Distribution, timing of attack, and oviposition of the banana weevil, *Cosmopolites sordidus*, on banana crop residues in Uganda

M. Masanza[1,2], C.S. Gold[1,*] & A. van Huis[2]

[1]*International Institute of Tropical Agriculture, PO Box 7878, Kampala, Uganda;* [2]*Laboratory of Entomology, Wageningen University, PO Box 8031, Wageningen, 6700 EH, the Netherlands*

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Abstract

Crop sanitation (removal and chopping of residue corms and pseudostems following plant harvest) has been recommended as a 'best bet' means of reducing banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), populations. However, it has been unclear when such practices should be carried out and what types of residues should be destroyed. Therefore, trials were conducted in Uganda to determine *C. sordidus* distribution, timing of attack, and oviposition on crop residues and growing plants. Assessments were performed in on-station trials on different aged standing and prostrate residues by destructive sampling. Similar data were collected from farmers' fields maintained at low, moderate, and high levels of sanitation. In the on-station trial, oviposition occurred on up to 120-day-old residues, although most occurred within 30 days of harvest. In a second on-station experiment, oviposition on standing residues was not significantly affected by residue age. By contrast, oviposition on prostrate residues was two times higher on 4-week-old than on 2-week-old residues, while the number of larvae on 8-week-old residues was three times higher than on 2-week-old residues. The number of adults was twice as high on 16-week-old residues as that on 2-week-old residues for both prostrate and standing residues. Farmers' fields maintained at high sanitation had 50% fewer eggs per residue than farms with low sanitation levels. In general, the number of immatures per residue was 50% higher on banana corms than on pseudostems. Numbers of larvae per residue were three times more abundant at low than at high sanitation levels. Residues in fields with high sanitation supported 50% fewer adults than residues in low sanitation fields. The results suggest that removal and splitting of corms after harvest is effective and practical in destroying immature growth stages of the pest and that such practices should be carried out soon after harvest.

Introduction

The banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), is an important pest of East African highland banana (*Musa* spp. (Musaceae), genome group AAA-EA) (Sebasigari & Stover, 1988; Gold et al., 1999). Damage is caused by the larvae, which tunnel in the corm and pseudostem. *Cosmopolites sordidus* attack interferes with water and nutrient uptake resulting in plant loss, delayed maturation, reduced bunch weights, and shortened plantation life (Rukazambuga et al., 1998; Gold et al., 2004a). Damage also weakens the plant base leading to snapping and toppling. In severe attacks, yield losses can reach 100% (Sengooba, unpubl.). This pest has been implicated as a principal cause of highland banana decline in central Uganda (Gold et al., 1999).

Bananas are rhizomatous herbaceous plants (Stover & Simmonds, 1987). A mat consists of an underground corm from which one or more plants (shoots) emerge. The shoot consists of a pseudostem, comprised of leaf sheaths, and a true stem that grows through its center and bears the flower and fruit. New plants (ratoons) are produced by suckers emerging from lateral buds in the corm. Normally, a banana mat consists of three or more plant generations (ratoons or crop cycles) at any one time. Plant density is

*Correspondence: IITA, PO Box 7878, Kampala, Uganda.
E-mail: c.gold@cgiar.org

controlled by the farmer through desuckering. Following harvest, the shoot dies back and the supporting portion of the corm eventually rots.

Integrated pest management of *C. sordidus* has been reviewed by Gold et al. (2001). Cultural controls offer management tools that are readily available to the resource-poor banana growers, who produce most of the highland bananas in eastern Africa. Crop sanitation (i.e., destruction of banana residues), for example, was first proposed as a means of *C. sordidus* control in the 1920s (Froggatt, 1924; Ghesquiere, 1925) and continues to be widely recommended (Seshu Reddy et al., 1998). This entails uprooting and chopping the corms and pseudostems of harvested plants into small pieces for rapid desiccation so that larvae present will die (Treverrow et al., 1991). These practices also accelerate nutrient recycling within banana stands. Banana residues are purported to be adult refuges, food sources, and breeding sites for *C. sordidus*. It is believed that destruction of these residues lowers *C. sordidus* adult populations and reduces damage on growing plants in susceptible clones (Gold et al., 2001). Few data are available, however, to demonstrate the effects of crop sanitation on *C. sordidus* population dynamics and damage.

In Uganda, farmers' sanitation practices on crop residues include (1) cutting of harvested stems, (2) chopping and spreading of cut stems, (3) covering of old corms with soil, (4) removal of corms, and (5) chopping of corms. These practices may be realized from 0 to more than 90 days after harvest. Moreover, crop sanitation is a labour-demanding management practice. As a result, farmer implementation of sanitation practices ranges from haphazard to systematic, depending on resource level and perception of benefits. Some farmers believe that postharvest stumps feed the followers (suckers) with water and nutrients and that removal of these residues would retard sucker development (Wortmann et al., 1994).

A survey on crop sanitation practices as a control strategy against this pest in Ntungamo district showed that 75% of the farmers practiced only low levels of sanitation, while 5% effected high levels of sanitation (Masanza, 2003). Farmers suggested two reasons for low adoption rates: (1) the practice was labour-intensive and removal of older, partially rotted stumps was less time-consuming than removing freshly harvested stumps, and (2) they were unclear as to the importance of crop sanitation in reducing *C. sordidus* pest problems. By contrast, farmers in the Masaka district were far more likely to implement higher levels of crop sanitation (Ssennyonga et al., 1999). This difference reflected the greater commercial orientation and higher resource base of farmers in Masaka than in Ntungamo districts.

The biology of *C. sordidus* has been reviewed by Gold et al. (2001). It is a K-selected insect (Pianka, 1970) with a long life span (i.e., up to 4 years) and low fecundity (less than four eggs per week). The adults are free-living, negatively phototactic, and positively hydrophilic. Most adults are closely associated with the banana mat or cut residues (Gold et al., 2004b). Eggs are placed singly in the corm and leaf sheaths near soil level. Crop residues are favoured oviposition sites. Abera et al. (1999) found 19–32% of oviposition on residues, while Rukazambuga (1996) observed 200 eggs on a single stump. The larvae prefer to feed in the corm although they will also attack the pseudostem and true stem. Development has been reported as 1 week for eggs, 3–4 weeks for the larval stage, and 1 week for the pupal stage. Developmental periods may be extended on less suitable host materials (Mesquita & Caldas, 1986). In some resistant cultivars, larval survivorship is considerably higher on residues than growing plants, suggesting a breakdown in defense mechanisms following harvest (Gold & Bagabe, 1997). On highland banana, it is unclear whether *C. sordidus* females accept older residues and whether or not larvae can successfully develop in them. In this context, it is important to know which types of residues serve as host material for *C. sordidus* (i.e., attract ovipositing females and are most suitable for larval development) and the timing of its attack. Such information could provide important insights into the types of residues that should be destroyed and when the optimal time for practicing crop sanitation might be.

The objective of this study was to determine which types of crop residues are most susceptible to *C. sordidus* attack under field conditions. This was done by assessing *C. sordidus* oviposition levels and the distribution of *C. sordidus* stages on differently aged residues (compared to standing plants) at three sites in Uganda.

Materials and methods

Research on *C. sordidus* distribution on different ages and types of crop residues was performed on farmers' fields in Ntungamo district and in on-station trials at the Kawanda Agricultural Research Institute and the International Institute of Tropical Agriculture's Sendusu Farm adjacent to the Namulonge Agriculture and Animal Research Institute, Uganda.

Site descriptions

Ntungamo district is in south-western Uganda along the Mbarara-Kabale road. Banana is the principal food crop as well as a leading cash crop at the study site (Ntungamo subcounty, around 0°53′ S and 30°14′ E). Most production is on small farms (<1 ha) with low levels of management. *Cosmopolites sordidus* is an important production constraint, although considerable variation in population densities and damage were found between farms. Selected farms ranged in elevation from 1300 to 1560 m above sea level. Mean precipitation in the subcounty ranges from 800 to 1500 mm rainfall per year with bimodal distribution (March–May and September–December). Mean daily temperatures are 15 °C minimum and 28 °C maximum.

Kawanda (0°25′ N, 32°32′ E) is 13 km north of Kampala and 1195 m above sea level with bimodal rainfall (March–May; September–December) averaging 1190 mm per year, and average daily temperatures of 15 °C minimum and 27 °C maximum. Sendusu (0°32′ N, 32°32′ E) is 1260 meters above sea level with bimodal rainfall (March–May, September–December) averaging 1200 mm per year and mean temperatures of 17 °C minimum and 27 °C maximum.

Experiment 1: *Cosmopolites sordidus* ovipositional preferences and distribution on crop residues in farmers' fields in Ntungamo

Two established multicultivar highland banana stands (>50 years old) with high *C. sordidus* population densities (mean pseudostem trap capture after 3 days = 3.2 weevils) were selected for the study. Each field was 1 ha in size and maintained at a low sanitation level.

Residues were either left in situ on the mat or cut and left lying intact in the field. Chopping and spreading of residues was not practised on either farm. The fields had differently aged standing and prostrate residues scattered haphazardly throughout the farm. Most common were (1) standing stumps consisting of the corm and 0.5–2.0 m of pseudostem, and (2) prostrate stems that had been detached from the mat between ground level to 10 cm below the soil surface. These residues were grouped into five age class treatments on the basis of farmer information and residue appearance: (1) 0–7 days after harvest (DAH), (2) 8–14 DAH, (3) 15–30 DAH, (4) 31–60 DAH, and (5) 61–120 DAH. In general, fresh residues were green and firm, while older residues turned dark brown with inner tissues in varying states of decomposition.

Sampling was conducted during the rainy season of March–April 1999. Data were collected on haphazardly selected crop residues, identified to cultivar, age, and location (standing or prostrate). Stumps were extracted from the soil using a digging spear. These were first examined visually for adults in the leaf sheaths and attached to the corm. The leaf sheaths were examined visually for eggs and the outer surface of the corm was then carefully pared using sharp knives to expose the eggs according to the methods of Abera (1997). The corm and pseudostem were then carefully dissected to expose immatures and other adults. On the first farm, 53 standing and 25 prostrate residues were sampled, while 264 standing and 126 prostate residues were sampled on the second farm.

Experiment 2: *Cosmopolites sordidus* ovipositional preferences and distribution on crop residues in on-station trials at Kawanda and Sendusu

This study was carried out to look at *C. sordidus* egg and larval distribution on two types of residues (i.e., standing and prostrate) at five different times (0, 2, 4, 8, and 16 weeks) after harvest. At Kawanda, the study was carried out in a 4-year-old highland banana (cv. Atwalira) stand comprised of four plots (30 × 70 m) separated by 20 m grass alleys. Planting density was 3.0 × 2.5 m with 280 mats per plot. In Sendusu, we used a 6-year-old highland banana stand (cv. Atwalira) comprised of two plots (115 × 12.5 m) separated by a 20-m grass alley. Each plot had about 50 mats of widely spaced bananas after disappearance of many of the original banana mats as a result of *C. sordidus* attack. Of these, we selected a total of 50 mats (30 from one plot and 20 from the other) to ensure enough samples for five replicates per treatment.

In each stand, plant density was maintained at three plants (one flowered, one preflowered, and one sucker) per mat. Mature bunches were harvested continually. One week before implementation of treatments, *C. sordidus* density in both stands was estimated at 9000 weevils ha^{-1} using mark and recapture methods described by Gold and Bagabe (1997).

As bananas were harvested in each field, randomly collected plants were assigned to different treatments. Standing residues comprised banana stumps left in situ (i.e., still attached to the mat) for which the pseudostem had been cut 1.5 m above the ground. For prostrate residues, the corm was cut 10 cm below the collar with 1.5 m of pseudostem attached. These were placed flat on the ground at least 1 m away from the mats. The date of harvest was noted and residues were sampled at fixed intervals after harvest.

Cosmopolites sordidus oviposition and larval infestation were evaluated on standing residues at 0, 2, 4, 8, and 16 weeks after harvest, and prostrate residues at 2, 4, 8, and 16 weeks after harvest. At each site, five residues per treatment were sampled during both the wet (March–April 2000) and the dry (July–August 2000) season. Stumps were extracted from the soil using a digging spear to remove as much of the corm as possible (in older and partially rotten residues, removal of the entire corm was sometimes not possible). The condition of the corms was determined by its moistness. Each stump was first examined visually for adults as in experiment 1. The leaf sheaths were also examined visually for eggs. Then the corm was carefully pared using sharp knives to expose additional eggs. The corm was then dissected carefully to expose immatures and other adults. The same was done for pseudostems.

Experiment 3: *Cosmopolites sordidus* ovipositional preferences and distribution on crop residues in implemented treatments in farmers' fields in Ntungamo

Following the conclusion of a 2-year study on the effects of increasing sanitation levels on *C. sordidus* population levels and damage in farmers' fields in Ntungamo (Masanza et al., 2004), a follow-up study was carried out on pest distribution on 15 farms. Each of these banana stands was more than 2 years old at the onset of the original study and initially used low levels of crop sanitation. Five of the farmers (controls) had continued low levels of sanitation (pseudostems and corms left attached to mat, or cut in large pieces and left intact on ground within the banana stand until they rot). Five farmers maintained moderate levels of sanitation (at 4–6 week intervals, residues cut at soil level, chopped into small pieces and spread out to dry; old corms left on mat but covered with soil). Five farmers implemented high levels of sanitation (at weekly intervals, pseudostems cut, chopped into small pieces and spread out to dry; corms removed from mat at depth of 5 cm and chopped into pieces). Mean pseudostem trap capture rates (3 days after trap placement) of *C. sordidus* were 2.3 adults in low sanitation fields, 1.7 adults under moderate sanitation, and 1.1 adults in high sanitation fields. Estimates of *C. sordidus* population densities ranged from 4300 to 8000 adults ha^{-1} (4–7 weevils per mat).

Trials were then implemented during the rainy season between September and December 2001. Work focused on a single highland banana cultivar, Enyeru, which was common on all farms. Each farmer was asked to allow us to manage crop residues for this cultivar. Fifty fresh residues per farm were either (1) cut at 1.5 m above the collar and then left in situ, or (2) cut near the soil level with at least 10 cm of corm and placed as large pieces prostrate on the ground at least 1 m from the mat. We then sampled the following treatments: (1) fresh maiden suckers, (2) recently harvested standing residues (1–7 DAH), (3) old standing residues (8–30 DAH), (4) very old standing residues (60–112 DAH), (5) old prostrate residues (8–30 DAH), and (6) very old prostrate residues (60–112 DAH). Ten maiden suckers and 10 residues per treatment were assessed on each farm. Fresh residues were green and firm, while older residues turned dark brown with inner tissues in increasing states of decomposition over time. Plants for assessment were harvested over time, noting dates of harvest. The residues were accordingly labelled for ease of assessment.

First, the residues were searched for adults externally attached or in the soil under prostrate residues or within 2.5 cm of standing residues. The surface of the residue corms and leaf sheaths were closely examined for eggs. The corms and pseudostems were then systematically dissected using sharp knives to reveal the presence of immature stages and additional adults.

Data analysis

Data from experiment 1 were analysed on a SAS general linear model (GLM) procedure on responses of number of eggs, larvae, pupae, teneral adults and adults by residue age, residue placement (standing or prostrate), location on residue (corm or pseudostem), and by clone/cultivar. Responses for *C. sordidus* development stage by residue age and location were first square root transformed before analysis for stabilizing variances and then re-transformed. Means were separated using Ryan–Einot–Gabriel–Welsch multiple range test (REGWQ).

For data from experiment 2, two sets of analyses were performed on numbers of eggs, larvae, pupae, and adults on standing vs. prostrate and crop residue age. Mean of eggs, larvae, pupae, and adults per residue for both sites were subjected to preliminary analysis to detect site and seasonal differences. When no such differences were observed, the means were pooled and subjected to GLM of SAS. Means were compared using pairwise comparison t-test of LS means generated from analysis using SAS (SAS Institute, 1997).

For experiment 3, GLM of SAS was used to analyse data on number of eggs, larvae, pupae, and adults. Least square (LS) means by sanitation level and crop residue type/age were obtained. Treatment effects were separated using the pairwise comparison t-test of LS means.

Results

Experiment 1: *Cosmopolites sordidus* ovipositional preferences and distribution on crop residues in farmers' fields in Ntungamo

In spite of relatively high banana weevil infestation levels in the experimental fields, observed oviposition levels were low (Table 1). Nevertheless, females accepted all stages of crop residues including up to 120 days after harvest (Table 1). Oviposition was greatest, however, on younger crop residues, while other weevil stages were mostly similar across residue age classes. Oviposition levels were also similar (1) on standing and prostrate residues and (2) on residue corms and pseudostems. All of the crop residues examined in this study appeared suitable for larval development (Table 2).

Experiment 2: *Cosmopolites sordidus* ovipositional preferences and distribution on crop residues in on-station trials at Kawanda and Sendusu

More *C. sordidus* adults were associated with older than younger standing and prostrate residues (Table 3). The numbers of adults were similar at comparable stage

Table 1 Mean number of *Cosmopolites sordidus* eggs, larvae, pupae, teneral adults, and adults by crop residue age in farmers' fields in Ntungamo district, Uganda

Age of residue (days after harvest)	Mean number of each banana weevil growth stage				
	Eggs	Larvae	Pupae	Teneral adults	Adults
0–7	2.4a	4.3a	0.7b	0.5a	3.1a
8–14	1.5abc	3.1a	1.7a	0.7a	4.3a
15–30	1.7ab	4.3a	1.2ab	0.5a	3.1a
31–60	0.7c	3.1a	1.2ab	0.5a	2.4a
61–120	0.9c	2.4a	0.7b	0.7a	4.3a

In columns, means followed by the same letter are not significantly (P>0.05) different by Ryan–Ginot–Gabriel–Welsch Multiple Range test.

Table 2 Number of *Cosmopolites sordidus* eggs on standing (n = 124) and prostrate (n = 116) residues in farmers' fields in Ntungamo district, Uganda

Residue type		Age of banana residue (days after harvest)				
		1–7	8–14	15–30	31–60	61–120
Standing	Corm	1.2a	1.0a	1.3a	0.7a	0.7a
	Pseudostem	1.2a	0.6a	0.4a	0.1a	0.7a
Prostrate	Corm	0.5a	0.4a	0.7a	0.1a	0.0a
	Pseudostem	0.0a	0.1a	0.0a	0.0a	0.0a

In columns, means with the same letter are not significantly (P>0.05) different by RyanEinot–Gabriel–Welsch Multiple Range test.

standing and prostrate residues. Ovipositing females accepted all stages of residues. The greatest number of eggs was found on 4-week-old prostrate residues, but there was no clear trend between residue age or location and egg numbers. Peak numbers of larvae were found on 4- and 8-week-old prostrate residues, while there was no difference among treatments in numbers of pupae.

Experiment 3: *Cosmopolites sordidus* ovipositional preferences and distribution on crop residues in implemented treatments in farmers' fields in Ntungamo

Numbers of *C. sordidus* adults and immature stages were related to levels of crop sanitation with lowest population densities on farms maintained at high levels of crop sanitation (Figure 1). More *C. sordidus* of each stage were associated with residue corms than with pseudostems for each sanitation level (Figure 2). Similar trends were found between *C. sordidus* stage and residue age under different sanitation levels, so the data from the fields were pooled (Figure 2). In this experiment, oviposition levels on crop residues were 10 times higher than in experiment 1, which had been undertaken in the same subcounty 2 years earlier. High levels of oviposition occurred on crop residues of all ages, although older residues tended to have fewer eggs. Eggs were also more abundant on each of the residue treatments than on fresh suckers. Larval numbers were also lowest on suckers and tended to increase with residue age (Figure 3). More larvae were present on prostrate than standing residues. Pupal and adult numbers were also higher on prostrate than standing residues and lowest on suckers.

Table 3 Number of *Cosmopolites sordidus* eggs, larvae, pupae, and adults by age of standing and prostrate banana (cv. Atwalira) residues in on-station trials at the Kawanda Agricultural Research Institute and IITA's Sendusu farm, Uganda (pooled data)

Residues	Weeks after harvest	Eggs	Larvae	Pupae	Adults	Moistness
Standing	0	3.2 ± 1.08b	4.7 ± 1.96b	0.9 ± 0.41a	4.9 ± 1.55b	Moderate
	2	4.4 ± 1.34a	4.0 ± 2.44b	0.4 ± 0.51a	3.9 ± 1.93b	Moderate
	4	3.3 ± 1.33b	5.1 ± 2.43b	0.4 ± 0.51a	4.0 ± 1.91b	Moderate
	8	4.2 ± 1.29a	4.0 ± 2.36b	0.4 ± 0.49a	6.2 ± 1.87ab	Moderate
	16	2.6 ± 1.75b	2.0 ± 3.16b	0.1 ± 0.67a	7.7 ± 2.52a	Very moist
Prostrate	2	2.3 ± 1.12b	3.4 ± 2.04b	0.2 ± 0.43a	3.3 ± 1.61b	Moderate
	4	4.8 ± 1.33a	7.6 ± 2.42a	0.6 ± 0.51a	3.5 ± 1.92b	Moderate
	8	3.3 ± 1.25b	10.1 ± 2.28a	0.8 ± 0.48a	5.6 ± 1.80ab	Very moist
	16	1.2 ± 1.05b	3.9 ± 1.92b	0.7 ± 0.40a	8.0 ± 1.52a	Very moist

In columns, means followed by the same letter are not significantly different (P>0.05) by pairwise comparison t-test.

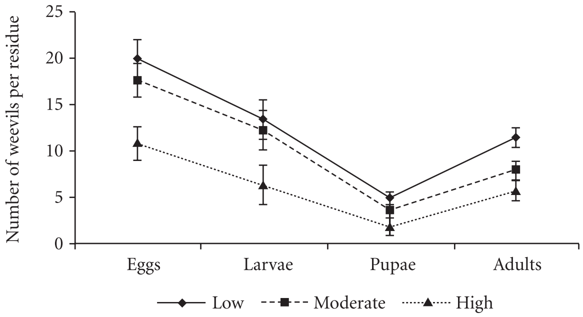

Figure 1 The number of *Cosmopolites sordidus* at different development stages (LS means ± SE) in crop residues in farmers' fields maintained at low, moderate, and high sanitation levels in Ntungamo district, Uganda.

Discussion

Destruction of crop residues has been widely recommended as a means of controlling *C. sordidus* in banana fields in the East African Great Lakes region and elsewhere (Gold et al., 2001). In our studies, female *C. sordidus* were attracted to and accepted all sampled crop residues for oviposition including those from plants that had been harvested 2–4 months earlier. Oviposition was, however, somewhat lower on older than younger residues. All of these residues also appeared to be satisfactory substrates for larval development. More larvae were found on older residues although, from the data, it is unclear if this reflected differential oviposition rates or higher levels of larval survival. Oviposition rates and larval numbers were higher on all stages of residues than on maiden suckers. However, we were unable to determine the relative numbers of eggs on residues compared to flowering plants which are more favoured for oviposition than maiden suckers (Abera, 1997), as farmers were reluctant to let us destroy such plants.

Higher numbers of *C. sordidus* adults on older residues might be related to the increased moisture found in these materials. *Cosmopolites sordidus* adults are highly sensitive to soil moisture and will rapidly die if left on a dry substrate (Roth & Willis, 1963; Gold et al., 2001). It is also possible that decaying host tissues release increased levels of volatiles that attract adult *C. sordidus*. Budenberg et al. (1993) suggested that kairomones emitted from host plant tissue are important in host plant location.

In this study, oviposition rates tended to be higher on corms than on pseudostems although egg density was low and differences were not significant. The greater attraction of adult *C. sordidus* to corms than to pseudostems is well known (Gold et al., 2001). However, our results contrast with those of Abera (1997) who found most oviposition to be on pseudostems. These differences may have reflected levels of high mat, by which the corm emerges from the ground and is more exposed to ovipositing *C. sordidus*. In Ntungamo, many plantations were more than 50 years old and high mat was common.

Oviposition rates were similar among standing and prostrate residues, yet prostrate residues supported higher numbers of larvae. In other studies, higher numbers of larvae were also found in prostrate than in standing residues for the resistant cultivars Kisubi (AB) in Uganda (Gold & Bagabe, 1997) and Pisang Awak (ABB) in Indonesia (CS Gold, unpubl.) It is possible that ovipositing females are able to place their eggs directly onto the corm or true stem on prostrate residues, while on standing stumps they are more likely to place their eggs on the pseudostem. Survivorship rates of young larvae have been shown to be greater on corms than on pseudostems (G Night, unpubl.). Thus, cutting and leaving residues intact within banana fields may exacerbate *C. sordidus* problems. Therefore, it is important to chop up cut residues to hasten desiccation of the material.

Lower *C. sordidus* levels on residues in fields maintained at high levels of crop sanitation suggest that this method does have an impact on pest populations. This strongly suggests that removal and splitting of corms after harvest is of practical importance in destroying especially immature growth stages of the pest. The data from this study suggest that oviposition on residues peaks within the first month after harvest but continues for at least another 3 months. Because all crop residues house immature *C. sordidus* stages, chopping them to small pieces as early as possible, preferably within 2 weeks after harvest, should destroy a large proportion of the pest population.

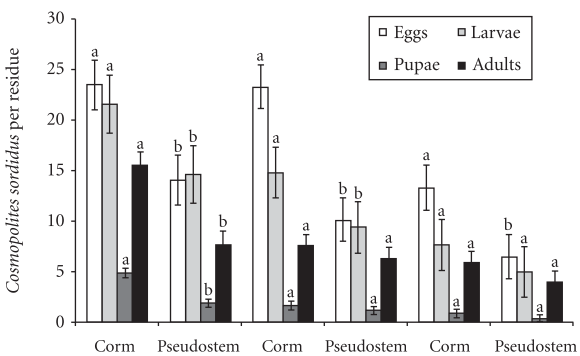

Figure 2 The number of different development stages of *Cosmopolites sordidus* in corms and pseudostem of crop residues in farmers' fields maintained at different sanitation levels for 1 year in Ntungamo district, Uganda. Means of weevil numbers of a certain development stage and within each sanitation level followed by the same letter are not significantly different (pairwise comparison t-test of LS means).

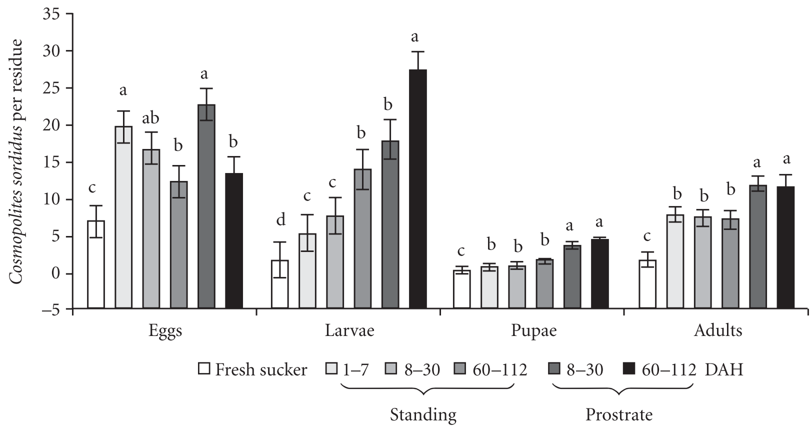

Figure 3 The number of *Cosmopolites sordidus* eggs, larvae, pupae, and adults by age of standing and prostrate crop residues of different ages (DAH: days after harvest) in farmers' fields maintained at low, moderate, and high sanitation levels for 1 year in Ntungamo district, Uganda. For each weevil development stage, means followed with the same letter are not significantly different (pairwise comparison *t*-test of LS means).

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