Upwind Flight of *Prostephanus truncatus* is Mediated by Aggregation Pheromone but not Food Volatiles

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Abstract—Flight bioassays were carried out to investigate the response of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) to maize volatiles in comparison to the male-produced aggregation pheromone. Upwind attraction of flying *P. truncatus* is mediated by the male-produced aggregation pheromone. In contrast, beetles showed no response to maize grains or volatiles, and no interactions between aggregation pheromone and maize volatiles were recorded. This absence of upwind flight to food volatiles, or any synergism between pheromone and food volatiles suggests that the male-produced aggregation pheromone is the only known long-range semiochemical used by *P. truncatus* for dispersal and host-selection. These results are in contrast with those on several other stored-product species, and suggest that *P. truncatus* may not use maize volatiles as long-range host finding kairomones in nature. We propose a hypothesis for the process of dispersal and host colonisation by *P. truncatus*. © 1998 Elsevier Science Ltd. All rights reserved

Key words—*Prostephanus truncatus*, larger grain borer, stored-product insect, Coleoptera, Bostrichidae, host-plant, pheromone, kairomone, wind tunnel, synergism

INTRODUCTION

Many phytophagous insects, including stored-product insects (Barrer, 1983; Stubbs *et al.*, 1985, Pierce *et al.*, 1990; Subramanyam *et al.*, 1992; Dowdy *et al.*, 1993; Phillips *et al.*, 1993) use host-derived kairomones, pheromones or both to locate suitable hosts (Metcalf, 1987). For *Carpophilus* spp. food volatiles and pheromones are known to interact in stimulating a response (e.g. Bartelt *et al.*, 1992; James *et al.*, 1994). For other species aggregation pheromones act synergistically with food volatiles (e.g. Walgenbach *et al.*, 1987; Dowd and Bartelt, 1991; Dowdy *et al.*, 1993). A knowledge of the interaction between stored-products insects and their plant hosts may have important practical applications such as in the development of food-baited trapping systems.

The larger grain borer, *Prostephanus truncatus* (Horn) is a member of the coleopteran family Bostrichidae, which consists principally of wood borers (Chittenden, 1911). Although it is a serious pest of farm-stored maize and cassava in the tropics (Hodges, 1986), large widespread

populations of *P. truncatus* occur in the bush, suggesting that the major reservoir for the pest is probably wood (Rees *et al.*, 1990; Nang'ayo *et al.*, 1993).

The two-component male-produced aggregation pheromone of *P. truncatus* elicits attraction of walking conspecifics in laboratory bioassays (Cork *et al.*, 1991; Boughton and Fadamiro, 1996), as well as flying beetles in a wind tunnel (Fadamiro, 1995), and in the field (Dendy *et al.*, 1989; Farrell and Key, 1992; Tigar *et al.*, 1993). *Prostephanus truncatus* adults are attracted over short distances to maize grain (Hodges, 1994, citing Detmers, 1990) and dried cassava (Wright *et al.*, 1993). However, field studies in Africa (Wright *et al.*, 1993), and Central America (Tigar *et al.*, 1994) suggest that *P. truncatus* is not attracted at long-range to maize grain or cob or to dried cassava.

Coupled gas chromatographic (GC)-electroantennographic detection (EAD) analyses using *P. truncatus* have led to the identification of ten antennally-active compounds in maize volatiles, and nine in cassava volatiles (Pike *et al.*, 1994). The bioactivity of these compounds was confirmed using a pitfall bioassay (Pike *et al.*, 1994). As a next logical step to the above initial positive results, we were interested in the study of upwind flight behaviour of *P. truncatus* to different blends of the active components of the maize volatiles that had been identified by Pike *et al.* (1994).

We report the results of the wind tunnel studies on the responses of *P. truncatus* to maize-grain volatiles and aggregation pheromone alone and together.

MATERIALS AND METHODS

Wind tunnel bioassays

Adult *P. truncatus* (Tanzanian strain which had been reared in the lab for about five years) were reared on whole, clean maize at $30 \pm 1°C$ and $65 \pm 5\%$ r.h. under a L12:D12 photoperiod. Beetles of known age were collected from cultures established on milled grain that passed through an Endecotts sieve, 3.35 mm mesh, to ease removal of beetles (Fadamiro, 1995). Intact beetles used in bioassays were sexed using the method of Shires and McCarthy (1976). Flying beetles were bioassayed 10–12 h into the photophase in a clear, rectangular, glass wind tunnel, $160 \times 75 \times 75$ cm (Fadamiro, 1995), at $29 \pm 1°C$, $30 \pm 5\%$ r.h., 3700 lux, and 20 ± 1 cm/s wind speed.

Pheromone

The male-produced aggregation pheromone of *P. truncatus* has two components, 1-methylethyl (2*E*)-2-methyl-2-pentenoate (Trunc-call 1 or T1) and 1-methylethyl (*E,E*)-2, 4-dimethyl-2, 4-heptadienoate (Trunc-call 2 or T2) (Cork *et al.*, 1991, D. Hall, pers. comm.). A 1:1 blend of T1:T2 and dichloromethane solvent were supplied by the Natural Resources Institute, Chatham, U.K. (NRI) in polythene vial dispensers ($20 \times 9 \times 1.5$ mm). They were stored separately at $-50°C$ before use. An optimal 0.2 mg dose of the pheromone was used in the bioassays (Fadamiro, 1995).

Maize volatiles

Pesticide-free, clean, American yellow maize grain packaged in thick polythene bags were frozen and then stored in a cold room at 3–4°C. Prior to use in bioassays, whole maize grains were allowed to warm up to $20 \pm 5°C$ overnight. Volatiles from freshly harvested whole maize were collected (Pike *et al.*, 1994) by placing 3 kg of grain in a 3 litre Buchner flask and drawing in air through a filter of activated charcoal via a tube to the base of the flask and out through a collecting filter containing Porapak Q (50–80 mesh; 200 mg). The Porapak was precleaned by washing thoroughly with dichloromethane and drying under nitrogen. Breakthrough of volatiles was prevented by connecting two filters in series. Collections were made for 7-day periods at 27°C and 70% r.h. Trapped volatiles were eluted with dichloromethane (4×500 μl) purified by passage through neutral alumina. Samples were analyzed by capillary GC on (25 m $\times 0.32$ mm i.d. columns) coated with polar CP-Wax 52CB (Chrompack) or non-polar CP-Sil 5CB (Chrompack) with helium carrier gas at 0.4 kg/cm^2, splitless injection and oven temperature held at 50°C for

Table   The composition of synthetic and natural maize volatile mixtures used in this study

Volatile blend	Components/ratio
	Nonanal 8, decanal 8, hexanoic acid 50 (50 ng/μl), nonanoic acid 25, vanillin 1, 2 phenyl-ethanol 6
2	Blend 1 plus tetradecanal 2 ng/μl
3	Blend 1 minus hexanoic acid
4	Blend 1 minus nonanoic acid
5	Hexanoic (50 ng/μl) and nonanoic acids in 2:1 ratio
	Blend 1 plus 2-octenal (5 ng/μl), 2-nonenal (5 ng/μl), octan-3-ol (3 ng/μl), octen-3-ol (2 ng/μl)
	A whole entrainment sample from maize (natural maize volatiles)

2 min then programmed to rise from 50°C to 230°C at 6°C/min. Quantitative analyses used flame ionization detection (220°C). Six blends of five synthetic maize volatiles were tested, as was the natural blend of captured maize volatiles (Table 1).

Response to maize vs pheromone

Five treatments, presented singly, were tested in the wind tunnel. These were:

1. No-food control, comprising an empty 9 cm Petri dish + solvent vial.
2. Whole-grain maize, 9 cm Petri dish containing 50 mg of fresh maize + solvent vial.
3. Infested maize, 9 cm Petri dish containing 50 mg of *P. truncatus*-infested maize + solvent vial.
4. Pheromone, empty 9 cm Petri dish + 0.2 mg pheromone vial.
5. Maize-pheromone, 9 cm Petri dish containing 50 mg of fresh grain + 0.2 mg pheromone vial (to test for interaction between maize and pheromone).

The two constituents of each treatment were placed ≤ 1 cm apart on a 20 cm high platform located 35 cm downwind of the air-outlet screen, and 70 cm upwind of a beetle release platform. For each treatment, 10 unsexed beetles were placed on the release platform. Data recorded during the following 10 min were: number of beetles taking-off; number landing upwind of the release platform within ≤ 50 cm of the upwind screen; number orienting to treatment by flying upwind at the level of and to within 10 cm of the treatment; and number landing on the upwind platform holding the treatment. Each treatment was tested six times with a fresh group of 10 beetles. Data were analyzed using a Kruskal-Wallis (non-parametric) test (Sokal and Rohlf, 1981).

Response to maize volatiles vs pheromone

A dose response experiment was undertaken with 20, 50, 100 and 200 μl of blend 1 (Table 1), the complete synthetic blend. The blend doses were dispensed on to a small triangular piece of filter paper using a disposable microcap pipette. The filter paper was then suspended by a 20 cm high plastic peg clamp 70 cm upwind of the beetle release platform. Twenty unsexed beetles were released and the following data recorded for 10 min: numbers of beetles taking-off; numbers orienting (as above); and number landing on the treatment source (the peg or the filter paper). There were three replicates per treatment.

In a second experiment, nine treatments were tested singly in randomized order: the seven synthetic maize volatile blends (100 μl dose); 100 μl of dichloromethane solvent control; and 0.2 mg of pheromone. All nine treatments were run in a day and replicated four times, except for blend 7 (Table 1) which was replicated only twice due to shortage of material. Responses of 20 released beetles, per stimulus were observed as above for 7.5 min.

Two-choice experiment: pheromone + solvent vs pheromone + maize volatiles

This experiment was designed to test if flying beetles would discriminate between pheromone alone and a pheromone + host volatiles source when simultaneously presented in the wind tunnel.

The design of this experiment was similar to that described by Fadamiro *et al.* (1996). The two sources were suspended 20 cm high, 12.5 cm apart and 100 cm upwind of the centered beetle release platform. One of the sources consisted of 0.2 mg pheromone in a polythene vial plus

Table 2. Responses of *P. truncatus* to whole-maize grain vs pheromone. A total of 60 beetles were released per treatment in six replicates. Values in the same column having the same letter are not significantly different (*P* > 0.05). Chi-square values for numbers taking-off, landing upwind, orienting and landing on the treatment source are 2.63, 12.27, 19.43 and 25.61, respectively

Treatment	No. taking off	No. landing upwind	No. orienting to treatment source	No. landing on treatment source
		6ᵃ	0ᵃ	0ᵃ
		8ᵃ	5ᵃ	0ᵃ
		9ᵃ	4ᵃ	1ᵃ
		17ᵇ	15ᵇ	15ᵇ
		18ᵇ	17ᵇ	17ᵇ
		=0.02	<0.0006	<0.0001

100 μl of the dichloromethane solvent placed closely side by side. The other source was a vial with 0.2 mg of pheromone beside a vial containing 100 μl of blend 7 (Table 1). Ten male and 10 female beetles were released together downwind of the two odour sources and the data recorded for 10 min were: number of beetles orienting to each source; and number and sex of beetles landing on each source. The two sources were alternated between tests to control for possible bias in the wind tunnel. This experiment was repeated six times and data were analyzed using Chi-square tests (Parker, 1979).

RESULTS

Response to maize vs pheromone

The numbers of beetles taking off were not significantly different among the five treatments (Table 2). However, significantly more beetles landed upwind, oriented upwind, and landed on the treatment source in the two treatments containing pheromone than in the other three treatments which were not different from each other (Table 2).

Response to maize volatiles vs pheromone

With the exception of the 100 μl dose of maize volatile blend 1, to which three beetles oriented, no flying beetles oriented to or landed on the source of maize volatiles at any dose (Table 3). However, about 65% of flying beetles landed on the pheromone treatment source.

In the second experiment, flying *P. truncatus* were generally unresponsive to all seven volatile blends including blend 7, the natural maize volatiles (Table 4). However, over 80% of flying beetles responded to the pheromone source.

Two-choice experiment: pheromone + solvent vs pheromone + maize volatiles

There were no significant differences in the numbers or sex ratios of beetles orienting to, and landing on sources of pheromone + solvent, or pheromone + maize volatiles (Table 5).

DISCUSSION

Apart from confirming pheromone-mediated upwind flight of *P. truncatus*, the results of the first two experiments (Tables 2 and 3) suggest that *P. truncatus* are not attracted from long

Table 3. Response of *P. truncatus* to different doses of synthetic maize volatile blend.   A total of 60 beetles were released per treatment

Treatment	No. taking off	No. orienting to treatment source	No. landing on treatment source
Blend 1, 20 μl		0	0
Blend 1, 50 μl		0	0
Blend 1, 100 μl		3	0
Blend 1, 200 μl		0	0
20 μl dichloromethane solvent control		0	0
0.2 mg pheromone	14	9	9

Table 4. Responses of *P. truncatus* to maize volatiles vs pheromone. Treatments presented singly in 100 μl doses. Eighty beetles were tested per treatment except for blend 7 for which only 40 beetles were tested

Treatment	No. taking-off	No. orienting to treatment source	No. landing on treatment source
Blend 1		0	0
Blend 2		0	0
Blend 3		0	0
Blend 4		0	0
Blend 5			0
Blend 6		1	0
Blend 7		0	0
Solvent control		0	0
0.2 mg pheromone		12	11

range (≥ 70 cm) to maize or maize volatiles. This contrasts with the results of 'pitfall' bioassays in which *P. truncatus* responded over a short range (≤ 5 cm) to maize and cassava volatiles (Pike *et al.*, 1994).

Stored-product beetles that respond positively to host-plant volatiles include: *Trogoderma* spp. (Dermestidae) (Nara *et al.*, 1981), *Oryzaephilus* spp. (Cucujidae) (Mikolajczak *et al.*, 1984; Stubbs *et al.*, 1985; White, 1989; Pierce *et al.*, 1990), *Tribolium* spp. (Tenebrionidae) (Phillips *et al.*, 1993), and *Sitophilus* spp. (Curculionidae) (Phillips *et al.*, 1993; Pike *et al.*, 1994). Dowdy *et al.* (1993) report that *Rhyzopertha dominica* (Bostrichidae) was more responsive to infested than clean wheat, possibly because of pheromone in infested grain. Pierce *et al.* (1990) concluded that *Oryzaephilus* spp. may use some components of host volatiles as host-finding kairomones in nature. However, the majority of the above mentioned studies employed pitfall olfactometers (walking bioassays). Only rarely, e.g. for *Carpophilus lugubris* Murray (Nitidulidae) has response by flying beetles to food odours been recorded in the wind tunnel (Lin and Phelan, 1991), or in the field (Lin *et al.*, 1992). It seems reasonable that food volatiles could mediate food finding in the dusky sap beetle, *C. lugubris* and other nitidulids, since they are naturally closely associated with ripening fruits and vegetables (Lin *et al.*, 1992).

A flight bioassay may be a more realistic model of beetle field responses than bioassays employing walking beetles (Domek *et al.*, 1990) and can act as a good predictor of chemically mediated host finding in the field (Lin and Phelan, 1991; Lin *et al.*, 1992). This may account for the contrast between our results and those of Pike *et al.* (1994). However, our results support the results of field studies in Togo (Wright *et al.*, 1993) and Mexico (Tigar *et al.*, 1994) which detected no long-range attraction of adult *P. truncatus* to maize grain or cobs.

In neither single- nor two-choice flight bioassays did the addition of maize to a pheromone source alter the level of beetles' response (Tables 2 and 5). The absence of interaction between aggregation pheromone and maize volatiles is in contrast to many studies in which synergism occurred between aggregation pheromones and host volatiles, e.g. for: *Carpophilus* spp. (Nitidulidae) (Dowd and Bartelt, 1991; Bartelt *et al.*, 1992; Lin *et al.*, 1992; James *et al.*, 1994); *Sitophilus* spp. (Curculionidae) (Walgenbach *et al.*, 1987); and *Oryzaephilus* spp. (Cucujidae) (Oehlschlager *et al.*, 1988).

Because *P. truncatus* is principally a wood borer (Chittenden, 1911) with great abundance in the natural environment (Nang'ayo *et al.*, 1993), one might not expect it to be specifically attracted to maize-plant materials. Hodges (1994) has suggested that *P. truncatus* bores test burrows into any sufficiently soft substrate, eventually locating suitable foods such as maize and

Table 5. Response of *P. truncatus* to two simultaneously presented sources of pheromone or pheromone plus maize volatiles (Blend 7). Chi-square values for numbers orienting, landing and sex ratio are 0.024, 0.031, and 0.125, respectively

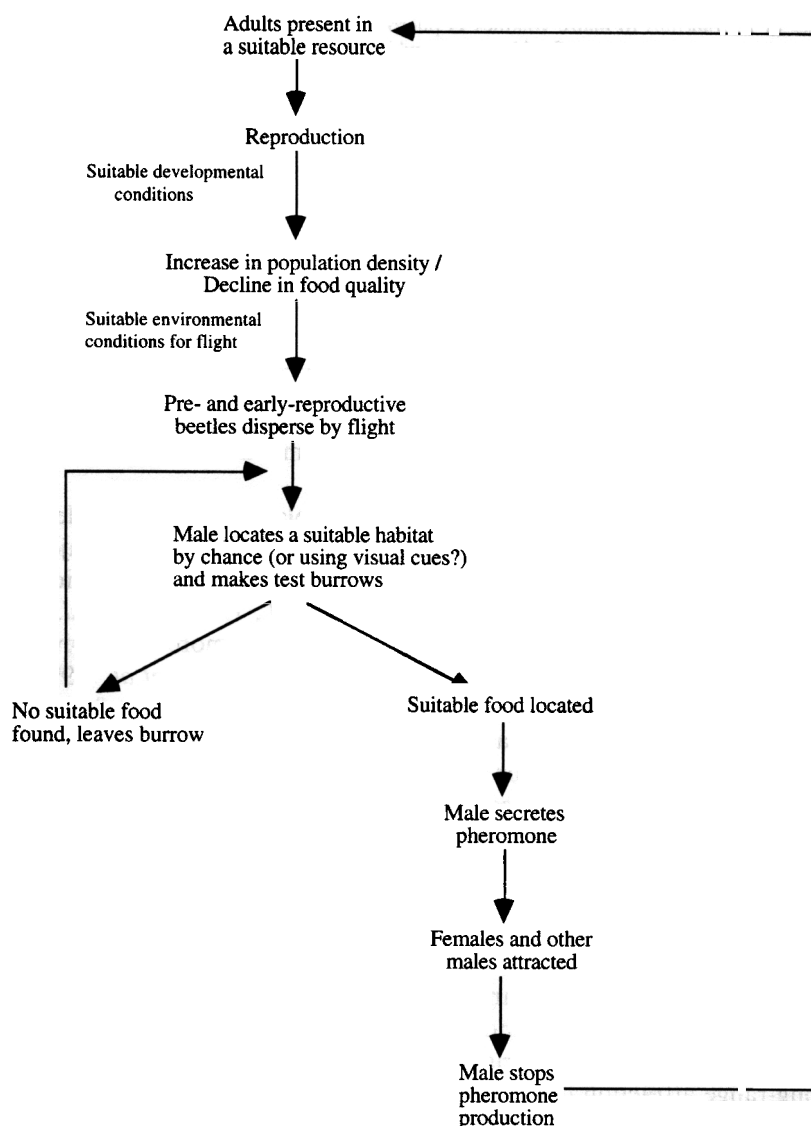| Treatment	No. orienting to source	No. landing on source	Sex ratio of beetles that landed on source (male:female)
	22	15	7:8
	20	17	9:8
	>0.5	>0.5	>0.5

Fig. 1. Dispersal and host colonization hypothesis for *P. truncatus*.

cassava. A similar means of host selection is apparently used by some Scolytidae attacking wood (Wood, 1982). Kennedy's hypothesis of a requisite dispersal phase prior to responding to olfactory stimuli (Kennedy, 1986) seems unlikely to apply to *P. truncatus*, since it did not appear to require a dispersal phase before orienting to pheromone. On-going field trapping studies in Kenya have shown that the addition of synthetic maize volatiles to pheromone makes no contribution to trap catch, thus providing further evidence that they play no role in host selection (Hodges, unpublished data).

Dispersal and resource colonization by P. truncatus

A hypothesis for dispersal and resource colonization by *P. truncatus* is presented in Fig. 1, and this largely parallels the host selection hypothesis proposed by Hodges (1994).

Under favourable developmental conditions adults in a resource of high quality continue to reproduce, leading to an increase in population density and consequently a decline in the quality of the resource. Conditions such as crowding, competition or increase in larval mortality may signal a decline in resource quality, influence ontogeny, and cause some beetles to disperse to a new resource before conditions become totally unfavourable. Under suitable environmental conditions for flight (Fadamiro, 1995), pre-reproductive and reproductively active young adults

disperse by flight in search of a suitable resource (Fadamiro, 1997). On arrival at a suitable site, possibly by chance or by the use of visual cues, the male makes test burrows in search of food (Hodges, 1986). If no suitable food is found, the beetle leaves the burrow to try again elsewhere. However, if suitable food is found the male secretes a pheromone that attracts females and other males (Fadamiro and Wyatt, 1996), for the successful colonization of the resource. Once enough beetles have been attracted as signalled by the presence of females, or of female chemical-residues, the male stops pheromone production (Smith *et al.*, 1996), possibly to limit intra- and inter-specific competition, as well as the risk of predation. Meanwhile, male and female beetles in the newly-colonized site, under favourable conditions begin to mate and reproduce, leading to an increase in population density and declining food quality. This will eventually lead to dispersal and the cycle continues. The natural environment may serve as a transient niche for dispersing *P. truncatus* (Nang'ayo *et al.*, 1993), and as an alternative host during the off-season of suitable food crops such as maize. This proposed host colonization process involving the male-produced aggregation pheromone might have been evolved primarily for the natural environment (wood) of the beetle, but as the larger grain borer has only recently adapted to the storage habitat, the process is still followed there.

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