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Multifunctional coreid bug pheromones for efficient bioprotection against legume pests and enhanced food productivity

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Abstract

Background In Africa, food legumes such as cowpeas and beans constitute important sources of proteins for millions of rural and urban populations. However, attacks by multiple pest species can reduce yields by up to 80%. Smallholder farmers protect their crops against pests using conventional insecticides, thereby contributing to insecticide resistance and jeopardizing food safety. To date, no alternative sustainable practices are available to reduce insecticide use in the management of legume pests. This study aimed to provide a sustainable alternative to insecticide use based on semiochemicals to manage multiple legume pest species and enhance food productivity.

Results Using coupled gas chromatography-mass spectrometry (GC–MS) and coupled GC-electroantennographic detection (EAD) analyses, we identified 2-methylbutyl 2-methylbutanoate as the male-produced aggregation pheromone of the legume pest, *Clavigralla elongata*, a coreid bug species specific to East Africa. In multi-site field trials conducted in West Africa and East Africa, 2-methylbutyl 2-methylbutanoate and its analogue, isopentyl butanoate, previously identified from the pan-tropical coreid bug, *C. tomentosicollis*, both lured multiple legume insect pest species including from the *Clavigralla* genus, the legume pod-borer *Maruca vitrata*, flower thrips *Megalurothrips sjostedti*, and whitefly *Bemisia tabaci* into traps. Additionally, both pheromones lured the *Clavigralla* natural enemy parasitoid *Gryon fulviventris* into traps. The whitefly was only captured in pheromone-baited traps in East Africa. Deployment of an optimized pheromone trapping system significantly reduced legume pests and increased natural enemy density by up to sixfold compared to farmer practice (insecticide-treatment) and control. Legume yields for pheromone and insecticide treatments were comparable, ~ 320–590% higher than untreated controls.

Conclusion These findings establish coreid bug pheromones as effective novel multifunctional semiochemical-based tools for sustainable legume pest management and production without insecticide use.

Keywords *Clavigralla* spp., *Maruca vitrata*, Whiteflies, Thrips, Aggregation pheromone, Natural enemy, Legumes

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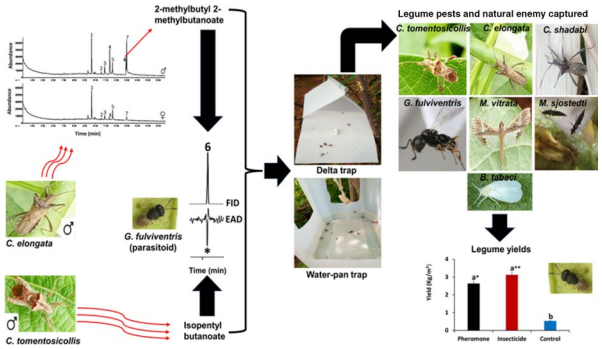
Graphical abstract



Background

Eco-responsive and sustainable crop production systems are key in ensuring food and nutritional security, agricultural incomes, and conservation of insect biodiversity [1, 2]. Food security in sub-Saharan Africa (SSA) is largely contingent on agricultural production systems (e.g. rainfed farming systems, dualistic farming systems) and pest management strategies. However, the farming systems and especially pest control strategies, which mirror global applications using insecticides, have limitations and significant risks to human and environmental health [3, 4]. Among the commodities affected by these risks are grain legumes including cowpea (*Vigna unguiculata* Walp.) and French beans (*Phaseolus vulgaris* L.), which are important sources of food and soil fertility, as well as providing income for small-scale farmers [5, 6]. In 2021, global production of cowpea was at 8.99 million metric tons of cowpea harvested from 14.5 million hectares of production land [7], of which 83% is from West Africa [8]. The global annual dry bean production is estimated at 27.5 million metric tons, of which 26% is from Africa [9]. Of this amount, 600,013 metric tons, with an approximate market value of USD 20 million per year was reported from Kenya, the largest producer of French beans in East Africa [10, 11]. Cultivation of these crops faces limitations due to both abiotic and biotic stressors, notably including infestations by multiple arthropod pests such as the brown pod-sucking bugs of the *Clavigralla* genus (Heteroptera: Coreidae), the legume pod-borer *Maruca vitrata* Fabricius (Lepidoptera: Crambidae), flower thrips *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), and whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) [12–16]. Of the *Clavigralla* species, *C. tomentosicollis* is pan-tropical in SSA, whereas *C. shadabi* and *C. elongata* are specific to west and east Africa, respectively. In SSA, the larval and adult stages of these insects are most damaging, feeding on the reproductive tissues of the plant, such as flower buds and pods, causing yield losses of up to 100% [17–25]. Current management methods, including the use of natural enemies and biopesticides, target individual pests, which are inadequate and costly for legume production. As such, legume farmers use broad-spectrum insecticides (acetak (acetamiprid 200 SL), oshothane, imaxi 200SC, dichlorodiphenyltrichloroethane (DDT), malathion, permethrin, imidacloprid, etc.) to control pests, which are harmful to the environment and human health and have resulted in resistance buildup in populations, making these approaches ineffective [26, 27].

Bioprotection of legumes is critical to their sustainable production. Recently, in a laboratory study, we demonstrated that the male-produced aggregation pheromone isopentyl butanoate of the pantropical coreid pod-sucking bug, *C. tomentosicollis*, attracted both sexes of the bug and its natural enemy, the parasitoid *G. fulviventris* [28]. This finding presents bio-protection potential opportunities to explore the use of coreid bug pheromones to improve smallholder legume productivity in farmer grown fields. Here, we provide field-based evidence in two countries in Africa—Benin (West Africa) and Kenya (East Africa) to show the multifunctional bioprotection potential of two coreid aggregation pheromones: isopentyl butanoate, previously identified from *C. tomentosicollis* [28], and newly identified 2-methylbutyl 2-methylbutanoate in the current study from *C. elongata*, a species-specific to East Africa. In farmer-grown

legume fields (Zou and Collines), both pheromones attracted multiple legume pest species and natural enemies. Furthermore, we demonstrated the effective use of 2-methylbutyl 2-methylbutanoate for sustainable legume production in a yield assessment study conducted in Kenya.

Results

We first observed the multifunctional bioprotection potential of isopentyl butanoate in a preliminary field trial conducted in a small-scale farmer mono-crop of cowpea at Ahoyeme (Benin). White delta and water-pan traps were baited with three doses (0.5 mg, 2.5 mg, and 5 mg) of the pheromone (Fig. S1), and their bioprotection potential was recorded for two coreid pod-sucking bugs, *C. tomentosicollis* and *C. shadabi,* the parasitoid natural enemy of *Clavigralla* species *G. fulviventris* and flower thrips *M. sjostedti* (Fig. S2a, b, c, e; Table S1). Trap captures for the legume pod borer *M. vitrata*, were not significantly different from the control ($P > 0.05$) (Fig. S2d). Interestingly, trap captures of both *C. tomentosicollis* and *C. shadabi*, increased with increasing pheromone dose, but with up to four-fold more of the former captured than the latter coreid ($P < 0.001$; $P < 0.01$). On the other hand, trap captures of the parasitoid *G. fulviventris*, decreased with increasing pheromone dose with significant difference ($P < 0.001$). These promising results prompted us to identify the aggregation pheromone of *C. elongata*, which is specific to East Africa, to test whether this multi-functional bioprotection potential is also applied to it.

Identification of the aggregation pheromone of *Clavigralla elongata*

Coupled gas chromatography–mass spectrometric (GC–MS) analysis of the air-borne volatile extracts of sexually mature *Clavigralla elongata* adults (7–8 days old) identified seven components: **1**—*α*-pinene, **2**—*β*-pinene, **3**—myrcene, **4**—isopentyl butanoate, **5**—1,8-cineole, **6**—2-methylbutyl 2-methylbutanoate and **7**—2-methylbutyl isovalerate, with peak **6**, as a male-specific component (Fig. 1a–c). In coupled GC-electroantennographic detection (EAD) assays, antennae of both male and female *C. elongata*, and female of the natural enemy parasitoid, *G. fulviventris*, consistently detected both the natural and synthetic 2-methylbutyl 2-methylbutanoate (Fig. 1d, e). Peak **5**, 1,8-cineole, was detected by antennae of both sexes of *C. elongata*, whereas peak **7**, 2-methylbutyl isovalerate, was detected by male antenna only. Additionally, GC-EAD-active peaks were recorded which varied with the antennae of the different sexes of this insect species and its parasitoid between the retention times 4 min and 7 min, which were all identified by GC–MS as column impurities, mainly siloxanes. Likewise, in Fig. 1e, GC-EAD-active peaks recorded between 2 and 6 min using the synthetic standard of 2-methylbutyl 2-methylbutanoate were identified as the column impurities siloxanes. These results suggest that 2-methylbutyl 2-methylbutanoate is a candidate aggregation pheromone of *C. elongata* that may attract both its sexes and potentially the natural enemy parasitoid *G. fulviventris.* Furthermore, these results show that the aggregation pheromone of *C. elongata* is structurally related to the male-specific aggregation pheromone ester isopentyl butanoate, previously identified from *C. tomentosicollis* (Fig. 1b) [28].

Multifunctional bio-crop protection potential of coreid pod-sucking bug pheromones in farmers' field—Benin (West Africa)

To confirm our preliminary results obtained in the cowpea field at Ahoyeme (Benin), we evaluated the bioprotection potential of the candidate *C. elongata* aggregation pheromone 2-methylbutyl 2-methylbutanoate and isopentyl butanoate, previously identified for *C. tomentosicollis* at two different legume growing sites, Zou and Collines, central Benin (Fig. 2A). Pheromone-baited traps, irrespective of the pheromone used, dose, and site, captured the same legume pests and natural enemies (Figs. 2B, C, 3A, B; Table 1, Tables S2a, and S2b), as previously observed in our preliminary field tests with isopentyl butanoate (Fig. S1, and Table S1). However, trap captures varied with the site, pheromone, pheromone dose ($P < 0.001$), and trap type ($P < 0.05$) (Fig. 3A, B; Table 1, Tables S2a and S2b, Table S4a). Although the pattern of trap capture was similar at both sites for the two coreid pheromones, in general, trap capture was comparatively higher at Zou than Collines (Table Sa). Strikingly, at both Zou and Collines, similar to our preliminary results, trap captures of *C. tomentosicollis* and *C. shadabi*, increased with increasing pheromone dose of isopentyl butanoate, with trap captures being higher in the former than the latter insect ($P < 0.001$) (Fig. 3A, B). At the two sites, both *C. tomentosicollis* and *C. shadabi* were significantly lured into pheromone-baited water-pan than delta traps ($P < 0.05$–$P < 0.001$). However, at Zou, delta traps baited with 2-methylbutyl 2-methylbutanoate significantly lured the highest number of legume pests, first being the thrips species *M. sjostedti* ($P < 0.001$) (Fig. 3A_e, j, Table S2a), followed by the parasitoid *G. fulviventris* ($P < 0.001$) (Fig. 3A, B_c, h; Table S2a and S2b). The highest capture of the parasitoid with 2-methylbutyl 2-methylbutanoate was recorded at a dose of 2.5 mg but at 0.5 mg and 5 mg for isopentyl butanoate ($P < 0.001$; $P > 0.05$). On the other hand, *M. vitrata* was significantly lured into water-pan traps than delta traps baited with

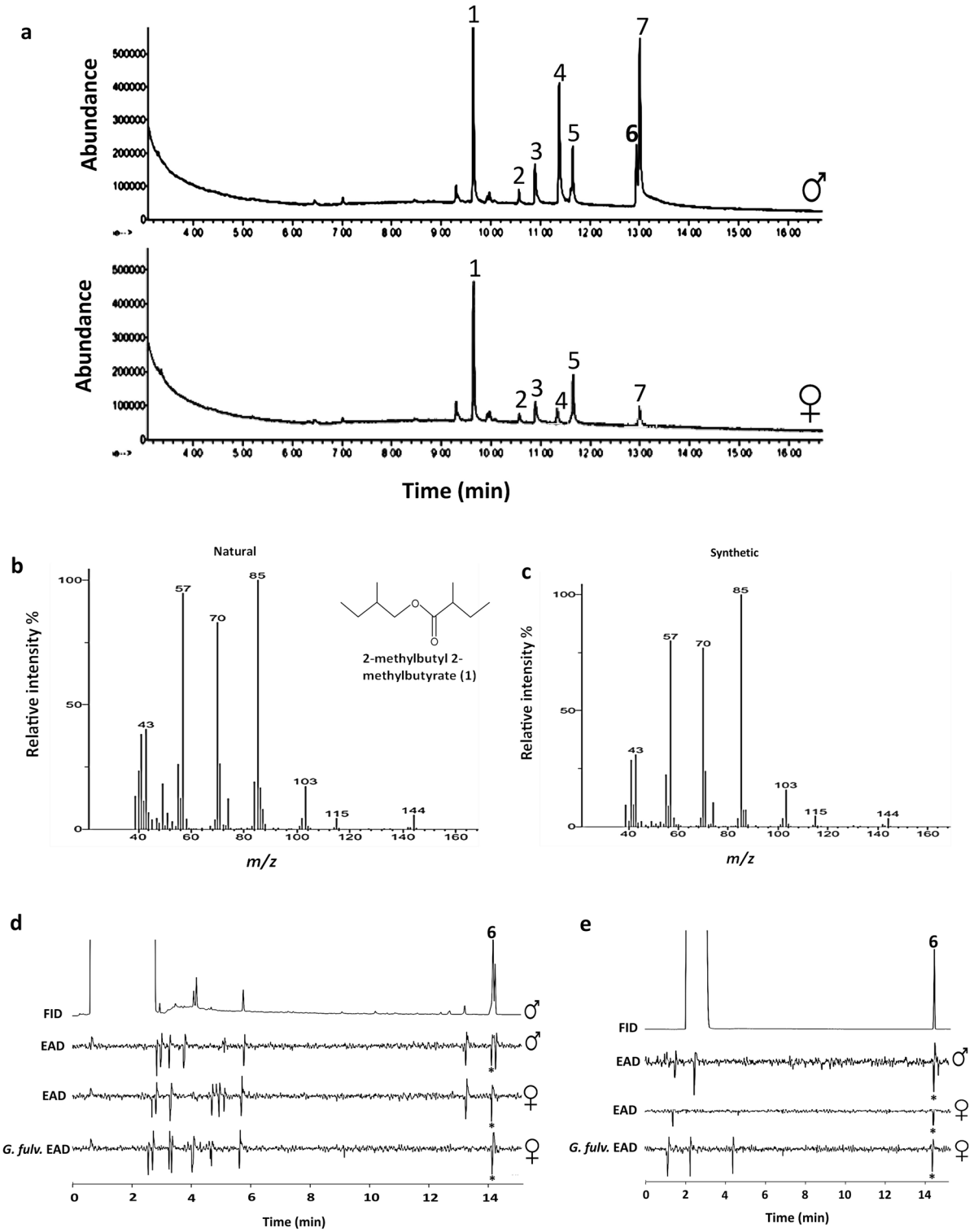


Fig. 1 Representative chemical profiles of **a** *Clavigralla elongata* male and female adult volatiles showing male-specific peak 6**, b** Mass spectra of male-specific peak **6** identified as 2-methylbutyl 2-methylbutanoate in natural volatile extract, and **c** synthetic standard, **d** coupled GC-EAD analysis showing antennal detection by *C. elongata* male and female, and *G. fulviventris* of peak **6** in the crude volatiles, and (e) synthetic standard. The symbol (♀) represents female and (♂) male and *G. fulv*. means *Gryon fulviventris*

2-methylbutyl 2-methylbutanoate at both sites ($P < 0.05$), but it was the reverse for isopentyl butanoate ($P > 0.05$) (Fig. 3A, B, Table 1, Tables S2a and S2b). Furthermore, at Collines, trap captures with the aggregation pheromone isopentyl butanoate of *C. tomentosicollis* followed a dose–response pattern (Fig. 3B_f), with 36% males and 41% females lured into the traps.

Validation of the Benin field results in farmers' field—Kenya (East Africa)

Given the results obtained from the Benin field trials, we evaluated the multifunctional bioprotection potential of the two aggregation pheromones against legume pests at two legume growing sites, Machakos and Embu, in eastern Kenya (Fig. 3). Unlike Benin, where legumes are often grown as mono-crops, in Kenya farmers plant legumes as both mono- and inter-crops. The same design and identical pheromone doses and trap types were used as was done in the Benin field trials. This study was carried out for 4 weeks at both sites. At Machakos, site 1 was an intercrop of French bean and maize, whereas site 2 was a monocrop of French bean. On the other hand, at Embu, site 1 was a mono-crop of French bean, and site 2 was an intercrop of pigeon pea and cowpea. Overall, traps baited with the pheromone with 2-methylbutyl 2-methylbutanoate identified from males of *C. elongata* captured 43% males and 49% females, confirming that it is, indeed, an aggregation pheromone. Trap captures mirrored the trap captures recorded in Benin. For each insect species, trap captures varied with the pheromone, dose ($P > 0.001$), trap type ($P > 0.001$), and site (Fig. 4A, B; Table 2, Table S3a and b; Table S4b). Trap captures were generally higher at the Machakos than at Embu sites. Surprisingly, pheromone-baited traps captured whiteflies at both sites in Kenya, but only in traps baited with the pheromone 2-methylbutyl 2-methylbutanoate identified for *C. elongata* at all the doses tested with a significant difference for dose (0.5 mg) ($P < 0.05$) (Table S3a). In general, at both sites, trap captures were highest for whiteflies, followed by thrips, and both were significantly lured into pheromone-baited delta traps than water-pan traps ($P < 0.001$; $P < 0.01$ respectively) (Fig. 4A, 4B- e and f; Table 2, Table S3a). As noted for the Benin sites, trap captures of the parasitoid *G. fulviventris* with the two different pheromones were also intermediate ($P < 0.01$), with no clear preference for any of the two trap types ($P > 0.05$). The highest capture of the parasitoid was recorded for isopentyl butanoate at a dose of 0.5 mg at the Machakos site ($P < 0.01$). Next were trap captures of the legume pod borer *M. vitrata,* which was significantly lured into pheromone-baited delta traps than water-pan traps ($P < 0.05$). Interestingly, although the pheromones are *Clavigralla* species-derived, trap captures were lowest but comparable for the two *Clavigralla* species. Both *C. elongata* and *C. tomentosicollis* were significantly lured into pheromone-baited water-pan traps than delta traps ($P < 0.05$) and generally followed a dose–response pattern for isopentyl butanoate at the Machakos site (Fig. 4A_g, h), and 2-methylbutyl 2-methylbutanoate at the Embu site (Fig. 4B_a, b). They lured multiple pests and natural enemies into traps. The results show that, unlike Benin, whiteflies are additional pests of legumes in Kenya (Table 2).

Notably, pheromone-baited trap captures for both sexes were similar (Table S5) across West and East Africa: *C. tomentosicollis*-Benin (males: 43%–45%, females: 41%–51%); and Kenya (males: 48% (both sites), females: 41%–45%); and *C. elongata*-Kenya (males: 36%–46%, females: 46%–59%).

Yield assessment

Given the almost identical multifunctional performance of the coreid-sucking bug pheromones in Benin and Kenya, next, we tested the bioprotection potential of the pheromone of *C. elongata* (2-methylbutyl 2-methylbutanote) in field trials at two different farmer-field sites (sites 1 and 2) in Machakos (Kenya) for 4 weeks and measured legume yields. Here, only the water-pan trap, which performed better at the various sites in Benin and Kenya for *Clavigralla* species was used. It was baited with the pheromone dose (5 mg) which elicited the highest attraction, and we used the same experimental design as in the previous experiments in both countries. The experiment was conducted in a mono-crop field of French bean (Vanilla cultivar). Overall, while the density of the parasitoid *G. fulviventris* increased with time, it was the opposite for *Clavigralla* spp. ($P < 0.01$, and $P < 0.05$) in the pheromone treatments compared to control at both sites (Fig. 5A_a, d). On the other hand, in the insecticide-treated field, both pest and parasitoid densities decreased with time compared to the control fields at both sites (Fig. 5A-b, e).

(See figure on next page.)

Fig. 2 **A** A map showing the experimental sites in Benin (West Africa) and Kenya (East Africa), and **B** pictures of legume pests trapped at the experimental sites: (**a**) *Clavigralla tomentosicollis*, (**b**) *C. elongata*, (**c**) *C. shadabi*, (**d**) *Gryon fulviventris* (**e**) *Maruca vitrata,* (**f**) parasitoid *G. fulviventris* on *Clavigralla* eggs in the field, (**g**) *Megalurothrips sjostedti*, and (**h**) *Bemisia tabaci*. **C** field layout of pheromone-baited and -unbaited delta traps and water pan traps in different legume cropping systems (mono- and intercrop) in Benin and Kenya

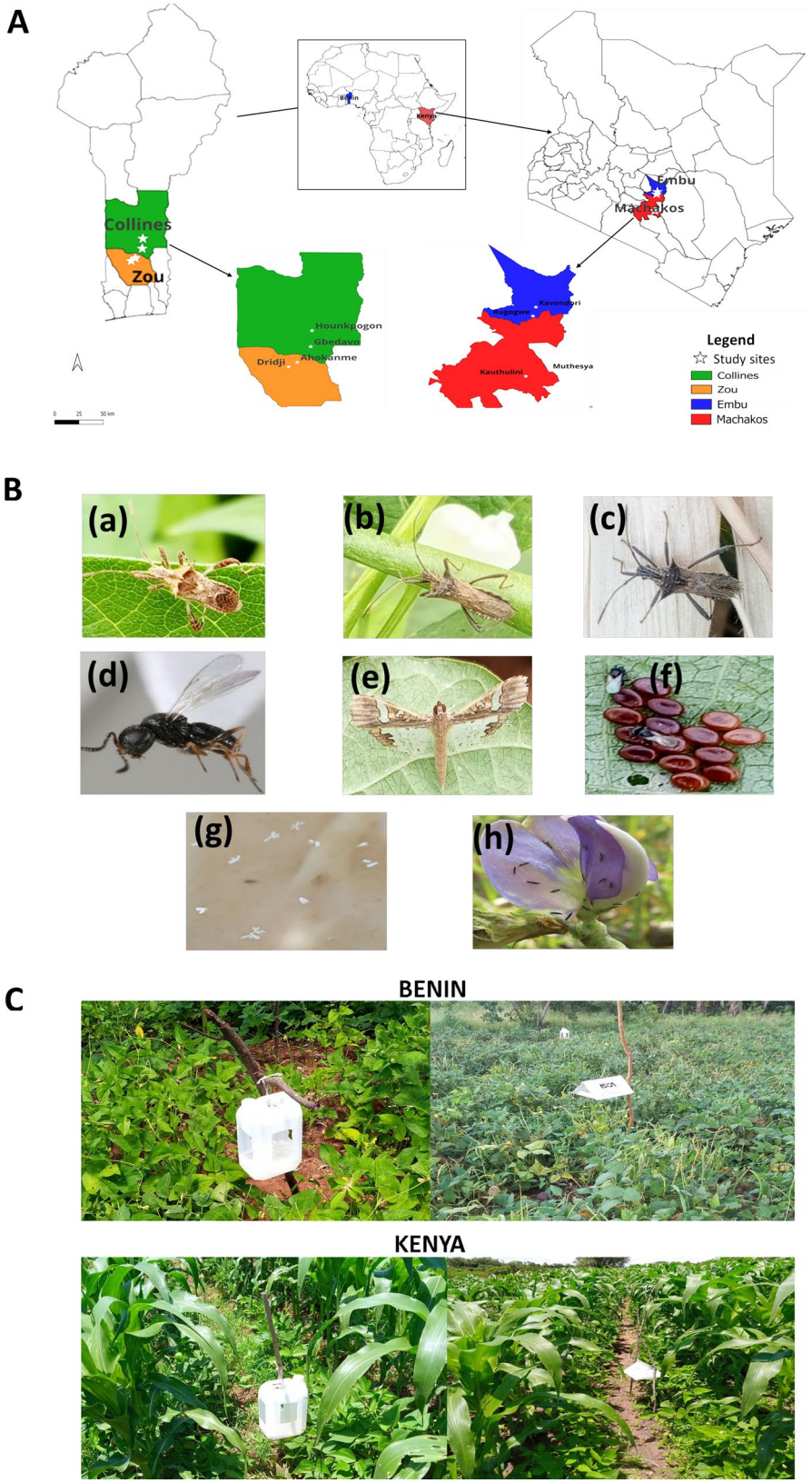


Fig. 2 (See legend on previous page.)

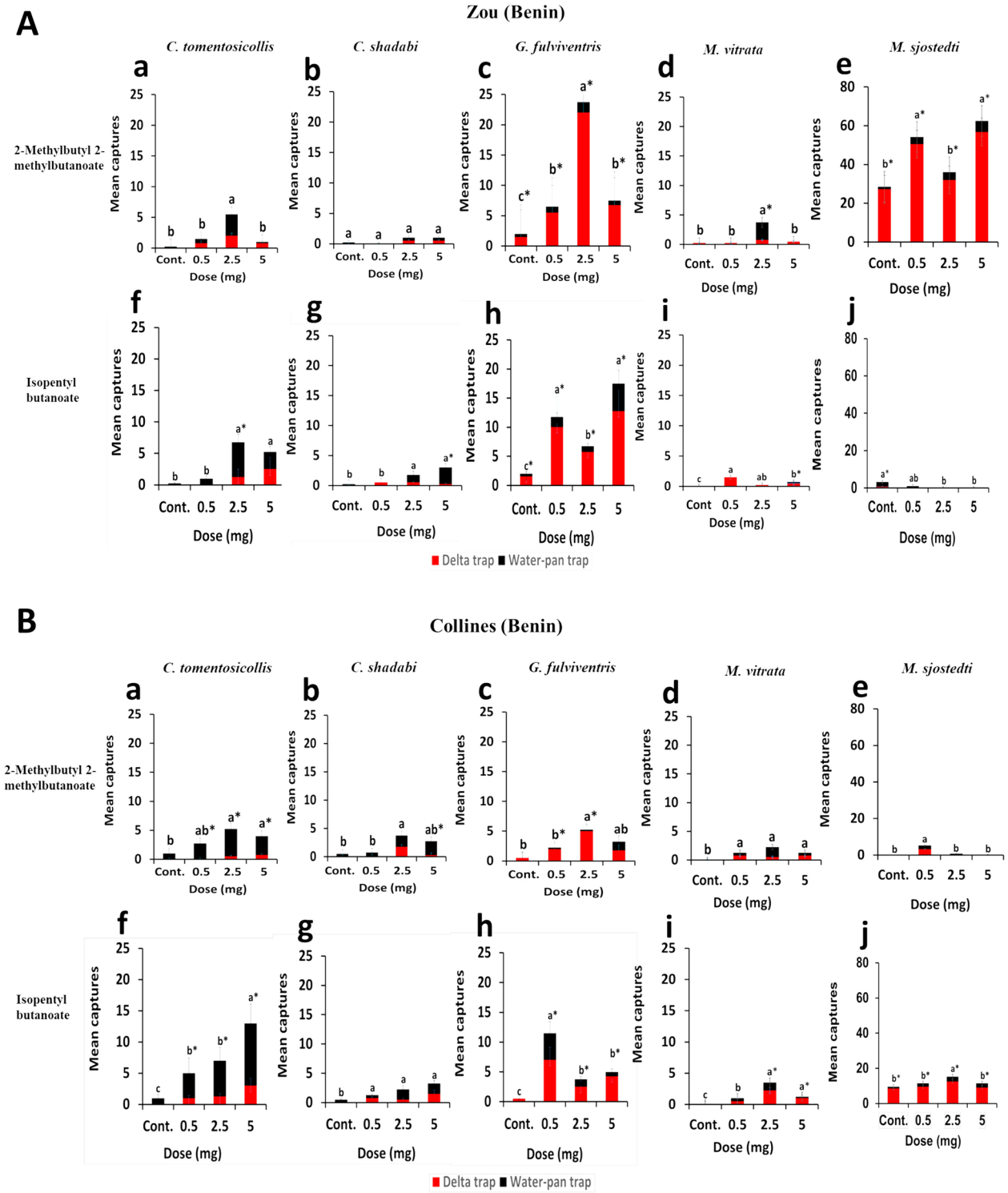


Fig. 3 Mean ± SE of trap captures of legume pests and natural enemy *Gryon fulviventris* with delta traps and water-pan traps with the aggregation pheromones of *C. elongata* (2-methylbutyl 2-methylbutanoate) and *Clavigralla tomentosicollis* (isopentyl butanoate) at different doses at two sites–Zou and Collines, Benin. The lowercase letters on the bar graphs compare each dose with the respective control captures, and the asterisks on the bar graphs indicate the significant differences between the delta trap and the water-pan trap captures. Means with different letters differ significantly (Tukey's honestly significant difference test (Tukey's HSD), $P < 0.05$)

Table 1 Effect of different doses of 2-methylbutyl 2-methylbutanoate and isopentyl butanoate on captures of legume pests in different agroecological zones in Benin

	Dose (mg)	2-Methylbutyl 2-methylbutanoate				Isopentyl butanoate			
		Zou		Collines		Zou		Collines	
		Mean ± SE	*P* value	Mean ± SE	*P* value	Mean ± SE	*P* value	Mean ± SE	*P* value
C. tomentosicollis	0.5	3.0 ± 0.0 **b**	< 0.001	5.5 ± 5.5 **ab**	< 0.05	2.0 ± 1.0 **b**	< 0.001	10.0 ± 2.5 **b**	< 0.01
	2.5	11.0 ± 3.0 **a**		10.5 ± 8.5 **a**		13.0 ± 3.0 **a**		14.0 ± 3.5 **b**	
	5	2.0 ± 1.0 **b**		8.0 ± 5.0 **a**		14.0 ± 3.5 a		26.0 ± 6.8 **a**	
	Control	0.0 ± 0.0 **b**		1.4 ± 1.0 **b**		0.0 ± 0.0 **b**		1.0 ± 1.0 **c**	
C. shadabi	0.5	0.5 ± 0.5 **a**	> 0.05	1.5 ± 1.5 **b**	< 0.001	0.5 ± 0.5 **b**	< 0.05	2.5 ± 0.5 **bc**	< 0.001
	2.5	2.0 ± 0.0 **a**		7.5 ± 0.5 **a**		3.5 ± 1.5 **ab**		4..5 ± 2.5 **ab**	
	5	1.5 ± 0.5 **a**		5.5 ± 4.5 **ab**		6.0 ± 3.0 **a**		6.5 ± 3.0 **a**	
	Control	0.5 ± 0.5 **a**		0.0 ± 0.0 **b**		0.5 ± 0.5 **b**		0.0 ± 0.0 **c**	
G. fulviventris	0.5	13.0 ± 9.0 **b**	< 0.001	4.5 ± 3.5 **b**	< 0.001	23.0 ± 10.0 **b**	< 0.05	23.0 ± 5.0 **a**	< 0.001
	2.5	47.5 ± 40.5 **a**		10.5 ± 9.5 **a**		13.5 ± 6.5 **c**		7.5 ± 2.5 **b**	
	5	15.0 ± 12.0 **b**		6.5 ± 0.5 **ab**		34.5 ± 15.5 **b**		10.0 ± 7.0 **ab**	
	Control	3.0 ± 3.0 **c**		1.0 ± 1.0 **b**		3.0 ± 3.0 **c**		1.0 ± 1.0 **b**	
M. vitrata	0.5	0.5 ± 0.5 **b**	< 0.001	4.0 ± 1.0 **a**	< 0.05	3.0 ± 1.5 **a**	> 0.05	4.0 ± 2.0 **a**	< 0.001
	2.5	8.5 ± 6.5 **a**		7.0 ± 2.0 **a**		0.5 ± 0.5 **a**		9.5 ± 3.5 **a**	
	5	1.0 ± 1.0 **b**		7.0 ± 2.0 **a**		1.0 ± 1.0 **a**		6.0 ± 2.5 **ab**	
	Control	0.5 ± 0.5 **b**		0.0 ± 0.0 **b**		0.5 ± 0.5 **a**		0.0 ± 0.0 **c**	
M. sjostedti	0.5	10.5 ± 2.5 **a**	> 0.05	108.5 ± 93.5 **a**	< 0.001	23.0 ± 15.0 **b**	> 0.05	2.0 ± 2.0 **ab**	< 0.001
	2.5	1.5 ± 1.5 **b**		72.0 ± 56.0 **c**		30.5 ± 19.5 **a**		0.0 ± 0.0 **b**	
	5	0.5 ± 0.5 **b**		125.0 ± 102.0 **a**		23.0 ± 13.0 **b**		0.0 ± 0.0 **b**	
	Control	0.0 ± 0.0 **b**		57.0 ± 52.0 **d**		19.0 ± 15.0 **b**		6.5 ± 3.5 **a**	

Means with different letters in a column by insect species differ significantly (ANOVA, Tukey's HSD), $P < 0.05$). SE = Standard Error

French bean yields across study sites were significantly greater by 319% and 331%, respectively at site 1, and 492% and 584%, respectively, at site 2 than their respective control fields (Table S7; Fig. 5B). However, whereas at site 1, legume yields from pheromone- and insecticide-treated fields were not significantly different ($P > 0.05$), they were slightly different in site 2. These results demonstrated the bioprotection efficiency of *C. elongata* aggregation pheromone in significantly reducing legume pest densities while increasing natural enemy density and potential use in legume production (Table S6_Fig. 5B_a, b) without insecticide use.

Discussion

Our data demonstrates that aggregation pheromones of *Clavigralla* species are multifunctional and that they contribute to sustainable bioprotection and productivity of food legumes. The pheromones effectively lured multiple legume pests including the coreid pod-sucking bug species *C. tomentosicollis*, *C. elongata* and *C. shadabi,* the legume pod borer *Maruca vitrata*, flower thrips *Megalurothrips sjostedti,* and more importantly, the whitefly *Bemisia tabaci*, which was only recorded in the experiments conducted in pheromone-baited traps in Kenya. More importantly, for the *Clavigralla* species, which showed cross-attraction to each other's pheromones, our results align with previous studies which have documented similar pheromone cross-attraction in hemipteran bugs. For example, *Piezodorus hybneri* (Gmelin) is attracted to both its pheromone blend comprised of β-sesquiphellandrene, (*R*)−15-hexadecanolide, and methyl (*Z*)−8-hexadecenoate and its competitor's *Riptortus pedestris* (Fabricius) pheromone (*E*)−2-hexenyl (*E*)−2-hexenoate depending upon environmental conditions [29]. Likewise, *Halyomorpha halys* (Stål) and *Acrosternum hilare* (Say) are both attracted to the brown-winged green bug's *Plautia stali* Scott aggregation pheromone (methyl (2*E*,4*E*,6*Z*)-decatrienoate) and its isomers [30, 31]. The aggregation pheromone methyl (*E*,*Z*)−2,4-decadienoate of *Euschistus* stink bugs also attracts nymphs of other stink bugs [32]. These examples show that the common chemical class among these aggregation pheromones is an ester, which suggests that it may be the most conserved chemical class in hemipteran bugs.

Both pheromone dose and trap type revealed differential responses in the different insects captured in traps. This suggests different sensitivities to the pheromones, and different potential behavioral uses by the different

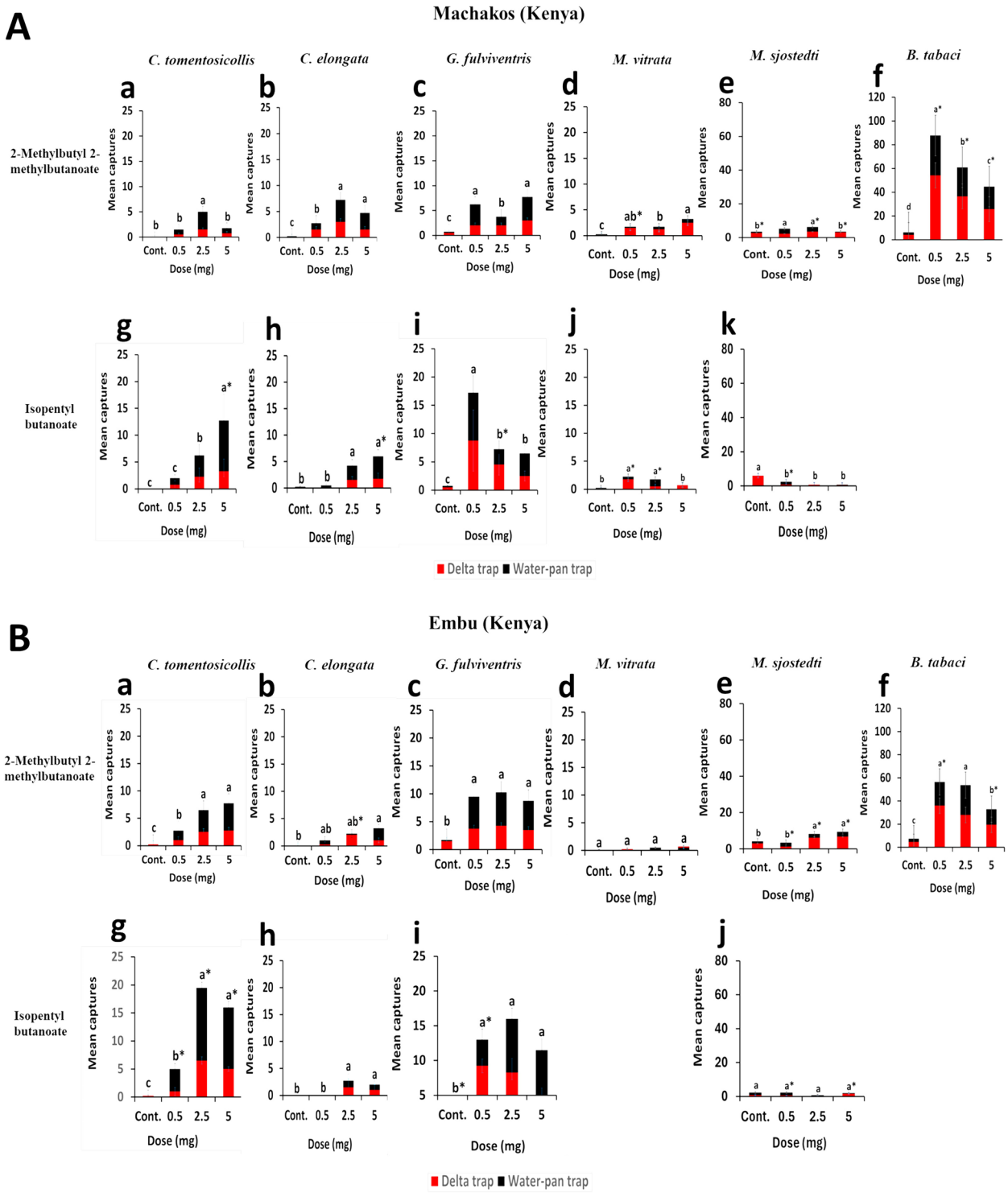


Fig. 4 Mean ± SE of trap captures of legume pests and natural enemy *Gryon fulviventris* with delta traps and water-pan traps with the aggregation pheromones of *C. elongata* (2-methylbutyl 2-methylbutanoate) and *Clavigralla tomentosicollis* (isopentyl butanoate) at different doses at two sites Machakos and Embu, Kenya. The lowercase letters on the bar graphs compare each dose with the respective control captures, and the asterisks on the bar graphs indicate the significant differences between the delta trap and the water-pan trap captures. Means with different letters differ significantly (Tukey's honestly significant difference test (Tukey's HSD), $P < 0.05$)

Table 2 Effect of different doses of 2-methylbutyl 2-methylbutanoate and isopentyl butanoate on captures of legume pests in different agroecological zones in Kenya

	Dose (mg)	2-Methylbutyl 2-methylbutanoate				Isopentyl butanoate			
		Machakos		Embu		Machakos		Embu	
		Mean ± SE	*P* value	Mean ± SE	*P* value	Mean ± SE	*P* value	Mean ± SE	*P* value
C. tomentosicollis	0.5	3.0 ± 1.0 **b**	< 0.001	5.5 ± 1.5 **b**	< 0.001	4.0 ± 1.0 **c**	< 0.001	9.5 ± 4.5 **c**	< 0.001
	2.5	11.0 ± 4.0 **a**		13.0 ± 3.0 **a**		12.5 ± 3.5 **b**		39.0 ± 13.0 **a**	
	5	3.0 ± 1.0 **b**		15.0 ± 5.0 **a**		25.0 ± 12.5 **a**		33.0 ± 12.0 **b**	
	Control	0.0 ± 0.0 **b**		0.0 ± 0.0 **c**		0.0 ± 0.0 **c**		0.0 ± 0.0 **b**	
C. elongata	0.5	5.5 ± 1.5 **b**	< 0.001	2.0 ± 1.0 **ab**	< 0.05	1.0 ± 1.0 **c**	< 0.001	0.0 ± 0.0 **b**	< 0.001
	2.5	13.5 ± 1.5 **a**		4.5 ± 3.5 **ab**		8.5 ± 2.5 **b**		5.5 ± 2.0 **a**	
	5	10.0 ± 3.0 **a**		6.5 ± 2.5 **a**		15.0 ± 6.5 **a**		4.0 ± 1.5 **b**	
	Control	0.0 ± 0.0 **c**		0.5 ± 0.5 **b**		0.0 ± 0.0 **c**		0.5 ± 0.5 **b**	
G. fulviventris	0.5	12.5 ± 3.5 **a**	< 0.001	19.5 ± 4.5 **a**	< 0.001	35.0 ± 7.5 **a**	< 0.001	27.5 ± 12.5 **ab**	< 0.001
	2.5	7.5 ± 0.5 **b**		20.5 ± 3.5 **a**		14.5 ± 3.5 **b**		31.5 ± 13.5 **a**	
	5	14.5 ± 3.5 **a**		16.5 ± 4.5 **a**		10.5 ± 1.5 **c**		23.0 ± 5.0 **b**	
	Control	0.5 ± 0.5 **c**		1.0 ± 0.0 **b**		0.5 ± 0.5 **d**		1.0 ± 0.0 **c**	
M. vitrata	0.5	5.5 ± 4.5 **ab**	< 0.05	0.5 ± 0.5 **a**	> 0.05	5.5 ± 4.5 **a**	> 0.05	–	–
	2.5	3.5 ± 1.5 **b**		0.5 ± 0.5 **a**		2.5 ± 0.5 a**b**		–	
	5	10.0 ± 4.0 **a**		0.5 ± 0.5 **a**		4.0 ± 1.5 **ab**		–	
	Control	1.5 ± 0.5 **c**		0.0 ± 0.0 **a**		1.5 ± 0.5 **b**		–	
M. sjostedti	0.5	10.5 ± 1.5 **a**	< 0.05	7.0 ± 2.0 **b**	< 0.01	5.0 ± 2.0 **b**	> 0.05	4.5 ± 2.5 **a**	> 0.05
	2.5	12.5 ± 1.5 **a**		16.5 ± 8.5 **a**		1.5 ± 1.5 **b**		1.5.0 ± 0.5 **a**	
	5	7.0 ± 5.0 **a**		19.0 ± 8.0 **a**		1.5 ± 1.5 **b**		4.0 ± 2.5 **a**	
	Control	7.0 ± 4.0 **a**		8.5 ± 3.5 **b**		12.0 ± 12.0 **a**		4.5 ± 1.5 **a**	
B. tabaci	0.5	175.5 ± 41.5 **a**	< 0.001	113.0 ± 31.0 **a**	< 0.001	–	–	–	–
	2.5	122.0 ± 24.0 **b**		108.5 ± 23.5 **a**		–		–	
	5	89.5 ± 13.5 **c**		66.0 ± 12.5 **b**		–		–	
	Control	10.5 ± 1.0 **d**		15.0 ± 4.0 **c**		–		–	

Means with different letters in a column by insect species differ significantly (ANOVA, Tukey's HSD), $P < 0.05$). SE = Standard Error

insects as follows: coreid pod-sucking bugs—they serve as aggregation pheromones for both sexes [28]; (we suggest that an analogous identification and field assays on the aggregation pheromone of *C. shadabi* could establish chemical structural relationships with other coreid bug pheromones and its multifunctional bioprotection potential); parasitoid *G. fulviventris*—they may serve as kairomones for the parasitoid to find its egg host [28, 32–34]; legume pod borer *M. vitrata,* whitefly *B. tabaci,* and flower thrips *M. sjostedti*, they may serve as chemical cues for finding food or an oviposition site [35]. The fact that 2-methylbutyl 2-methylbutanoate and isopentyl butanoate have been reported as associated with the aroma of fruits and flowers [35], it is not surprising to find a diversity of insects including these legume pests attracted to traps baited with these pheromone esters. The evolutionary histories of these species may likely contribute to their capacity to respond to coreid-sucking bug pheromones. Interestingly, a previous study identified the esters butyl butanoate and octyl butanoate in the headspace volatiles of cut cowpea flower buds and flowers [36], and in coupled GC-EAD assays, antennae of *M. vitrata* detected these two compounds. However, no behavioral assays were carried out to determine responses of the pod borer to these chemicals. On the other hand, the male-produced aggregation pheromone of the flower thrips *M. sjostedti* is comprised of the two compounds, the ester (*R*)-lavandulyl 3-methylbutanoate, identified as the major compound and (*R*)-lavandulol as the minor compound, but remarkably, both sexes are attracted to the ester [37]. Likewise, the male-produced aggregation pheromone of *Frankliniella occidentalis* is also an ester, neryl (*S*)−2-methylbutanoate, and it attracts both sexes [38]. The commonly used attractant for various thrips species including *M. sjostedti* is the ester kairomone methyl isonicotinate [38]. Thus, these examples demonstrate that certain esters may be ubiquitous attractants for thrips which would require additional research. Surprisingly, whiteflies known to respond to semiochemicals, mainly green leaf volatiles, such as

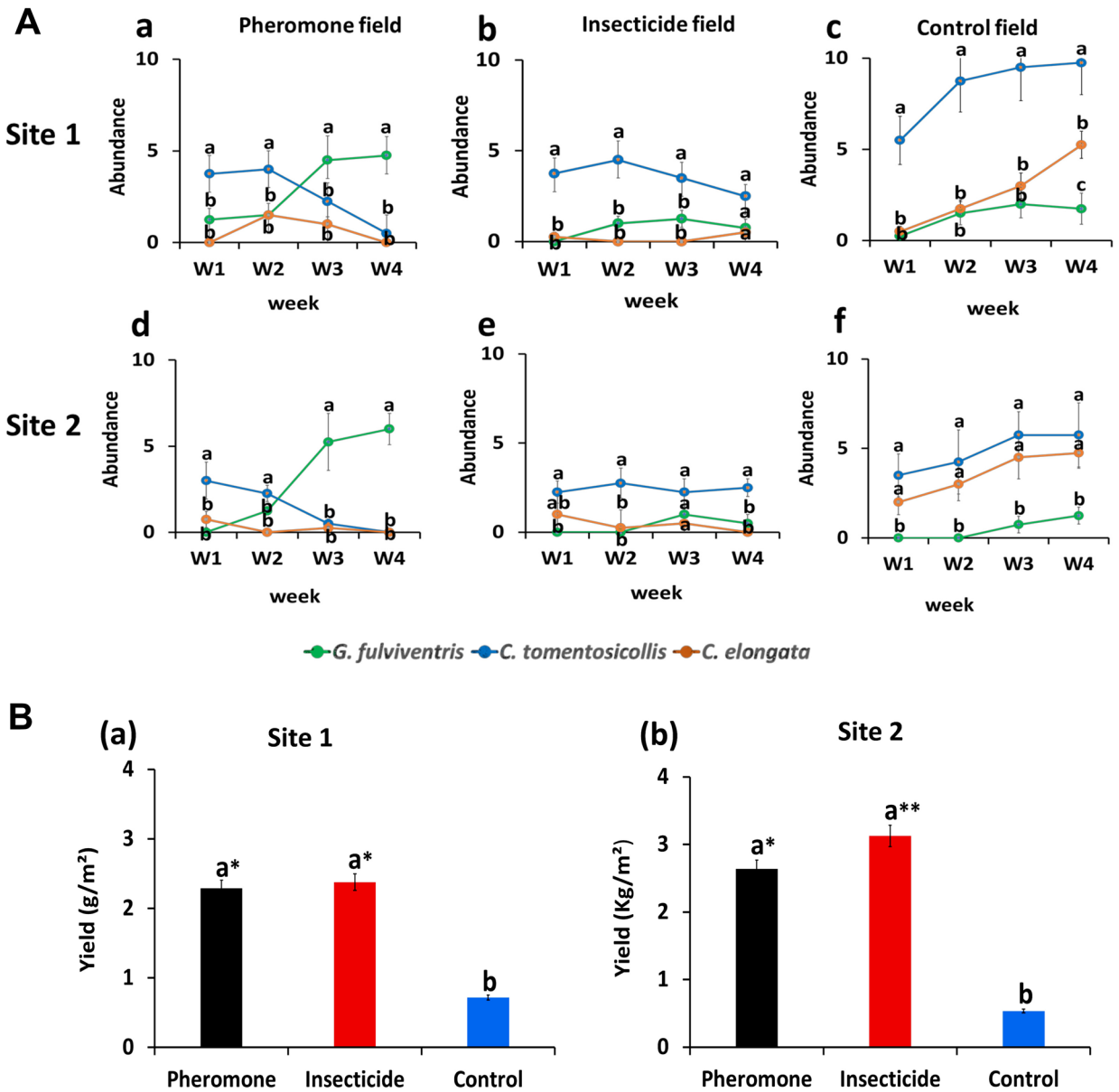


Fig. 5 Abundance of *Clavigralla* species and their parasitoid *G. fulviventris* at different experimental times in pheromone and insecticide-treated fields, and control (**A**), with figures a-c in site 1, and d-f in site 2. Mean ± SE of the harvested yield of different treatment fields (**B**): pheromone, insecticide, and control fields, (**a**) in site 1 and (**b**) in site 2. The graphs were generated using the mean abundance of insects recorded weekly. The lowercase letters on the bar graphs compare treatment yield with the respective control yield captures, and the asterisks on the bar graphs indicate the significant differences between the yield of pheromone and insecticide-treated fields. Means with different letters differ significantly (Tukey's honestly significant difference test (Tukey's HSD), $P < 0.05$). W1-W4 represents experimental weeks. The first collection was done three days before the installation of experiments and repeated every week after the installation of the experiment for 3 weeks

2-hexenal [39, 40], were captured into traps baited with pheromones derived from esters. This suggests further research into olfactory-mediated behaviors in whiteflies.

The fact that we recorded higher captures of whiteflies and thrips in Kenya (East Africa), but thrips only in Benin (West Africa) may reflect landscape and climatic differences as factors that contribute to pest infestations. A recent study reported that a greater diversity of plants in the landscape within and outside the farm area had a greater effect on the incidence of whiteflies and thrips on crops [41, 42]. It is likely that the cropping system, that is, monocrop versus intercrop, may contribute to the differential trap captures, which should also be investigated further. The variation of climatic factors (altitude,

land, temperature, and water pattern) is well-known to initiate pest incidences in crops [43–45]. For example, the variation in altitude and temperature influences the abundance of *M. vitrata* which was highest at lowland altitudes and lowest temperatures and lowest density at high altitudes and high temperatures [43]. Previous studies have shown that increasing temperature enhances whiteflies and thrips densities and favours the infestation of crops [46, 47]. A comprehensive study that captures climatic factors is needed to confirm these suggestions.

For the *Clavigralla* species, trapped predominantly in water-pan traps than delta traps may reflect their feeding behavior, sucking on plant tissues, which contain moisture [48, 49]. As such, we cannot rule out the influence of moisture on trap captures of these species. On the other hand, a greater proportion of the parasitoid *G. fulviventris*, was lured into delta traps than water-pan traps. This may be associated with their smaller size, contributing to them getting easily stuck on sticky surfaces [50], the same for whiteflies and thrips. It appeared that *Maruca vitrata*, showed no discrimination between pheromone-baited delta traps and water-pan traps, which would require further investigation, in particular their host finding trend and capacity [49].

Bioprotection studies, using the pheromone-treatment reduced *Clavigralla* density through efficient biological control of the pests by its natural enemies in the legume field. In the control field, high pest density but low natural enemy density caused significant damage and low yield of legumes. On the other hand, the insecticide treatment appeared to have acted indiscriminatory killing both the pests and natural enemies. It is important to note that insecticide-treatment could introduce negative effects, such as insecticide residues in crops and resistance to pests, which may need investigation.

Conclusion

We conclude that coreid pod-sucking bug pheromones lured multiple legume pests into traps. They also lured the natural enemy, a parasitoid of coreid pod-sucking bugs *Gryon fulviventris*, a promising biocontrol agent that can suppress the population of *Clavigralla* species in the field. As such, they are effective and novel multifunctional semiochemical-based tools for sustainable legume pest management and production without insecticide use. However, our finding of whiteflies in pheromone-baited traps in Kenya but not in Benin would require additional experiments to confirm these results. To make these pheromones accessible, cheap, and disseminated throughout the continent, we recommend that future studies should: (1) optimize the formulation of the lures for long-term multifunctional effects; (2) test the lures in many different agroecosystems in Africa; and (3) assess their integration with other biorationals to establish their full bioprotection potential in legume pest management and food productivity.

Materials and methods

Insects

Adult *C. elongata* males and females were collected on 2 weeks sprayed French beans and pigeon peas from Machakos (01° 10.836′ S, 037° 28.397′ E) and Embu (01° 09.698′ S, 037° 29.958′ E) in separate containers and then transferred to the insectary at the International Centre of Insect Physiology, (*icipe*) Nairobi, Kenya. They were reared on young healthy pods of French bean (*Phaseolus vulgaris*, Fabaceae) in cylindrical clear plastic cages (18 cm diameter × 6.5 cm high) (Foodmate 2 L, Kenpoly, Nairobi, Kenya) with a ventilated lid at 25 ± 2 °C and 45–70% relative humidity with a photoperiod of 12:12 h (Light: Dark) as previously described [28]. *Clavigralla tomentosicollis* egg batches collected from both areas in Kenya were incubated separately in clear plastic cages (9.0 cm diameter × 4.5 cm height) (0.5 L Foodmate, Kenpoly, Nairobi, Kenya) with ventilated lids. The parasitoid, *Gryon fulviventris* which emerged from *Clavigralla* eggs were collected using an aspirator and introduced into a cage containing *C. tomentosicollis* eggs that were less than 48 h old. They were fed on droplets of a 10% honey solution and reared using the same laboratory conditions.

Identification of the aggregation pheromone of *Clavigralla elongata*

Volatiles were collected separately from sexually mature *C. elongata* adult males and females of similar age (30 each; 7–8 days old, N = 4), and no insects (control), as previously described for *C. tomentosicollis* volatiles [28] in quick-fit glass jars (250 mL each) (Sigma Scientific, Gainesville, FL, USA) for 24 h at a flow rate of 260 mL min^{-1}. Super Q traps were each eluted with 200 µl GC grade dichloromethane (Analytical grade, Sigma-Aldrich, St, Louis, MO) and stored at −80 °C until required for analysis.

Volatiles from both sexes of adult *C. elongata* (1 µl each), were analysed by coupled gas chromatography/mass spectrometry (GC/MS) on an Agilent Technologies Inc. Series B 7890 GC coupled to a 5977A MS (inert XL/EI/CI MSD) triple-axis mass detector, equipped with an HP-5 low bleed capillary column (30 m × 0.25 mm i.d., 0.25 µm) (J &W, Folsom, CA, USA) in the electron impact mode at 70 eV. The GC oven temperature was 35 °C for 5 min with a rise of 10 °C min^{-1} to 280 °C for 10.5 min, then 5 °C min^{-1} to 285 °C and held at this temperature for 9 min. Compounds were tentatively identified by comparison of their mass spectral data with library data: Adams2, Chemecol, and NIST11. In addition, the identities of several compounds were confirmed by comparison

of their mass spectral data and retention times with those of authentic standards that were available.

Additionally, antennally-active compounds were identified using coupled gas chromatography/electroantennographic detection (GC/EAD) analysis using antennae of *C. elongata* males and females (7–8 days old adult) and *G. fulviventris* females (3–5 days old). The GC/EAD used an HP 7890 Series II gas chromatograph (Agilent Technologies, Palo Alto, California, USA) equipped with an HP-5 MS capillary column with similar dimensions and oven conditions as described for the GC/MS analysis. Carrier gas was high-purity nitrogen at a flow rate of 1 mL/min. Samples were injected in a splitless mode at 250 °C with a split valve delay of 1 min. Column effluent split was 1:1 with a fused silica outlet splitter (Alltech Associates Inc. Deerfield, IL), which allowed for simultaneous detection by a flame ionization detector (FID) and electroantennographic detector (EAD). The antennal preparation was made by filling in two sharpened glass capillaries with Ringer saline solution (Kugel 1997) (1.36 g KH_2PO_4, 0.24 g KCl, 0.08 g $CaCl_2$, 1.22 g $MgCl_2$, 4.8 mL KOH, 35.08 g $C_6H_{12}O_6$ (glucose), and 0.35 g NaCl dissolved in 0.5L of distilled water). One of the capillaries was inserted into the excised head/pro-thorax. The distal end of the antenna was then placed in a saline-filled electrode. The antennal signal was detected through an amplifier (Syntech, Hilversum, The Netherlands), which was acquired and processed by an IDAC-2 data acquisition controller (Syntech, Hilversum, The Netherlands) and later analyzed with EAG 2000 GC/EAD software (Syntech) to generate simultaneous FID and EAD signals on a computer. Aliquots (3 µl) of volatile samples and commercially purchased synthetic EAD-active compounds dissolved in dichloromethane were analysed. GC-EAD analysis was replicated a minimum of five times, and EAD responses were considered positive when three or more positive responses to the same sample were recorded.

Chemicals

Synthetic standards of isopentyl butanoate, 2-methylbutyl-2-methylbutanoate, were purchased from Sigma-Aldrich, Germany (purity ≥ 97%). Dichloromethane was purchased from Sigma Aldrich, Germany, and its purity was ≥ 95%.

Bio-crop protection potential of coreid pod-sucking bug pheromones in farmers' fields-Benin (West Africa)

Field experiments were carried out at farmers' legume farms in central Benin at two sites: Zou and Collines (Fig. 2), during two different rainy seasons (June 2019 for preliminary trial), (October–November 2020, and May–June 2021) to test the attractiveness of the two different pheromones to *Clavigralla* species and their key natural enemy, the parasitoid *G. fulviventris*. The experimental crops (cowpea and French bean) are seasonal and annual plants. At both Zou and Collines, pheromone-baited traps were evaluated at two sites each on farm sizes that were 100 m × 100 m of cowpea (Tawa and Kpodji-guèguè cultivars) mono-crops: Zou-Site 1A (07° 25.558′ N, 002° 02.203′ E); Site 1B (07° 24.770′ N, 002° 01.664′ E); Collines-Site 2A (07° 37001′ N, 002° 17.199′ E); Site 2B (07° 38.599′ N, 002° 17.866′ E). Pheromone-baited and -unbaited traps were set 20 m apart and 10 m from the plot border in a complete randomized design after 41 days of planting, which corresponds to the podding stage of cowpeas (Fig. S1, Fig. 2C) when legume pests are most active. Two *Clavigralla* aggregation pheromones were used to prepare the lures: isopentyl butanoate, from *C. tomentosicollis* and 2-methylbutyl-2-methylbutanoate, newly identified from *C. elongata*. Three different doses: 0.5 mg, 2.5 mg, and 5 mg of dichloromethane solutions of the two pheromones were prepared separately as lures. All samples, 500 µL each, were loaded into hexane-extracted rubber septa (1-cm-internal diameter × 2-cm-high) (Sigma-Aldrich, MA, United States) and air-dried in a hood. White delta traps (20.5-cm-outer diameter × 12-cm-high) (Kenya Biologics, Nairobi, Kenya) and water-pan traps made from 5L water bottles (16-cm-length × 10-cm-wide × 28-cm-high) purchased locally (open market) were used. We created an entry point (11-cm-wide × 7-cm-high) on each face of the bottle. Water placed at the bottom of the bottle served as a trap for insects that were attracted to the lure, which was hung 3 cm above the water surface with a white string. All the traps were baited with the rubber septa lures. Control traps were baited with rubber septa loaded with a similar volume of dichloromethane (500 µL) and air-dried. Additional lures that were prepared were kept in ziplock plastic bags, sealed, and stored at − 20 °C until use. The traps were suspended 30 cm above the crop canopy using galvanized wire and wood. The experiments were conducted for 4 weeks during two consecutive rainy seasons (long and short) at 24–38 °C and 44–70% relative humidity.

The position of the traps was changed every 48 h in the same design. The traps were checked and emptied in the morning (8:00–12:00) in every 2 days and the number of insects captured was separated by species and counted visually. The sticky plates were changed at each data collection. The lures were changed after 14 days. The water-pan trap was filled with clean water up to ¾ level, which retains and kills the insects that approach the lures. The water was sieved with a white net (0.4 × 0.7 mm), and the numbers of legume pests and natural enemies captured were recorded. The water in the container was replaced every 48 h. Furthermore, the numbers of males and females of *C. elongata* and *C. tomentosicollis* captured were recorded at each

collection date regardless of the type of trap and pheromone dose used.

Validation of the Benin field results in farmers' fields-Kenya (East Africa)

This study was carried out to validate the results obtained from Benin. The same design as in the Benin field experiments was used at two different farmer-field sites for 4 weeks (May–June 2020, and September–October 2023). These sites were located in Machakos: Site 1A (01° 10.836′ S, 037° 28.397′ E) (mixed intercrop of French bean (Vanilla cultivar) and maize (PHB 3253 cultivar), and Site 1B (01° 09.698′ S, 037° 29.958′ E), French bean (Vanilla cultivar) (mono-crop). Likewise, at the Embu farmer field, two sites were used: Site 2A (01° 09.698′ S, 037° 29.958′ E), French bean (Samantha cultivar) monocrop; Site 2B (01° 10.835′ S, 037° 28.401′ E) (mixed intercrop of pigeon pea (Kathumani cultivar) and cowpea (Black eye cultivar). Traps were set up after 35 days of planting which corresponds to the podding stage of French beans when legume pests are most active. Conditions at the study sites varied between 18 and 26 °C and 65–80% relative humidity.

Yield assessment

To evaluate the potential use of *Clavigralla* pheromones in legume production, water pan traps were baited with the most effective dose (5 mg) of 2-methylbutyl 2-methylbutanoate and assessed for their effectiveness in French bean production. Farm plots at two different sites in Machakos County were used, each split into three fenced plots of 40 m × 20 m (800 m^2) each. The plots were prepared in the same way according to farmer practices and planted on the same day on each site. The distance between plants was 15 cm (with 2–3 seeds per hole) and 40 cm between rows. The plots were weeded twice, the first at 3 weeks after planting, and the second at 5 weeks after planting. The fertilizers nitrogen, phosphorus, and potassium (NPK) 12:32:16 and calcium ammonium nitrate (CAN) 27:2.4:5.3 were applied 28 days after planting at the rate of 0.25 g/hole (farmer practice) (County Agriculture Office, Machakos, Kenya, *personal communication*). The insecticide-treated fields were treated with a mixture of an insecticide Acetak (with Active Ingredient (AI) acetamiprid 200 SL, 0.25–0.5 mL/L) and a fungicide Oshothane (with AI mancozeb, 2.5 g/L). The first application of the mixture of insecticide-fungicide was done 33 days after planting and repeated every week for 3 weeks to simulate farmer practice. The population dynamics of *Clavigralla* species and their egg parasitoids were monitored every week for 4 m^2 (1 m^2 × 4 plots) in each treatment field and for the natural enemy from batches of 30 eggs of *C. tomentosicollis* collected from the fields. The number (from each plot) of coreid bugs present in each field was also recorded at each collection. The first sampling occurred a day before the installation of the pheromone traps and the spray of pesticides. Eggs collected from different plots and treatments were incubated separately in the laboratory in sterile clear plastic boxes (9 cm diameter and 4.5 cm height) with ventilated lids for 21 days, which exceeds the date of expected parasitoid emergence date by 7 days. The number of parasitoids that emerged from different collected eggs was recorded daily and pooled. The pheromone-baited water-pan traps were placed in the plots 32 days after planting. The lures were changed every 14 days, and the observations were carried out for 4 weeks. Mature pods harvested from the treated and control fields (800 m^2 each), were dried, shelled, and compared for physical quality (Fig. S3). The dry seeds were weighed using the sensible balance KERN EW_087620289 (Kern & Sohn GmbH.D, Balingen, Germany).

Data analyses

All statistical analyses were carried out in R v.4.1.3 [51] at 5% significance level. Data collected for each legume insect species captured (*C. tomentosicollis*, *C. elongata*, *C. shadabi*, *Maruca vitrata*, *Megalurothrips sjostedti*, *Bemisia tabaci*, *Gryon fulviventris*) by each pheromone at different doses in each location of Benin and Kenya were first tested for normality and homogeneity of variances using Shapiro–Wilk and Bartlett's tests, respectively. The number of each insect species captured was then analyzed against different doses of each pheromone in each location using analysis of variance (ANOVA) as they were normally distributed and homogeneous. Means were separated using Tukey's test with the honestly significant difference (HSD). Chi-square (χ^2) test was used to determine the significant difference between the two types of traps (delta trap and water-pan trap) at each level of pheromone doses. The same test was used to compare the number of each insect species captured in the two locations of Benin (Zou and Collines) and Kenya (Machakos and Embu) regardless of pheromone dose and trap type for the pest abundance in each location. Furthermore, the sex ratio was determined for *C. tomentosicollis* and *C. elongate* species and discriminated using Chi-square (χ^2) test. Moreover, the number of *C. tomentosicollis*, *C. elongata*, and the associated parasitoid *G. fulviventris* collected weekly during the experimentation period at each collection date, in each treatment, and at each site was first tested for normality and homogeneity of variances using Shapiro–Wilk and Bartlett's tests, respectively. The analysis of variance (ANOVA) was then performed to compare the density of each insect collected at each collection date in each treatment and at each site. The means were separated using Tukey's honestly significant test. The Chi-square test was used to discriminate yields from pheromone-treated, insecticide-treated, and control fields.

Abbreviations

APU	Arthropod Pathology Unit (APU)
ANOVA	Analysis of variance
BCEU	Behavioural and Chemical Ecology Unit (BCEU)
CAN	Calcium Ammonium Nitrate
CGIAR	Consultative Group on International Agricultural Research
GC-EAD	Gas chromatography-electroantennographic detection
GC–MS	Gas chromatography-mass spectrometry
HSD	Honestly significant difference
H	Hour
ICIPE	International Centre of Insect Physiology and Ecology
i.d.	Inside/inner diameter
IITA	International Institute of Tropical Agriculture
o.d	Outside/outer diameter
NPK	Nitrogen, phosphorus, and potassium
S	Supplementary
SDC	Swiss Agency for Development and Cooperation
SE	Standard error
SSA	sub-Saharan Africa
W	Week

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40538-024-00711-9.

Additional file 1.

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Author contributions
HK, FK, MT, and BT. conceptualized and designed the study. HK. conducted the experiments, collected and analysed the data. BT. confirmed the chemistry data. HK, XC, and HKK. prepared the lures and traps. HK, FK, MT, and BT. wrote the manuscript. BT. reviewed and edited the manuscript. FK, MT, and BT. sourced funding for the study. All authors approved the final manuscript.

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Data availability
No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
This study does not contain any experiments using any animal species that require ethical approval.

Consent for publication
This research is an original study published exclusively in this journal.

Competing interests
The authors declare no competing interests.

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