally from the two test chambers in a smooth and uniform plume. The position of the speed adjustment on the pump was then marked and used as the setting for all olfactometer tests. The actual flow rate of the air was not measured.

The lids of the Perspex boxes were firmly closed and made airtight with strong elastic bands.

Wooden arena

This was made from a circular piece of wood 750 mm in diameter (fig. 2). A strip of chipboard veneer was glued as a ring onto the sides of the circular base to make walls (w)

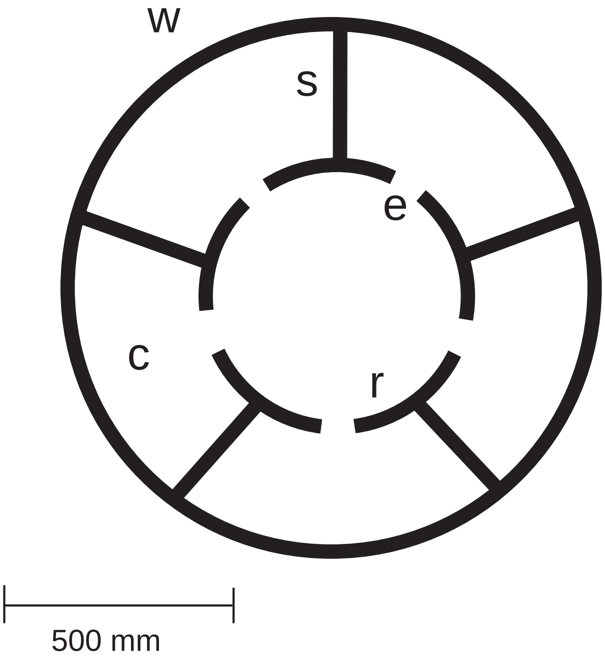

Fig. 2. The arena. c, compartments for test materials; e, entrances through a Perspex ring (r) enabling *Cosmopolites sordidus* to move from a central area into the compartments with test materials; s, Styrofoam dividers to form (in this example) five chambers for test materials; w, outer wall of arena.

220 mm high. The arena was covered with a glass lid to prevent escape of the weevils. A Perspex ring (r) 375 mm in diameter and 21 mm high formed an inner chamber within which the weevils were liberated. Grooves in the edge of the ring, as many as the number of substances to be compared, served as entrances (e) through which the weevils could pass. Strips of Styrofoam (s) radiating from the ring to the arena wall created compartments (c) within which the test materials were placed.

Bioassay

Cosmopolites sordidus from a culture maintained in the laboratory were starved for at least 12 h in a Perspex box lined with moistened filter paper. The beetles were not sexed, as previous work had shown no differences in the sexes in their response to volatiles (Budenberg *et al.*, 1993; Braimah, 1997). All tests were run in complete darkness to avoid any effect of uneven distribution of light on the responses of the weevils. For any test, an initial period of 60 min was allowed for the weevils to respond to the test materials. If more than 20% of the weevils had not responded to any of the materials at the end of the 60 min period the test was continued for a further 30 min, in order that the weevils not responding would not exceed 20%.

In the olfactometer tests, ten *C. sordidus* were introduced into the test apparatus at a time, and the tests were replicated six times with different weevils. At the end of the test period, the weevils in the two test chambers were counted. Weevils remaining in the release arena were recorded as ‘neutral’. After every three replicates, the olfactometer was cleaned first with absolute ethanol and then with household detergent. It was then left in a glassware drying oven for at least 30 min. Test materials were then exchanged between the chambers to compensate for any positional effects or preferences for either test chamber.

For arena tests, 20 *C. sordidus* were introduced into the inner chamber. At the end of the same test period timing as used with the olfactometer, the numbers of weevils in each compartment were recorded. Weevils that had not responded to any of the materials and remained in the inner chamber or any which had climbed the Styrofoam strips between compartments were recorded as ‘neutral’. The test was run eight times. The materials from which the arena was constructed made it impossible to be sure that contamination between odours in compartments would not occur if materials were exchanged between compartments between runs. However, the arena was rotated through 90° after each run so that at least there was compensation for any positional effects.

For each test, all replicates were run on the same day. Each of the materials used came from a single source and was divided into two. One half was used in the olfactometer and the other in the arena, and in each apparatus these halves were used repeatedly for all replicates since there was insufficient material to renew the material between replicates.

Preferences for different parts of the banana plant

The various parts were initially obtained from a mature wild type banana, *Musa velutina* (Wendl & Drude) (Musaceae), because it was then the only plant available that had flowered and could provide all the requisite plant parts. The plant was uprooted and divided into roots, pseudostem, rhizome, leaves, and flowers together with fruits. Eighty to one hundred milligrams of each of these parts were then all compared in the arena for attractiveness to the banana weevil. Subsequently, 50–60 g of all the other parts were compared with 20 g of dead banana leaves in the olfactometer for attraction to *C. sordidus*. Only a limited amount of dead leaf material was available, but it would have had a much higher fresh biomass before senescence. Twenty grams of dead banana leaves were also compared with distilled water as a control, both in the olfactometer and the arena. This served to ascertain the relative importance of humidity compared with host plant cues in the foraging responses of *C. sordidus*.

Later tests used banana material from ‘Cavendish’ cultivars (*Musa* AAA subgroup) as the material from the wild type was in short supply.

Air-dried and naturally senesced banana leaves

The experiment on the effect of senescence of leaf material on preferences of *C. sordidus* was carried out in two parts:

1. A green mature leaf was cut off the plant and completely air-dried in the glasshouse. Equal weights (20 g) of the dried leaf and naturally dead leaf material were compared in the olfactometer for attractiveness to *C. sordidus*.

2. A mature leaf that had turned yellow in the initial stages of senescence was cut and dried and was compared with dead leaf material as in **1** above.

Involvement of microbial organisms on dead leaves in the production of dead-leaf-based attractants

Halves of enough attached green mature leaves for the tests were washed with absolute ethanol to remove any microbes or their spores on the surface. They were left to dry for about 15 min and then enveloped in clear polythene held in place with Sellotape. The other halves were left exposed, and the leaves left on the plants until completely senesced and dry. Pieces of leaf obtained from the two halves were compared in the olfactometer for attractiveness to the weevil.

Comparison of dead banana leaves and dead leaves of other plants

Naturally senesced and dead leaves of cocoa *Theobroma cacao* L. (Sterculiaceae), cocoyam *Xanthosoma sagittifolium* (Araceae) and yam *Dioscorea rotundata* Poir. (Dioscoreaceae) were obtained from plants already in the glasshouse. Similar leaves of soybean *Glycine max* (L.) Merr. (Fabaceae) were obtained from harvested plants from a glasshouse experiment, and hay as a mixture of dry grasses was obtained from a local pet shop. Yam and cocoyam are commonly cultivated in association with bananas and plantains in most humid tropics (Jones, 1986). Hay was selected to represent weed stubble while soybean was chosen as a broad-leaved plant and a legume that is fast establishing itself as a food legume in most of Africa. Twenty-gram samples of these materials were used in the tests.

Analysis of data

For the olfactometer and arena tests with only two materials, the results were analysed by a χ^2 test incorporating a test for heterogeneity between replicates (Adams & van Emden, 1972). A significant heterogeneity between replicates casts doubt on a significant χ^2 between the two test materials. When more than two materials were compared in arena tests, data were analysed by analysis of variance for completely randomized designs. In all analyses, weevils that were recorded as 'neutral' were omitted from the analysis.

Results

Our interpretation of the results is limited by the fact that we did not conduct experiments to distinguish between attractant and arrestant properties of the plant materials. However, we consider that the olfactometer would have measured attractiveness. Arrestant properties would be more likely to affect the arena results, and these are interpreted here simply as preferences.

Preferences for different parts of the banana plant

The flowers and fruits were the least preferred parts tested ($P < 0.05$) (fig. 3). There is indeed no record in the literature of the flowers and fruits of banana being attacked by *C. sordidus*. The pseudostem and the leaves were the most preferred plant parts, but only the low preference for the flowers and fruits was statistically lower at $P = 0.05$. The number of *C. sordidus* attracted to the rhizome was intermediate between (and statistically inseparable from) the number attracted to the flowers/fruits and the other plant parts. A surprising result, in relation to the behaviour of the insect in the field, was that leaves were as preferred as pseudostem material.

While counting the weevils, it was noticed that most of those found on the leaves in the arena were sitting on the dead dry portions. Indeed, dead leaves proved more attractive than any other part of the banana plant in the olfactometer ($P < 0.05$, table 1). Similarly, in a second arena bioassay (table 2), of the plant parts tested only fresh roots were as preferred ($P < 0.05$) by the weevil as dead leaf material.

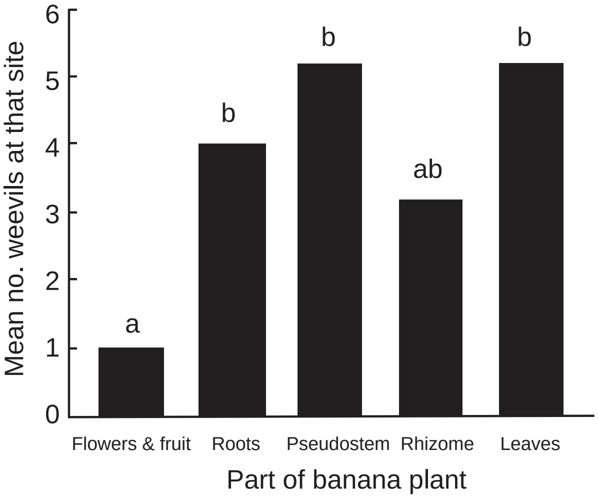

Fig. 3. Mean number of *Cosmopolites sordidus* recorded in arena test chambers containing different parts of banana plants. Columns with the same letter do not differ significantly at $P = 0.05$.

Table 1. Comparative attractiveness of a naturally senesced banana leaf and other banana materials to *Cosmopolities sordidus* in the olfactometer.

Test plant material	Percentage of *C. sordidus* responding to		$\chi^2_{1\text{ d.f.}}$	$\chi^2_{5\text{ d.f.}}$
	Test	Senesced		
Fresh leaf	4	96	21.2***	0.3^{ns}
Fresh root	32	68	4.2*	10.1^{ns}
Pseudostem	16	84	15.1**	10.3^{ns}
Air-dried leaf	15	85	24.1**	2.1^{ns}
Distilled water	26	74	30.4**	10.2^{ns}

^{ns} $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Air-dried and naturally senesced banana leaves

Both detached fresh and subsequently air-dried leaves (table 1) were clearly less attractive in the olfactometer than a leaf that had senesced naturally ($P < 0.001$). Naturally senesced leaves were also more attractive than leaves detached when yellow and then air-dried; the mean number of *C. sordidus* attracted was 4.0 and 1.3 respectively ($\chi^2_{1\text{ d.f}} = 8.00$, $P < 0.01$).

Involvement of microbial organisms on dead leaves in the production of dead-leaf-based attractants

Exposed halves of attached leaves and halves washed with ethanol and then covered in clear polythene until used in the olfactometer did not differ statistically in attractiveness to *C. sordidus*. The mean number of weevils attracted to the odour of exposed and covered half-leaves was respectively 1.15 and 1.90 ($\chi^2_{1\text{ d.f}} = 1.98$, $P < 0.05$). That the odour of the ethanol-sterilized half-leaves attracted numerically more *C. sordidus* than the odour from half-leaves exposed to microbial contamination was clear evidence that microbial organisms were not involved in the production of attractant odours from dead banana leaves.

Table 2. Mean number of *Cosmopolites sordidus* recorded in arena test chambers containing either a naturally senesced banana leaf or other banana materials.

Test plant material	Percentage of *C. sordidus* responding to		$\chi^2_{1\text{ d.f.}}$	$\chi^2_{7\text{ d.f.}}$
	Test	Senesced		
Fresh leaf	26	74	11.8***	2.1^{ns}
Fresh root	47	53	0.2^{ns}	3.1^{ns}
Pseudostem	27	73	10.4***	3.3^{ns}
Air-dried leaf	19	81	17.9***	1.9^{ns}
Rhizome	29	71	9.6**	4.6^{ns}
Distilled water	26	74	30.4***	10.2^{ns}

$^{ns}P > 0.05$; **$P < 0.01$; ***$P < 0.001$.

Comparison of dead banana leaves and dead leaves of other plants

In the olfactometer, dead yam leaves were more attractive to *C. sordidus* than dead banana leaves ($P < 0.001$, table 3). Although there was also an apparent attraction to dead cocoyam leaves over dead banana leaves ($P < 0.05$), the heterogeneity between replicates meant that this attraction could not be confirmed. Dead banana leaves were, however, found to be more attractive than cocoa and soybean leaves ($P < 0.05$). Hay was statistically similar to dead banana leaf in attractiveness to the weevil.

The arena comparison of the dead leaves of the non-banana plants tested in the olfactometer confirmed that dead leaves of yam and cocoyam were more preferred by *C. sordidus* than those of cocoa and soybean ($P < 0.05$, fig. 4). However, hay was not preferred to cocoa, a result which was not consistent with the olfactometer results. In these, there was no difference between hay and banana, yet banana had been preferred to cocoa.

Discussion

This is the first time that different parts of the banana plant have been shown to differ in how far they are preferred by *C. sordidus*. However, different parts of the oilseed rape plant *Brassica napus* L. (Brassicaceae) have been shown to differ in attractiveness to the cabbage seed weevil *Ceutorhynchus assimilis* (Paykull) (Coleoptera: Curculionidae) (Evans & Allen-Williams, 1989). Here it was the extract of the flowers (the part of the banana plant least preferred by *Cosmopolites sordidus*) which trapped most *Ceutorhynchus assimilis*.

The search for plant-produced semiochemicals which attract *Cosmopolites sordidus* has previously focused on fresh rhizome volatiles (Budenberg *et al.*, 1993; Braimah, 1997). Unfortunately, both singly and in combination, such volatiles have proved not to be attractive, and often repellent. The identification of dead banana leaf material as the source of an attractive semiochemical is therefore a breakthrough, and work is currently in progress to identify the chemical involved.

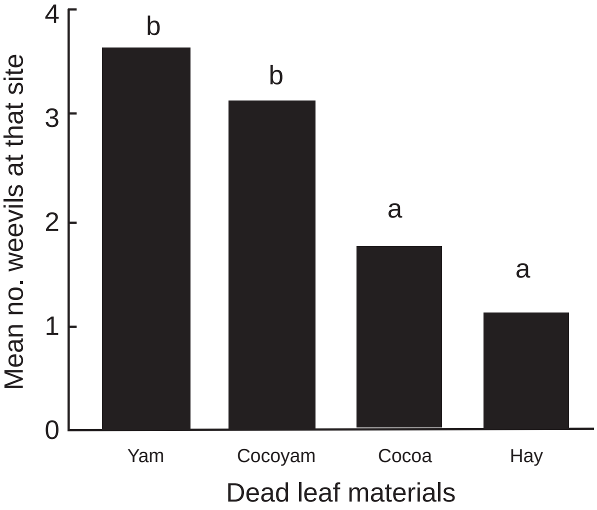

Fig. 4. Mean number of *Cosmopolites sordidus* recorded in arena test chambers containing dead leaves of some non-host plants. Columns with the same letter do not differ significantly at $P = 0.05$.

Table 3. Comparative attractiveness of a naturally senesced banana leaf and naturally senesced leaves of other plant species to *Cosmopolites sordidus* in the olfactometer.

Test plant material	Percentage of *C. sordidus* responding to senesced leaves of		χ^2 1 d.f.	χ^2 5 d.f.
	Test	Banana		
Cocoa	9	91	23.1***	7.9^{ns}
Cocoyam	69	31	6.4*	16.8*
Hay	60	40	1.0^{ns}	2.5^{ns}
Soybean	32	68	5.2*	3.2^{ns}
Yam	74	26	7.3**	10.9^{ns}

$^{ns}P > 0.05$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Difficulties of obtaining enough plant materials forced the first experiment on parts of the banana plant to rely on one batch of plant material from a wild type banana. However, the attractiveness to *Cosmopolites sordidus* of dead banana leaf material proved reproducible in subsequent experiments with new material from cultivated banana plants.

It appears that the process of leaf senescence has to progress naturally, with the leaf attached to the plant, for the attractive odours to develop, and that microbial metabolites are not involved. It is possible that a stepwise, enzyme-mediated process is involved. This is indicated by the failure of detached and dried leaves to produce the attractant. The process would result in rapid moisture loss inhibiting the enzymatic processes.

The attractiveness of dead banana leaf material to *C. sordidus* would help explain the high weevil numbers in abandoned banana plantations where dead leaf material accumulates freely (Sikora *et al.*, 1989). However, other factors such as higher moisture and darkness, provided by the debris and which would arrest the beetles, are equally likely to be important. The result is also relevant to the widespread use of dead banana leaf material for moisture conservation. One would expect the resident weevil population to increase and the efficiency of pseudostem traps to be reduced. Such effects have indeed been reported where banana material is used in this way (Price, 1993; Rukazambuga, 1996).

Roth & Willis (1963) and Ogengo-Latigo & Bakyalire (1993) have demonstrated the preference of adult *C. sordidus* for moist conditions. Both the arena and olfactometer bioassays showed that dead leaf material was considerably preferred over moisture (water). The combination of dead-leaf odours and moist conditions appears to be a cheap method of improving the efficacy of pseudostem traps.

Poor farm sanitation leads to banana plants with attached dead leaves, the accumulation of other plant debris and excess weed stubble. Such conditions have been blamed for high *C. sordidus* populations (Sikora *et al.*, 1989; Seshu-Reddy *et al.*, 1993). It was therefore important to elucidate how far the breakdown of non-specific green leaf compounds was involved in attracting weevils as opposed to the microclimatic conditions provided by the debris. In the comparison of dead banana leaf material with that for dead leaves of other plants, yam and cocoyam were included because they are commonly cultivated in association with bananas and plantains (Jones, 1986). They have been reported as alternative host plants of *C. sordidus* (Ittyeipe, 1986; Price,1994), probably wrongly, since Schmitt (1993) could only induce feeding on these crops by *C. sordidus* if the insects were severely starved. The preference of the weevils shown here for dead leaves of these plants would lead to adults being found on them in the field, and this may explain why it has been assumed that they are alternative hosts. Cocoa was included as a known non-host, and one which has been tested before and found less attractive than banana rhizome (Cerda *et al*., 1996). Soybean was included as another non-host, but one grown widely in Africa and often near or in banana plantations. Hay was chosen to represent weed stubble. That cocoa and soybean were not preferred indicates that *C. sordidus* can, as would be expected for what is believed to be a monophagous insect, discriminate between the dead leaves of a variety of plants. It is therefore worth pursuing the identification of the attractive compound with a view to using it to enhance the efficiency of traps for *C. sordidus*. That volatiles from the dead leaves of yam and possibly also cocoyam as well proved significantly more attractive than those from banana in the olfactometer was surprising, and the chemical(s) involved in this attraction also need to be identified. Other oligophagous insects have been found to respond to the odours of unrelated non-host plants (e.g. Colorado beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) by de Wilde *et al*. (1969) and Visser & Nielsen (1977) even though they are not found to congregate on such plants. This attractiveness of dead leaves of non-host plants often in spatial association with banana suggests that other stimuli, perhaps at close-range or even on contact, indicate to the weevil the suitability of the plants it encounters for breeding and feeding. In practical terms, the pruning and destruction of dead leaf materials of some other associated plants as well as of banana would be necessary to reduce colonization by *C. sordidus* in banana and plantain crops. That high populations of weevils are recorded in abandoned and poorly managed banana fields (see above) and that re-invasion of new banana crops is most rapid in fields with a recent history of banana cultivation (Afreh-Nuamah, 1993), can be explained by the prevalence of dead banana debris in such fields.

The discovery that it is the dead leaves of banana which produce semiochemicals that are attractive to the weevil provides the potential for enhancing the efficiency of split pseudostem and rhizome traps with a view to infecting arriving weevils with an entomopathogenic fungus (Treverrow *et al*., 1991; Kaaya *et al*., 1993).

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Sampling and Monitoring in Crop Protection: The Theoretical Basis for Designing Practical Decision Guides

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